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## **Entomology in Ecuador**

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Olivier Dangles**

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**En couverture.** *Dynastes hercules* (L. 1758) (Scarabaeidae : Dynastinae), Choco Forest, Equateur. C'est un des plus grands coléoptères connus. Certains mâles atteignent une longueur de 170 mm.

**Cover.** *Dynastes hercules* (L. 1758) (Scarabaeidae: Dynastinae), Choco Forest, Ecuador. *It is one of the largest beetle known. Some males reach 170 mm length.* Photo Olivier Dangles ([www.naturexpose.com](http://www.naturexpose.com)).

# Entomology in Ecuador

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The Western Amazonian basin has long been recognized as supporting one of the highest levels of biological diversity in the world. Insects are particularly abundant and species rich in this region, yet the task of describing new species, discovering their range, understanding the factors that govern their distribution and the degree of alteration in their community structure as a result of habitat degradation is still in its early stages. The wide diversity of habitats that Ecuador possesses in a small area makes it an ideal location for biodiversity and ecological research. Although the diversity of many groups (e.g. plants, birds, and frogs) has been the focus of numerous publications data on the entomological fauna in Ecuador are scarce, mostly limited to the response of insect diversity to altitudinal gradients. During the past decades, the Ecuadorian research in Entomology has been dominated by taxonomic studies. Face to the acute environmental awareness and called attention to the pressing problem of biodiversity conservation, this taxonomic knowledge has recently been refocused in an ecological perspective.

The nine contributions to this special issue aim to present some of the major lines of research developed in ecological entomology in Ecuador, mainly at the Museum of Zoology of the Catholic University of Quito (QCAZ), Invertebrate Section. The studies concern different ecosystems of Ecuador such as lowland Amazonian rainforests (Carpio *et al.* 2009, Checa *et al.* 2009), Montane cloud forest (Donoso & Ramón 2009) and Andean páramos (Moret 2009). Most studies however cover a wide range of biogeographic regions (Badher *et al.* 2009, Barragán *et al.* 2009, Donoso *et al.* 2009, Dangles *et al.* 2009) including comparisons with other regions from Latin America (Cárdenes *et al.* 2009). The coverage of taxa (e.g. Diptera, Isoptera, Hymenoptera, Lepidoptera, Coleoptera), thematic (e.g. taxonomy, biogeography, community ecology, conservation biology) and methodologies (e.g. multi-dimensional analysis, spatial statistics, niche modeling) was designed to highlight the diverse areas on which QCAZ entomologists have focused during the last years, giving a broad view of some of their scientific achievements.

In spite of their large topical range, the contributions to this special issue are united by a common theme: a focus on how a good knowledge of species taxonomy plays a crucial role in fostering and underpinning ecological research in the field of entomology. This is particularly important in tropical countries like Ecuador where the task of entomologists seems to have a time limit with a clock ticking faster and faster as human disturbance continues to increase. I hope that this special issue will not only provide a fresh view of entomo-

logical research performed in Ecuador but also foster interest from entomologists worldwide to come and perform research in this country which shelters one of the most species-rich but also most endangered insect fauna on Earth.

**Acknowledgements.** I am grateful to Brigitte Frérot, Pierre Rasmont, and Yves Carton for their enthusiasm in this special issue project and their support for making it a reality. I also thank all the members of the QCAZ Museum, Invertebrates Section for their dedicated contribution to this issue. Special thanks to Raphael Cárdenes, for his help in the coordination of the issue. Financial supports from the Pontificia Universidad Católica del Ecuador (Donación de Impuesto a la Renta), the IRD (UR-072) and the University of Delaware (Department of Entomology & Wildlife Ecology) for the publication of this special issue are greatly acknowledged.

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# The History of Entomology in Ecuador

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**Abstract.** This work is not intended to be a complete review of all publications about entomology in Ecuador. It compiles the history of entomology in Ecuador in a chronological order. It first provides observations about the influence of pre-Columbian cultures and the cultural heritage of indigenous populations. It then presents the contribution of the Spanish conquest and colonization chroniclers, the specialists that described American species during the Renaissance period and the great scientific expeditions. Finally the birth of Ecuadorian entomology as a science is described with the creation of institutes for applied research and the Ecuadorian museums of entomology.

**Résumé. Histoire de l'entomologie en Equateur.** Cette étude n'a pas pour objectif de faire une révision complète de toutes les publications sur le thème en Equateur, mais de présenter les grandes étapes de l'évolution de l'entomologie dans ce pays dans un ordre chronologique. Il présente tout d'abord des informations sur l'influence des cultures pré-colombiennes et de l'héritage culturel légué par les populations indigènes. Il présente ensuite la contribution des chroniqueurs de la conquête espagnole et de la colonisation, des spécialistes qui ont décrit les espèces américaines pendant la période de la Renaissance et des grandes expéditions scientifiques. Finalement, la naissance de l'entomologie en tant que science est décrite avec la création des instituts de recherche appliquée et des muséums équatoriens d'entomologie.

**Keywords:** Pre-columbian, Conquest of America, The great expeditions, The beginning of the 20th century.

## Pre-Columbian Ecuador

Pre-hispanic cultures had extensive knowledge of the insects of Ecuador and incorporated insects into mythology, art, cuisine and geography. For instance, insect motifs were used in different ceramic pieces implying that these creatures were involved in the every day lives of people from different cultures that inhabited these lands (Cummins *et al.* 1996; Melic 2003). There are a variety of ceramic pieces deposited at the Museo Antropológico del Banco Central del Ecuador that incorporate insects in their design (Fig. 1). This cultural heritage has been manifested in the use of insects as a food source by a variety cultures. Onore (1997) mentioned 82 species of insects that have been used as food in several indigenous cultures currently and historically. One of the most important examples is the beetle, *Platycoelia lutescens* Blanchard 1850 (Coleoptera: Scarabaeidae: Rutelinae), commonly called "catzo blanco" that is used in a seasonal dish during October and November in Quito's valleys

(Smith & Paucar 2000). Another example of insects used as food is the beetle larva known as "chontacuro", *Rhynchophorus palmarum* (L. 1758) (Coleoptera: Curculionidae). This larva is sold and cooked in various regions in the Amazon basin (Onore 1997; Barragán & Carpio 2008).

Within the American Indian cosmopolitan vision insects occupy an important role. Numerous prehispanic cultures considered certain insects as terrestrial incarnations of divine forces (Beutelspacher 1989). Butterflies are frequently represented in the art of various prehispanic cultures. In Mexican mythology, especially the Mayan culture, butterflies were considered to represent the souls of dead warriors killed in battles or sacrifices (Beutelspacher 1989). In other prehispanic cultures, butterflies were a sign of high rank and images were used to decorate pectorals, hair pins (tocados) and nose pieces (narigueras).

The use of insect names to designate particular localities also demonstrates the importance of these animals. There is an area near Quito named Cuzubamba, from the Kichwa roots: "cuzo" meaning worm or grub, and "pampa" meaning valley, implying the "valley of the grubs." Other insects represented bad fortune. Even today the moth, *Ascalapha odorata* L.

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1758 (Lepidoptera Noctuidae), commonly called “tandacuchi” (Fig. 2) is considered, by the people living in the central Ecuadorian Sierra (Andean region), as a messenger of death every time this moth gets inside their houses. Another example is the hemipteran, *Fulgora laternaria* L. 1758 (Hemiptera: Fulgoridae), commonly known as “machaca” (Fig. 3), that symbolizes lust. The belief is that if a person unintentionally comes in contact with this insect, this person must have sex otherwise he or she will die within a few hours (Medeiros Costa-Neto 2007). Before the arrival of the European conquistadors, the insect *Dactylopius* spp. Costa 1835 (Hemiptera: Coccidae), known as “cochinilla del nopal,” was used to dye the fabrics of the Incas throughout South America. After the conquest, this industry was an important business within the Spanish colony. The dye extracted from this insect was the second most valuable product exported from Nueva España in the 18<sup>th</sup> century, only after silver (Barragán & Carpio 2008).

### The Colonial Era in America

With the arrival of the Europeans, knowledge about



**Figure 1**

Tuza Culture (Carchi) Ceramic pieces deposited at the Reserva Arqueológica de la Dirección Cultural del Banco Central del Ecuador. Regional Quito. (A.Janeta).

the New World started to focus on nature with the first identification of specimens that numerous Spanish conquistadors brought back to Europe, together with gold and spices (Rodas 2003). One of the first reports, written in the conquest period, was the *Historia General y Natural de la Indias, Islas y Tierra firme del Mar Océano*, by Gonzalo Fernández de Oviedo and Valdez in 1535. This work is divided into 50 books. *Libro XV: El cual trata de los animales insectos* (Acosta-Solis 1977) described certain entomological curiosities such as beetles with lights known as “cucuyos”, *Pyrophorus* spp. (Coleoptera: Elateridae), “cochinillas del nopal”, *Dactylopius* spp. (Coccidae: Hemiptera), and stingless bees (Hymenoptera: Meliponinae) (Hogue 1993).

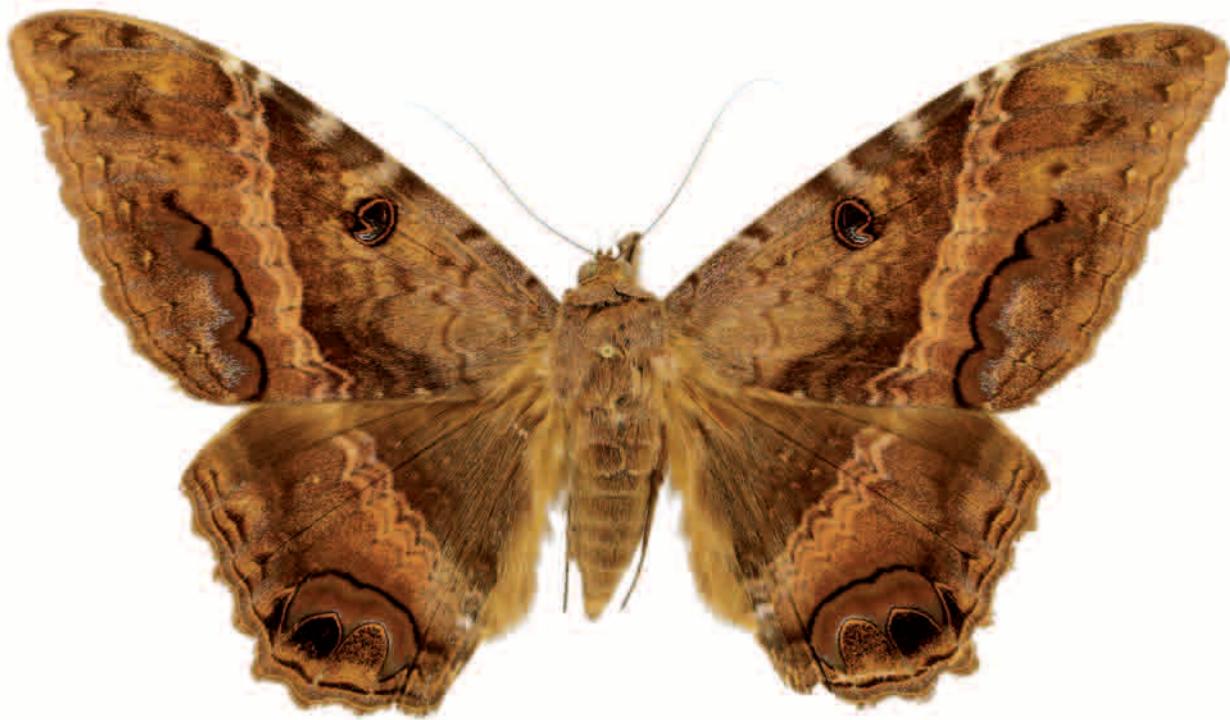
Father Juan de Velasco (1727–1792) in his *Historia del Reino de Quito en la América Meridional* in 1789 and Mario Cicala (1718–17..) and *Descripción Histórica Física de la Provincia de Quito de la Compañía de Jesús* the first to report details about the ancestral knowledge of the land that now constitutes Ecuador. He described certain aspects of Ecuadorian entomology (Velasco 1946; Cicala 2004). However, these reports were far from the centers of advanced science in Europe and were not consistent with the developing Linnean binomial classification system. Many of these initial reports from Nueva España were fantasies and exaggerated observations (Acosta Solis 1977).

### The Great Expeditions

#### De La Condamine, Humboldt, Darwin, Whymper and others

As a result of the Enlightenment in Europe, scientific academies mounted a series of expeditions to the colonies overseas. The French Geodesic Mission worked in Ecuador from 1735 to 1746 measuring the roundness of the Earth (Rodas 2003). The mission was directed by the French naturalist Charles Marie de La Condamine (1701–1774) and included the botanist Joseph de Jussieu (1704–1779) and the Spanish captain Antonio de Ulloa (1716–1795). Captain Ulloa represented the Spanish military before the French Academy of Sciences for this expedition to South America. The report *Noticias Americanas* (1772) contains specific statements about several Ecuadorian insects including a grasshopper plague that could have involved one of the species of *Schistocerca* (Orthoptera: Acrididae) (Hogue 1993).

One of the monumental expeditions conducted from 1799 to 1804 and without doubt the most impressive was the one carried out by Alexander Von Humboldt (Fig. 4) and Aimé Bonpland throughout



**Figure 2**  
*Ascalaphha odorata* L. 1758 (A. Janeta).



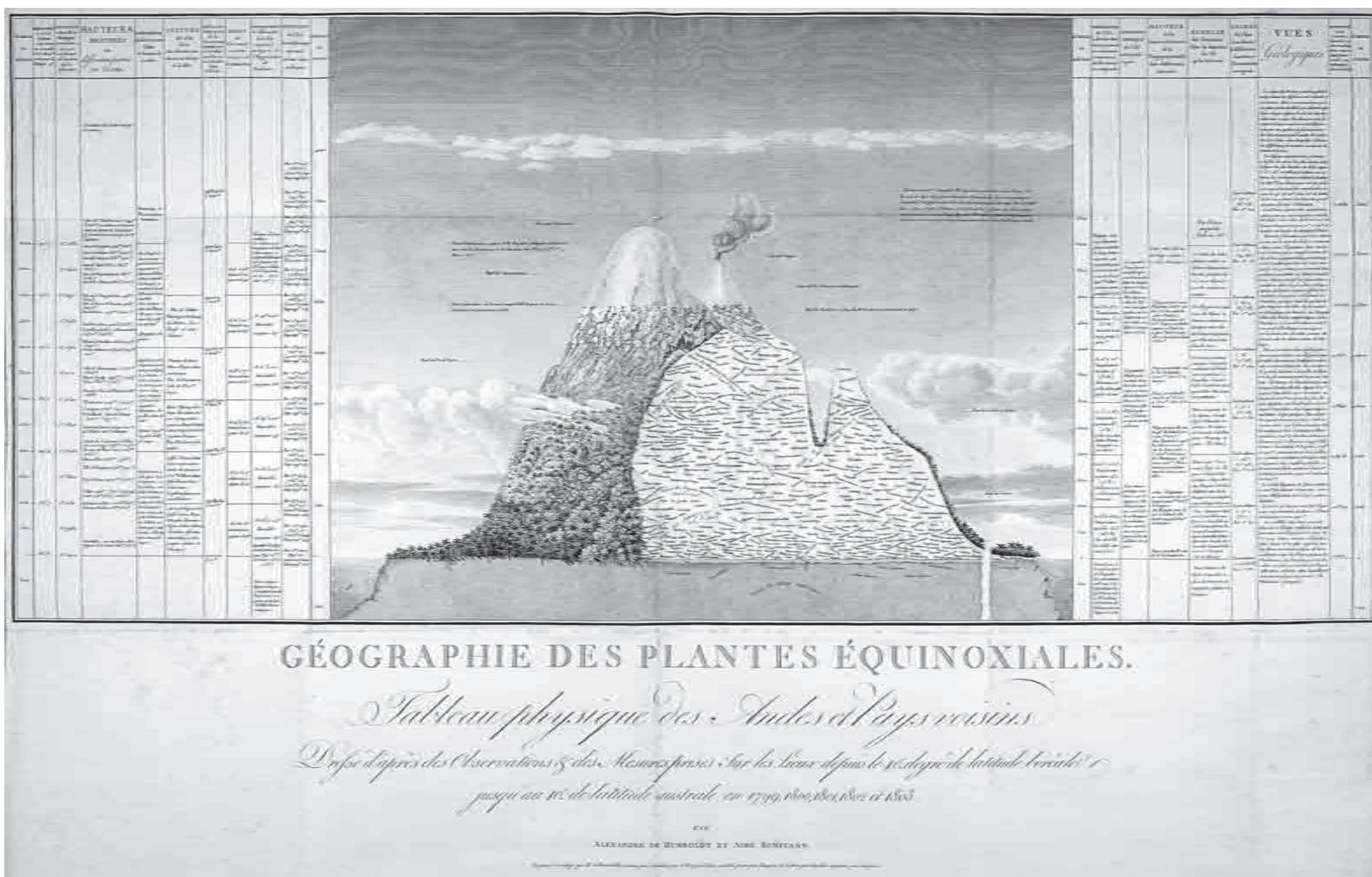
**Figure 3**  
*Fulgora laternaria* L. 1758 (A. Janeta).

America (Papavero *et al.* 1995). They made numerous and important observations concerning the biological aspects of insects and gathered an extensive collection of insects that later were described by Pierre André Latreille (Papavero 1971). Today, a great number of these specimens are deposited in the Muséum National d'Histoire Naturelle de Paris. Numerous scientists consider Humboldt as the father of biogeographic and ecological studies based on his narratives of his studies

in South America. One of his most detailed illustrations was of the Ecuadorian Andes, where he illustrated the diversity and distribution of plants according to altitude (Fig. 5). The influence of altitude is reflected in his manuscripts that described Ecuadorian species. One of his numerous publications is the Collection of Observations on Zoology and Comparative Anatomy (1805–1833) where he described in detail several observations on Ecuadorian insects. Humboldt's



**Figure 4**  
Alexander Von Humboldt by Friedrich Georg Weitsch 1806

**Figure 5**

Original from A. von Humboldt 1807. *Essai sur la géographie des plantes*. Courtesy Rare Book Collection, Missouri Botanical Garden Library. (C. Ulloa).

work in the New World was so important that he is considered as the first American scientist and discoverer. Von Humboldt met Simón Bolívar in Paris when Bolívar was still very young (Acosta Solis 1977).

Another great naturalists of the 19<sup>th</sup> century was Jean-Baptiste Boussingault (1802–1887) who acquired fame in Europe as a result of his ten-year trip through equatorial America. He was an impressive scientist and naturalist, an eminent agronomist, and an active chemist. Simón Bolívar, the liberator of Latin America and head of the government of Gran Colombia invited Boussingault to develop scientific research in the new republics (Acosta – Solís 1977; Boulaine 1995). In Ecuador, he was the first to notice the existence of a peculiar entomological fauna in the high Andes. In his attempt to reach the summit of Chimborazo (6268 m) and before arriving at the glacier of this mountain, he

collected several insects that Moret (2005) stated could have been carabid beetles (Coleoptera: Carabidae).

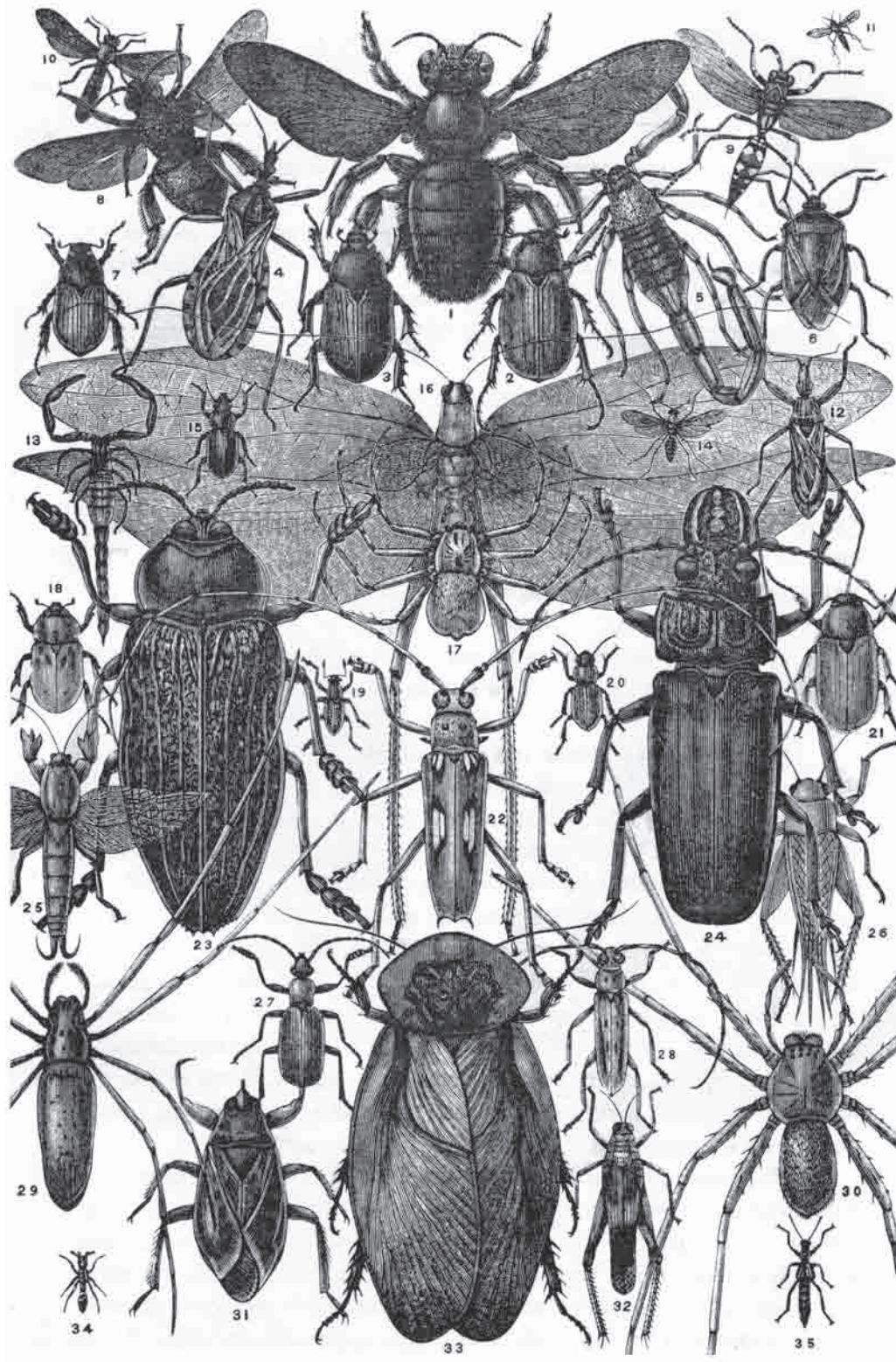
In the 19<sup>th</sup> century, one of the most outstanding visits to Ecuador was the one by Charles Darwin (1809–1882) on board the Beagle. In his book published in 1845, *Voyage of the Beagle*, Darwin (1989) cited the following on his arrival to the Galápagos Archipelago: “*I took great pains in collecting insects [of the Galápagos Islands], but excepting, Tierra del Fuego, I never saw in this respect so poor a country...*”. However, he emphasized that the few species he collected turned out to be new species. Darwin was always fond of entomology and his observations and collections of beetles helped him to clarify his ideas concerning the distribution of insects and sexual selection. His entomological observations strengthened his ideas in his monumental work, *The Origin of Species* in 1859 (Darwin 1985).

The Spanish Scientific Commission of the Pacific, in December 1864 and January 1865, went into the Ecuadorian Andes after travelling along the American coast (Cabodevilla 1998). Francisco de Paula Martínez, chronicler of the expedition, made excursions to two volcanoes near Quito, Guagua Pichincha and Antisana. He collected numerous insects that are housed today in the Madrid Museum of Natural History (Santos Mazorra 1994; López-Ocón 2003).

One of the most important surveys was the one by Edward Whymper (1840–1911) who arrived to Ecuador in 1879 and returned to London in 1880 (Fig. 6). He described his scientific observations in his work “*Travels amongts the great Andes of the Equator*”. Its first edition came out in 1891 and contained excellent descriptions of hundreds of insects that were collected in his journey. It also included a supplement that compiled species descriptions by contemporary scientists like Henry Walter Bates (1825–1892). Bates (1891) felt that the research done by Humboldt and Bonpland was unsatisfactory and that the observations done by Whymper had been superior in quantity and quality as he described hundreds of high altitude insects that were new to science (Moret 2005). Whymper not only gathered information about Ecuadorian mountains and volcanoes but also collected a great variety of insects. Several of these insects have been described in his honor, for example the scarab species, *Heterogomphus whymperi* Bates 1861 (Coleoptera: Scarabeidae). Ecuadorian biodiversity was reflected in an illustration by Whymper of the insects he found one night in his hotel room in Guayaquil (Fig 7). Whymper also suggested that diversity decreases in relation to higher altitude confirming Von Humboldt's observations. This observation was also made in the



**Figure 6**  
Edward Whymper. Museo Nazionale della Montagna “Duca degli Abruzzi”. Centro Documentazione - Torino.



**Figure 7**

Insects in Whymper bedroom in Guayaquil. (Whymper 1892).

preface table in the supplementary appendix written by Bates (Whymper 1892). Whymper's collections were noteworthy in that he noted with precision the date, locality, and altitude of each specimen. This practice was uncommon even for professional naturalists at that time (Moret 2005). Whymper's altitude measurements are exact in almost all instances even though he obtained those numbers using a heavy and fragile mercury barometer. This instrument was baptized as "baby" because one of his companions, Alpinist Jean-Antoine Carrel, had to carry it on his back to the peak of the volcano Chimborazo (Whymper 1892).

The Italian zoologist Enrico Festa visited Ecuador and collected numerous specimens that are now deposited at the Museo Regionale di Scienze Naturali Di Torino. Festa left Italy in mid-1895 to head a historic expedition to Ecuador, but a revolution and fighting between liberals and conservatives forced Festa to stop in Panama in the Darien jungles. While waiting several months until the political situation calmed down, Festa collected information and specimens from the Panamenian Chocó forest. He arrived in Guayaquil in September 1895, where he started his journey through Ecuador collecting every specimen he came across, from insects to large mammals. He ended his expedition in February 1898 when he returned to Europe. Much of his work was conducted in the Ecuadorian Andean region. He traveled from Cuenca in the south to Tulcán, the northern limit of Ecuador on the Colombian border (Festa 1909). He extensively collected specimens from all zoological taxa, however, much of the material collected by Festa was not published due to the vast size of his collections.

Many insect collections were made by important naturalists and men of science who travelled around Ecuador. Hugh Cuming (1791–1865) was an English naturalist and conchologist who has been described as the "Prince of Collectors" (Lovell 1864). Cuming travelled around South America from 1821 to 1830. His vast assemblage of materials were immediately distributed to museums and included 130,000 specimens of dried plant material, 30,000 shells, large numbers of birds, reptiles, quadrupeds and insects, and numerous living orchids (Lovell 1864). Herman Karsten (1817–1908) was a German geologist, botanist and naturalist who followed the example of Humboldt and travelled from North and to South America in 1844–1856. In Ecuador, he worked in the vicinity of the Pichincha and Sangay volcanoes and collected both plants and insects (Acosta Solís 1977). Another naturalist, Marc de Matham, also made entomological collections between 1887 and 1893 (Onore 2003), which were later studied by Vaurie (1969) and

Duckworth & Eichlin (1978). The German geologist, Alphons Stübel (1835–1904) travelled throughout the Ecuadorian Andes from 1870 to 1874. He focused on volcanism studies but also collected many insect specimens that were sent to the entomologist, Theodor Kirsch. Kirsch published the descriptions of many new insect species belonging to the families Chrysomelidae, Tenebrionidae, Scarabaeidae, and Carabidae among others (Moret 2005, Acosta-Solís 1977).

### **The Beginning of the 20<sup>th</sup> Century**

At the beginning of the 20<sup>th</sup> century, the Mission Géodésique de l'Equateur (1901–1906) organized by the military geographic service with the support of the Académie des Sciences de Paris came to Ecuador to measure the Equatorial meridian. They also collected insects that are now deposited at the Muséum National d'Histoire Naturelle de Paris and the British Museum. The French expedition collected a large number of specimens that were described in a series of volumes. Volume 10 deals with Entomology and Botany; Chapter 2 is devoted to Diptera, where 34 Nematocera species and 145 Banchycera species were reported. One of the described species was *Diadocera riveti* (Tabanidae) (Surcouf 1919) that was originally described as part of the genus *Tabanus* and was named in honor of Paul Rivet (1876–1958). Rivet was part of the expedition as a medical doctor and anthropologist but also dedicated himself to collect insects during his journey. Lieutenant colonel Robert Bourgeois, chief of the mission, was the brother of the coleopterist Jules Bourgeois (Moret 2005). For this reason, the insect specimens collected by his colleagues were well studied.

In the Galápagos Islands, the most significant work after Darwin was the expedition of the California Academy of Science in 1905 and 1906 with F.X. Williams as the entomologist (Peck 2001). The next most significant expedition was that of the Galápagos International Scientific Project (GISP) of 1964 organized by the University of California (Usinger 1972)

It is important to emphasize that from the beginning, natural history expeditions traveled the country collecting animals and plants using mainly the same roads and routes (Whymper 1892; Festa 1909; Onore 2003). Many of the collecting localities are named repeatedly. Benalcazar, Cieza de León, La Condamine, Bonpland, Ulloa, Humboldt, Whymper, and Festa followed routes used since pre-Columbian times and elaborated and improved by the Incas. These roads were named "Qhapac Ñan" (Inca road) and later the Spaniards used those roads as connections between

Guayaquil (the main port) and Quito, the Ecuadorian capital (Onore 2003).

The first Ecuadorian that dedicated himself to the study of insects was Francisco Campos Ribadeneira (1878–1943). He was an intellectual from Guayaquil and was considered as the zoologist of the country. He was a biology teacher at the Colegio Vicente Rocafuerte and a medical zoology professor at the University of Guayaquil, where he conducted studies in medical entomology. Campos collected numerous insects and created the first entomological collection in Ecuador (Moret 2005). Periodically, he also wrote important publications for the Revista del Colegio Vicente Rocafuerte and the Sociedad Médica Ecuatoriana that published the only scientific journal related to natural sciences. In 1926, he published *Contribución al estudio de los insectos del Callejón Interandino*. One of the surveys he presented at the second medical entomology congress was the *Contribución al Estudio de los Esfíngidos* where he presented 56 species from Ecuador (Campos 1930).

## **The Development of Entomology as a Science in Ecuador**

### **Medical entomology**

The relationship between insects and humans has been documented throughout history, from the mythical biblical plagues and the first observations of malaria by Hipocrates about 400 BC, through the miasmatic theory of disease and the devastating pests that caused high mortality to human populations. Many chroniclers commented on the nuisance of mosquitos and how plagues attacked crops. However, it was only at the end of the 19<sup>th</sup> century that insects were recognized as possible vectors of diseases such as malaria (Machado-Allison 2004).

The Ecuadorian government started programs to control tropical diseases in 1940 with creation of the Instituto Nacional de Higiene y Medicina Tropical (INHMT) “Leopoldo Izquieta Pérez”. This institute has the mission to identify vectors of tropical and infectious diseases and to establish an insectary to test insecticides (<http://www.inh.gov.ec/>). Another institution devoted to the control of insect vector of human disease is the Servicio Nacional de Erradicación de la Malaria (SNEM). This institute studies and controls populations of *Aedes aegypti* (L. 1762) (Diptera: Culicidae) and the Chagas Disease vectors *Panstrongylus rufotuberculatus* (Champion 1883), *Rhodnius ecuadoriensis* Lent & León 1958, *Triatoma*

*dimidiata* (Latrelle 1811) (Hemiptera: Triatominae), and other species.

In 1950, José Rodriguez started the first taxonomic study of Phlebotominae sandflies in Ecuador. He described a new vector species of Leishmaniasis, *Phlebotomus camposi* Rodriguez 1950 (Diptera: Psychodidae), (Rodriguez 1950, Rodriguez 1952a, 1952b, Rodríguez 1953a, 1953b; Rodríguez 1956). Luis León (1957) continued this research on Leishmaniasis in Ecuador, looking for other vectors and reservoirs of this disease.

### **Roberto Leví Castillo**

One of the most influent scientists in the development of medical entomology in Ecuador was a multi-talented man, Roberto Levi Castillo. He was a passionate stamp collector, historian, physician, chemist, professor and pilot in the Ecuadorian and US Armies. He was born in January 29 of 1921 in Guayaquil (Ecuador) and did post graduate work in Europe (1929–1931) and in the United States (1932–1937). In 1937, he was commissioned as a Second Lieutenant in the US Army with a specialization in military aviation. He fought with the Ecuadorian Army during the Peruvian invasion of the Ecuadorian territory in 1941. He returned to the United States in 1942, studied at the Cornell University Medical School and graduated as a physician with a specialization in Family Medicine in 1943. For one year, he worked with the allied military command during the Second World War controlling malaria outbreaks in Greece and France (Perez Pimentel 1994).

One of the most important results of Levi-Castillo's research was the discovery that varieties of a single *Anopheles* species are geographically specific (Levi-Castillo 1944a). This publication can be considered as an early insight to ideas concerning ecological speciation (Schluter, 2001) and vicariance biogeography (Wiley 1988). In 1945, he joined the Inter-American Cooperative Service for Public Health of the United States as epidemiologist and sanitary entomologist. He fought against Andean malaria caused by the mosquito *Anopheles pseudopunctipennis*. Returning to Ecuador, he was posted as professor of Chemistry at the Vicente Rocafuerte National School in 1947. Perez-Pimentel (1994) states that he had passionate scientific discussions with Dr. Francisco Campos suggesting they did not get along with each other and had different research viewpoints. In 1951, he was awarded a PhD in chemistry and pharmaceuticals from Guayaquil University. His doctoral research was an investigation of *Culex* resistance to insecticides, one of the first studies of this type.

Levi-Castillo's major contribution as entomologist was the detailed study of South American Anophelinae. He worked in the areas of taxonomy, systematics, biology, zoogeography, ecology, and control of this group of mosquitoes (Levi-Castillo 1953, Levi-Castillo 1949, Levi-Castillo 1947, Levi-Castillo 1945, Levi-Castillo 1944d). He experimented on the possible natural control of malaria vectors and published in highly rated international research journals (Levi-Castillo 1944c). His publications have been cited worldwide and in recognition, Dr. João Lane (University of São Paulo) named a *Culex* species in his honor (*C. levicastillo* Lane 1945). He also wrote about environmental problems and consequences caused by human perturbation of the environment. He was a pioneer in conservation thinking. In 1962 he renounced entomological research because of a strike at the University of Guayaquil which destroyed his hopes of training young entomologists. He said "I understood that my intellect was in advance

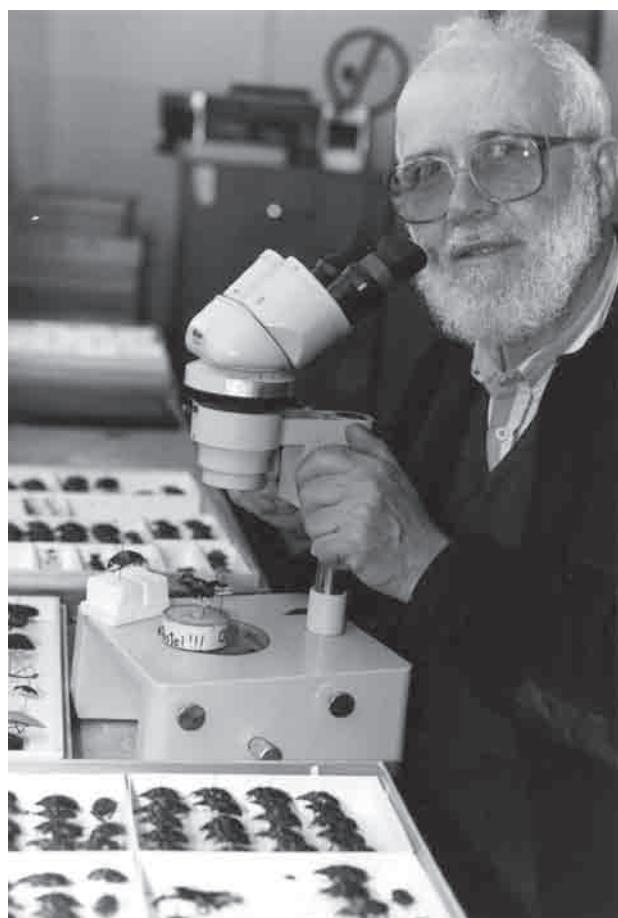
compared to the Ecuadorian academic environment, and that entomology could not be my way of life in a country where there were not the economic resources to finance so many diversified study-fields [...] I sold my laboratory equipment and burned my books to definitely abandon what sometime filled me with joy and illusions to give the chance to other challenges; looking for these, I found in stamp collecting, a new horizon". Since then he has stood out as one of the best Ecuadorian stamp-collectors (Perez Pimentel 1994).

### Agricultural entomology

In 1959, the government of Ecuador created INIAP (Instituto Autónomo de Investigaciones Agropecuarias). This institution prioritized scientific research as the foundation of agricultural development in Ecuador ([www.iniap-ecuador.gov.ec](http://www.iniap-ecuador.gov.ec)). Many agricultural engineers that work there studied agricultural entomology in Europe, United States, and other Latin American countries. The collaboration of countries such as the United States assisted the development of agricultural entomology in Ecuador.

The agricultural engineer, Gualberto Merino, was one of the pioneers of agricultural entomology research (Merino & Vázquez 1959). He started his work at the Ministerio de Agricultura in an effort to control the pest grasshopper *Schistocerca* sp. (Orthoptera: Acrididae) in the provinces of Loja and El Oro in southern Ecuador in 1945 and 1946. He used flame throwers at night to try to destroy the grasshoppers in their nocturnal refuges. This work was continued for two years without results until an undetermined pathogen reduced the population of grasshoppers, causing foul odors due to the decomposition of millions of dead insects (Merino, *pers. com.*).

Merino and his collaborators published more than 47 papers about different crop pests in Ecuador (Merino 2003). In the late 1940's, Ecuador started to import synthetic insecticides for pest control, including DDT. These insecticides were broadly used in eradication programs for agricultural pests, diseases vectors, and in schools to eliminate head lice on children. That period is known as the "green revolution" [The term "Green Revolution" generally refers to the use of improved varieties, fertilizer, irrigation and pesticides, but not pesticides in particular, that resulted in dramatic increasing in agricultural productivity. This most evident in Ecuador in the production of rice which benefited from improved varieties from IRRI] (Merino & Hernandez 1959; Merino & Vázquez 1960; Edwards 2004). It is important to emphasize the support of the Servicio Cooperativo Interamericano de Agricultura and the scientist, Harold Yust (1958) who made the



**Figure 8**  
Giovanni Onore (R. Cárdenas).

first inventory of Ecuadorian agricultural pests.

The control of pests with IPM techniques arrived late in Ecuador with replicas of experiences of other countries. Julio Molineros was a pioneer in research on fruit flies (Diptera:Tephritidae) (Molineros *et al.* 1992) and was responsible for the introduction of *Rodolia cardinalis* (Muslant 1850) (Coleoptera: Coccinellidae) for control of *Icerya purchasi* (Maskel 1878), (Hemiptera: Margarodidae), a major pest of [crop] in Ecuador.

### Museums of Natural History

The Museo Nacional de Ciencias Naturales was created in 1978 and was initially directed by the engineer Moreno who gave to the Museum his collection of Molusca and Lepidoptera. The objectives of the National Museum are the inventory and classification of the fauna and flora and the exhibition and diffusion of knowledge of Ecuador's biodiversity (see [www.mecn.gov.ec](http://www.mecn.gov.ec)). The collections at this museum have been acquired from national or foreign collectors. One of the important collection is the moths (Lepidoptera) that belonged to Thierry Porion. Today the museum collaborates in research with several museums and universities overseas, and generates its own projects in several entomological taxa (Venedictoff & Herbulet 1980).

The Museo de la Escuela Politécnica Nacional, directed by the Ecuadorian zoologist Professor Gustavo Orcés, created a section devoted to entomology at the end of the 1980's. This museum has an important collection that is available to the public. One of the outstanding researchers that have increased the number of specimens in that collection is Terry Erwin of the Smithsonian Institution who works with the personnel from that museum. Erwin and his collaborators have deposited a large number of insects collected from the canopy of trees of the Ecuadorian Amazon (Shpeley & Araujo 1997; Erwin 2000; Lucky *et al.* 2002). The collection has more than 10,000 dry invertebrate specimens and 1,600 invertebrate specimens in alcohol. The majority of these specimens has been collected by pesticide fogging of tree canopies.

### Creation of the Museum of Zoology at the Pontifical Catholic University of Ecuador

Giovanni Onore arrived in Ecuador from Italy in 1980 (Fig. 8). Onore is a Marianist missionary who worked in the Popular Republic of Congo for a decade strengthening agricultural production systems where insect pests were one of his priorities (Onore 1980, Fabres *et al.* 1981) His fondness for insects was evident since he was very young, so Africa unveiled a world full

of possibilities for research for him. He was a zoology professor at Brazzaville University (Jácome 2008).

When he arrived in Ecuador he worked in the Cotopaxi province in education. In 1981, he started to teach invertebrate zoology at the Pontificia Universidad Católica del Ecuador (PUCE). At PUCE he made one of the greatest contributions to entomology in Ecuador. He has published nearly 50 articles about Ecuadorian



**Figure 9**  
*Onorelucanus onorei* Lacroix & Bartolozzi 1989 (A. Janeta).

insects in forest entomology (Gara & Onore 1989, Onore & Maza 2003), agriculture entomology (Onore 1986), biodiversity (Onore & Davidson 1990, Somme *et al.* 1996), ethnozoology (Onore 1997), history of entomology (Onore 2003), and taxonomic descriptions of new species (Bartolozzi *et al.* 1991, Onore 1993, Bartolozzi & Onore 1993, Pampligioni *et al.* 2002, Onore & Morón 2004, Bartolozzi & Onore 2006). During his time as a university professor, he supervised more than 60 bachelors thesis, all related to insects (see Dangles *et al.* this issue). In recognition of his work, more than 150 insects have been named in his honor such as *Onorelucanus onorei* Lacroix & Bartolozzi 1989 (Coleoptera: Lucanidae) (Fig. 9).

One of the most important contributions of Onore has been the creation of the, Invertebrate Division within the Zoology Museum (QCAZ) at PUCE. This is a scientific collection that is the largest and most organized collection in Ecuador. It contains close to 2 million specimens from all regions of Ecuador (see Donoso *et al.* this issue). A large number of those specimens were collected by Onore in his travels throughout Ecuador. A great number of specimens were collected by his students that were assigned to prepare a scientific insect collection for the entomology class. This Museum is recognized internationally and has contact with the most important museums world-wide such as Staatliches Museum für Tierkunde Dresden (SMTD), Museum für Naturkunde der Humboldt Universität Berlin (ZMHB), Universidad Nacional de La Plata (MLPA), Institut Royal des Sciences Naturelles de Belgique (ISNB), Canadian National Collection of Insects Ottawa (CNCI), Muséum National d'Histoire Naturelle, Paris (MNHN), Museo Zoologico La Specola Florencia (MZUF), Museo Regionale Scienze Naturali Torino (MRSN), Museum d'Histoire Naturelle Genève (MHNG), The Natural History Museum London (BMNH), Los Angeles County Museum of Natural History Los Angeles (LACM), California Academy of Sciences San Francisco (CASC), Florida State Collection of Arthropods Gainesville (FSCA), Carnegie Museum of Natural History Pittsburgh (CMNH), University of Nebraska Lincoln (UNSM), American Museum of Natural History New York (AMNH), Smithsonian Institution Washington (USNM) (Onore 2003). The active exchange of specimens and information that has contributed to increase the knowledge of entomology in the country. Onore currently is the director of the Fundación Otonga, a private reserve in the cloud forest of Ecuador dedicated to conservation of this important habitat.

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# Entomology in Ecuador: Recent developments and future challenges

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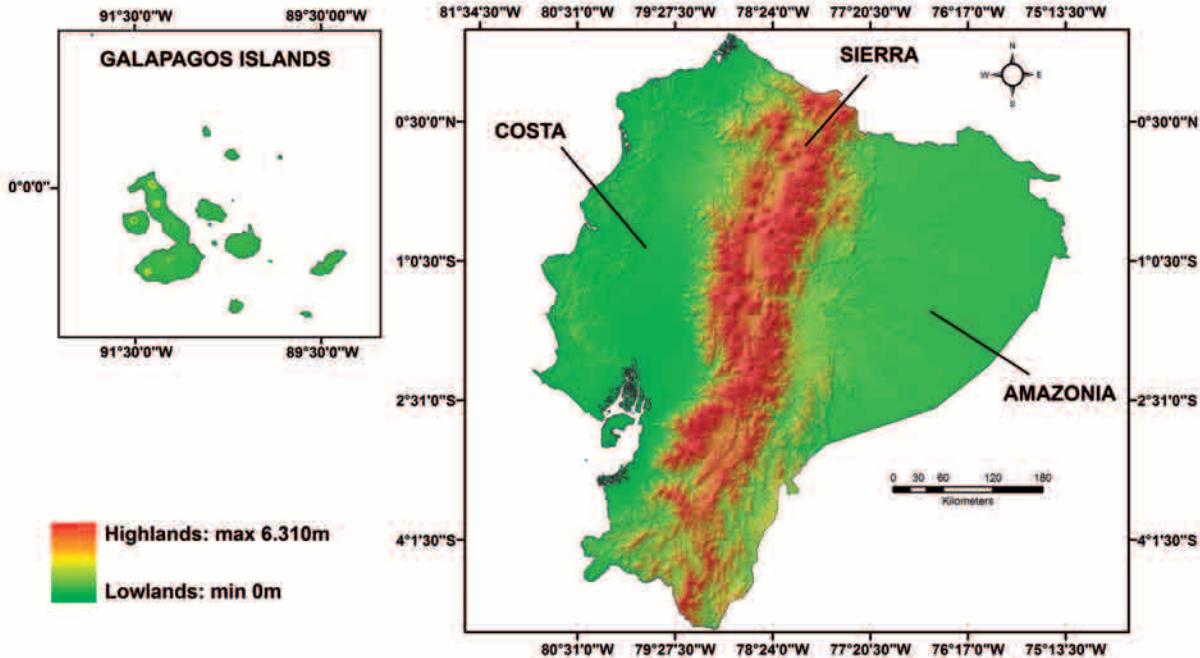
**Abstract.** We review and analyze the recent development and future challenges facing entomology as a science in Ecuador, a country with limited financial and human resources and numerous environmental problems. Taxonomic studies of the Ecuadorian insect fauna have been well developed for only a few groups (e.g. Papilionoidea, Carabidae) and remains in its infancy for most insect orders. This is due to the huge diversity of species living in a great diversity of habitats and the difficulty to identify most species. There is a lack of published basic biological information and to a high rate of endemism of many groups, especially in the Andes. The development of ecological entomology as a formal discipline in Ecuador is a very recent phenomenon, and has been mostly limited to descriptive studies of the environmental factors that govern insect diversity and abundance. We outline a set of research challenges regarding the impact of global environmental changes on insect communities and habitats they live in and propose potential strategies for the development of entomology in Ecuador. Both basic and applied research will be important in this context as well as international collaboration to strengthen the role of entomological science in decision making processes in the country.

**Résumé. L'entomologie en Equateur : développements récents et futurs défis.** Cet article est une révision et une analyse des récentes avancées et des futurs défis de l'entomologie en tant que science en Equateur, pays dont les ressources financières et humaines sont limitées et qui fait face à de nombreux problèmes environnementaux. La taxonomie de l'entomofaune d'Equateur a été étudiée en détail pour seulement quelques groupes (e.g. Papilionoidea, Carabidae) et reste fragmentaire pour la plupart des ordres d'insectes. Ceci est lié à l'existence d'une très grande diversité d'espèces vivant dans une grande diversité d'habitats et de la difficulté d'identifier la plupart de celles-ci. A cela s'ajoutent un manque réel de données publiées sur la biologie de la plupart des espèces ainsi qu'un fort taux d'endémisme de plusieurs groupes, notamment dans la région andine. Le développement de l'écologie entomologique en tant que discipline en Equateur est un phénomène très récent principalement restreint à des études descriptives sur les facteurs environnementaux qui influencent la diversité et l'abondance des insectes. Nous présentons des thématiques de recherches d'enjeu pour les futures années, notamment en relation avec l'étude de l'impact des changements globaux sur les communautés d'insectes et leurs habitats et nous proposons des stratégies pratiques pour le développement de l'entomologie en Equateur. Dans ce contexte, le développement combiné de la recherche fondamentale et appliquée, si possible dans le cadre de collaborations internationales, permettra de renforcer le rôle de l'entomologie dans les processus de décision à l'échelle du pays.

**Keywords:** Insect taxonomy, Ecology and evolution, Pests, Monitoring, Global changes.

The Neotropical region has long been recognized as supporting one of the highest levels of biological diversity in the world. Insects are particularly abundant and species rich in many Neotropical ecosystems, yet the extent of this diversity, the factors that govern its distribution and the degree of degradation as a result of anthropogenic changes are still incompletely known. The wide diversity of habitats that Ecuador possesses in a small area makes it an ideal location for biodiversity, ecological and evolutionary research. Although the

diversity of many groups (e.g. plants, birds and frogs) has been the focus of numerous publications, data on the entomological fauna in Ecuador are still very incomplete. In this paper, we aim to review and analyze recent developments and future challenges facing entomology as a science in Ecuador, a country with limited financial and human resources and numerous environmental problems. It is not our goal to present a comprehensive review of every paper in entomology published on the Ecuadorian insect fauna, but rather to cite studies, especially those published by, or in collaboration with, Ecuadorian entomologists, that we have found especially important and revealing to illustrate the development of entomology as a science in Ecuador.

**Figure 1**

Digital elevation map of Ecuador, including Galápagos Islands. Color bar indicates elevation range.

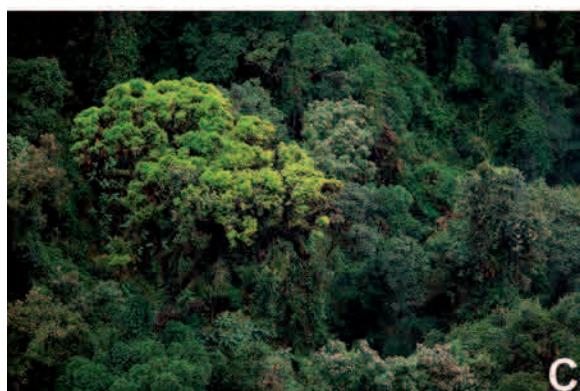
### Ecuador's biogeographic zones

The tropical Andes span more than 1.5 million km<sup>2</sup> from western Venezuela to northern Chile and Argentina, and include large portions of Colombia, Ecuador, Peru, and Bolivia. Ecuador is located in the Northern part of the region, bordered by Peru in the south and southeast, Colombia in the north and northeast and the Pacific Ocean in the west. With an area of only 283,560 km<sup>2</sup>, Ecuador is one of the smallest countries of South America. The great highs and lows of the Andes mountain range (fig. 1), with its snowcapped peaks, steep slopes, deep canyons, and isolated valleys, have led to the evolution of an amazing diversity of ecosystems, habitats and thus, species diversification (Hughes & Eastwood 2006; Chaves *et al.* 2007; Ribas *et al.* 2007). Recent studies demonstrate that Andes uplift was separated by relatively long periods of stability (tens of millions of years), and by rapid changes of 1.5 Km or more in relatively short periods of time (1 to 4 million years) (Garzione *et al.* 2008). This allowed the creation of new climatic and environmental niches in relatively short periods of times, and the adaptation of organisms to those habitats for long periods of time. The large variety and range of climatic regimes found in Ecuador have a major effect on the range of vegetation types that

define biogeographic zones (see Cárdenas *et al.*, this issue). Ecuador's territory is usually divided into four main natural regions: the Amazonian lowlands, the Andes, the Pacific coastal lowlands and the Galápagos Islands (fig. 1). We provide a short description of each region, which we think will guide the reader not only in this article, but also throughout the special issue. More details on the different biogeographic zones can be found in Ron *et al.* (in press).

Accounting for almost 40% of the total area of Ecuador, the Amazonian region gradually descends eastwards from the foothills of the Andes to altitudes of 200–400 m. The climate is tropical, humid and aseasonal. Monthly mean precipitation is approximately 2820 mm/ year with no month receiving less than 100 mm of rain (Valencia *et al.* 2004). Temperatures range from 22 °C (minima) to 32 °C (maxima). The absence of a prolonged dry season, together with warm temperatures throughout the year and a varied topography, make the region a hotspot of biodiversity (Myers *et al.* 2000). The only biogeographic region of this zone is the evergreen lowland wet forest with a canopy mostly 15–30 m tall and emergent trees reaching 50 m (fig. 2A).

The Ecuadorian Andes occupy the central third of Ecuador and are divided into two main cordilleras,



western and eastern. Transverse mountain bridges interconnect these two cordilleras forming ten inter-Andean basins with at least 30 peaks of volcanic origin and 25 mountains above 4,500 m (Ron *et al.* in press). The cordillera exhibit precipitous elevation gradients with a complex topography which creates a landscape with extreme climatic differences. Annual rainfall varies between less than 500 mm in the dry inter-Andean basins to above 6000 mm on the Eastern slope. Temperature varies as a function of elevation with small seasonal changes. Major biogeographic regions from East to West include Eastern foothill forest, Eastern montane forest (cloud forest), Páramo, Andean shrub, Western montane forest and Western foothill forest (figs. 2B, C, E).

On the Western slope of the Andes, the Pacific coast contains lowlands, river valleys, and a coastal cordillera with maximum elevations of 800–900 m. Natural ecosystems are dry scrub, deciduous forest, Chocó tropical forest, mangroves and Western montane forests at higher altitudes (mainly in Guayas and Esmeraldas provinces). Characterized as one of the wettest non-seasonal climates on Earth, the Chocó region is another of the top ten hotspots of biodiversity (Myers *et al.* 2000), (fig. 2F). Between the humid Chocoan forest and the dry Peruvian deserts, the dry coastal tropical forest is characterized by a North to South humidity gradient giving it a tremendous complexity of local climates and a great diversity of ecosystems (fig. 2G).

The Galápagos Archipelago comprises 12 large and numerous smaller islands and exposed rocks that have a total area of about 8,000 km<sup>2</sup>. All islands are oceanic and have never been connected to the continent by any sort of land bridge (Constant 2006). Located in the Pacific Ocean approximately 1000 km west of the continent, the Galápagos have a remarkably seasonal climate, largely influenced by shifts in cool water masses originating from the South of Peru and warm water masses from the North (Kricher 2006). Large islands have an altitudinal gradient of vegetation types from arid and transitional forests in the lower parts to moist forest and fern-sedge zones in the higher

elevations (Grant 1999, fig. 2H). The volcanic origin of these islands, many of which still have highly active volcanoes, has resulted in celebrated levels of species diversification and endemism (Kricher 2006).

## Recent advances in the entomological knowledge in Ecuador

### Taxonomy and distribution

Since the creation of the Invertebrate Section of the Museum of Zoology QCAZ of the Pontifical Catholic University of Ecuador (PUCE) in 1981 (see Barragán *et al.* this issue), investigations on entomology have focused mainly on the taxonomy and the biology of specific groups of insects. As in many entomological museums, two taxonomic groups have been the focuses of interest by both local and foreign entomological taxonomists: Lepidoptera and Coleoptera. Note that few other extensive entomological studies have been performed in specific regions of Ecuador such as the work by Peck (2001) on orders of insects of the Galápagos Islands

A database of Ecuadorian butterfly diversity and distribution has been developed by K. Willmott from the Florida Museum of Natural History and J. Hall from the National Museum of Natural History (online access: <http://www.butterfliesofecuador.com>). In addition to the information found on the “butterfly of Ecuador website”, four monographs have been published on Lepidoptera genera (Piñas & Manzano 1997), Arctiidae (Piñas & Manzano 2003a), Saturnidae (Piñas & Manzano 2003b), Papilionidae (Bolino & Onore 2001), and Sphingidae (Guevara *et al.* 2002). Willmott & Hall (2008) estimate that Ecuador contains approximately 2700 species of Papilioidea, about 50–55% of all Neotropical butterfly species and 25% of the world's species, making it one of the world's three most diverse countries along with Colombia and Peru. Exhaustive butterfly inventories in specific Ecuadorian regions over a single year, such as in the Amazonian forest with about 20,000 individuals collected (Checa 2006), and in the Chocó where about 10,000 individuals were collected (Velasco 2008), confirmed the huge abundance and diversity of species, many of them being represented by only one or two individuals. Since 1993, a total of 168 species and 49 genera of butterflies from Ecuador have been described by various authors (see Willmott & Hall 2008, for a complete list of references). About 200 species and 8 genera still require formal description. Even for a relatively well-studied group like Papilioidea, one highly distinctive and four cryptic undescribed species

### Figure 2

Photographs of some insect rich-ecosystems of Ecuador A. Canopy view of the Amazonian tropical forest (Yasuni National Park, 300 m a.s.l.), B. High altitude grasslands of páramo (Sangay National Park, 3600 m a.s.l.), C. Western montane forest (Yanacocha Reserve, 3200 m a.s.l.), D. Agricultural landscape (Carchi Province, 2800 m a.s.l.), E. Tropical rain forest (Misahualli, 300 m a.s.l.), F. Chocó evergreen forest (Canande Reserve, 1200 m a.s.l.), G. Coastal dry forest (300 m. a.s.l.), H. Coastal mangroves and arid forest (Galápagos National Park). Photo credits: A-D, H: O. Dangles; E: M. Guerra-V.; F: R. E. Cárdenas; G: G. Ramón.

have been recognized since 1998, all occurring in Andean habitats (Jasinski 1998; Willmott *et al.* 2001). More poorly studied groups, such as the Lycaenidae, Riodinidae and Satyridae, are likely to contain even higher proportions of new or unrecognized species (Willmot & Hall 2008) suggesting that Ecuador remains a source of many discoveries for lepidopterists.

Regarding the Coleoptera of Ecuador, and particularly Carabidae, the most complete study is by P. Moret on the Carabidae of the Páramo in the Ecuadorian Andes (Moret 2005). The Páramos are mountain ecosystems consisting of large areas of herbaceous plants and sclerophylous shrubs, above the tree line (3400–3600 m) and below the permanent snowline (4800–5000 m, fig. 2B). Based on the direct examination of about 8500 individuals, Moret (2005) reviewed 16 genera and 204 species, of which 57 were new to science. The flightless condition of most (96%) high Andean Carabidae implies reduced dispersal ability and has led to a great number of geographically restricted species. The author considered a total of 191 species (94%) as micro - or meso-endemic to the Ecuador Andes. This rate of endemism is similar to that found in the Andes near Mérida, Venezuela (91%, Perrault 1994), although Ecuadorian Carabidae exhibit a higher diversity, both at specific and generic levels. Endemism rates are lower among the Alpine Carabidae of the Alps (60%, Brandmayr *et al.* 2003) and the Pyrenees (44%, Moret 2005) with a higher number of genera and fewer species in each genera.

These detailed works on the Papilionoidea and Carabidae reveal three main characteristic of the Ecuadorian entomological fauna which can be

generalized to most taxonomic groups throughout the country: 1) the huge diversity of species in a great diversity of habitats, 2) the difficulty in identification of most species, and 3) the lack of published basic biological information, partly due to the high rate of endemism of many groups especially in the Andes (Table 1). For example, an exhaustive survey of stingless bees (Hymenoptera: Meliponinae) in 14 provinces of Ecuador by Coloma (1986) reported a total of 73 species, of which 13 were new species for science and 49 new records for Ecuador. Similarly, Ayala (1998) and Battiston & Picciau (2008) reported a total of 69 species of mantids (Mantodea) of which 10 were new to science. The high rate of endemism for many groups such as Coleoptera, especially in the Andean region, also complicates the work of taxonomists. For example, the Ecuadorian tiger beetle fauna (Coleoptera: Cicindelidae) contains 12 genera and 74 species, of which 26.0% are endemic (Nuñez *et al.* 1994; Pearson *et al.* 1999). This is the highest percent of endemism among all Andean countries (Nuñez *et al.* 1994). Similarly, 173 species of Dynastinae beetles (Coleoptera: Scarabeidae) have been reported in Ecuador, of which 35 are endemic, mainly from the genus *Cyclocephala* (Ortiz 1997). Finally, of the 283 species of Ecuadorian Rutelinae beetles, 26.8% are endemic (Paukar 1998; Smith 2003). The high rates of endemism observed for many insect groups (Table 1) represent a challenging issue for insect taxonomists not only in Ecuador but also in neighboring countries.

### Agricultural entomology

The development of entomology as a scientific

Table 1. Diversity of species and genera and percentage of endemism of several taxonomic groups of insects in Ecuador.

Order	Taxonomic group	Number of species	Number of genera	Main genera (nb. species)	% endemism in Ecuador	References
Hymenoptera	Meliponinae	73	17	Trigona(20), Melipona(8)	31.1	Coloma (1986)
	Formicidae	670	74	Pheidole (93), Camponotus (58)	10.7	Donoso (unpubl. data)
	Ithomiinae	116	32	Pteronymia (15), Oleria (14)	43.0	Gil (2001)
Diptera	Tabanidae	204	33	Tabanus (40), Esenbeckia (16)	12.2	Cárdenas & Buestan (this issue)
	Drosophila	112	1	-	36.6	Acurio & Rafael (unpubl. data)
Orthoptera	Caelifera	216	117	Jivarus (15), Orphulella (6)	55.0	Buzzetti & Carotti (2008)
	Mantodea	63	37	Vates (5), Acanthops (4)	34.8	Ayala (1998), Battiston & Picciau (2008)
Isoptera	all	62	28	Nasutitermes (15), Anoplotermes (6)	-	Bahder <i>et al.</i> (this issue)
Coleoptera	Cicindelidae	74	12	Cicindela (26), Odontocheila (14)	29.2	Nuñez <i>et al.</i> 1994
	Dynastinae	173	40	Cyclocephala(67), Ancognata(13)	20.2	Ortiz 1997
	Rutelinae	283	38	Platycelia (144), Anomala (64)	33.4	Paukar (1998), Smith (2003)
	Sacarabeinae	233	21	Onthophagus (31), Canthidium (25)	-	Carpio, unpubl. data
	Carabidae	377	83	Dyscolus (63), Blennidus (33)	40.8	Zapata (1997)

discipline in Ecuador has been fostered by demand-driven entomological research, especially research aimed at solving specific problems related to agriculture. Since the creation of the National Institute of Agronomical Research (INIAF, <http://www.iniaf-ecuador.gov.ec>) in 1959, this research has focused on the study of deleterious effects of insect pests on local crop production, e.g. fruit fly (Molineros *et al.* 1992; Feican *et al.* 1999), white fly (Peralta 1993), potato weevil (Gallegos *et al.* 1997), potato tuber moths (Pollet *et al.* 2003) or on the development of agro-industrial projects such as cultivation of purple African nightshade (*Solanum marginatum*, Moya 1985) or African palm (*Elaeis guinensis*, Martinez 1991).

If diversity is a main feature of the entomological fauna in natural habitats, this is also true for cultivated landscapes (fig. 2D). For example, Onore & Arregui (1989) identified 27 insect pest species associated with *Lupinus mutabilis*, a species of lupine grown in the Andes for its edible bean. Of the 27 species, 13 were Lepidoptera (e.g. the noctuids *Copitarsia* sp., *Agrostris* sp., *Autoplusia* sp.) whose larvae feed on lupine leaves and seeds. Another major Andean crop, quinoa (*Chenopodium quinoa*), is attacked by at least 18 pest species, mainly lepidopteran Noctuidae (*Copitarsia* sp., *Agrostris* sp.) (Fiallos 1989). Balsa (*Ochroma pyramidalis*), a large fast-growing tree that can grow up to 30 m, has 68 insect pests including 60 species of Lepidoptera, mainly Arctiidae and Saturniidae (Barragán 1997). Finally, sixteen defoliator species are associated with the IUCN red-listed *Podocarpus oleifolius* (Podocarpaceae) of which 12 belong to the Geometridae (e.g. *Anisodes atrimacula*, *Sabulodes boliviiana*) (Salazar 1998).

The origin and the implications of such pest diversity for agro-ecosystem productivity are virtually unknown. Whereas inter-specific competition may be a key factor limiting insect diversity and abundance on the same host plant, mutualistic mechanisms (such as resource partitioning, sequential attack of the host plant) can promote coexistence among species. For example, in a study on the lepidopteran larva community on *Podocarpus*, Salazar (1998) showed that some species are specialized on the apex of the needle-like leaves whereas others feed on edges or stems. Similarly, Mazoyer (2007) showed the existence of facilitation mechanisms among pairs of potato moth species (Gelechiidae). Some species increased their feeding rate and survival when the tuber had been first infested by another species. Insect diversity and abundance can also be shaped by predator communities; however the high diversity of insect predators in Ecuador makes this a complex issue. For example, Martinez (1991) reported that more than 50 species of parasitoids,

mainly hymenopteran Chalcididae and Eulophidae and dipteran Tachinidae, were associated with 44 species of defoliators, mainly Limacodidae and Brassolidae Lepidopterans, in African palm (*Elaeis guinensis*) crops.

### **Ecological entomology**

Because the complex patterns of uplift of the Andean cordillera and oceanic islands, a large number of speciation events took place in Ecuador. This makes this country not only a productive place for studies on insect taxonomy, but also on insect ecology, evolution, or biogeography (Peck 2001; Moret 2005; Jiggins *et al.* 2006). This unique environmental and evolutionary history has attracted a long list of explorers and naturalists such as Darwin, von Humboldt and Whymper who have played an important role in fostering an interest in South American natural history and evolution of insects (Barragán *et al.* this issue). Despite the biological diversity of Ecuador and the scientific interest it has generated in the past, the development of ecological entomology as a formal discipline in Ecuador is a very recent phenomenon. It has been mostly limited to descriptive studies on environmental factors that govern insect diversity and abundance in different types of natural habitats. Examples include the study of seasonality and stratification of butterfly and locust communities (DeVries *et al.* 1997; Amédégnato 2003; Checa 2006; Velasco 2008), the microdistribution of vector and pest insects (Suarez 2008; Dangles *et al.* 2008) or the altitudinal distribution of insect species (Brehm *et al.* 2003a, 2003b; Jacobsen 2004; Hilt & Fiedler 2006; Cárdenas 2007; Fiedler *et al.* 2008).

The succession of plant and animal communities along altitudinal gradients has been of major interest for ecologists, especially in temperate regions (Berner *et al.* 2004; Hodkinson 2005). More recently, a growing number of studies have investigated the diversity of insect assemblages along altitudinal gradients in species-rich tropical regions (Brühl *et al.* 1999; Axmacher *et al.* 2004), including Ecuador for several groups such as moths (Geometridae: Hilt & Fiedler 2006, Gelechiidae: Dangles *et al.* 2008) Dipteron Tabanidae (Cárdenas 2007), and aquatic insects (Jacobsen 2004). The works by Jacobsen on streams and rivers (fig. 2E) represent the most complete study ever realized in the country on the ecological and physiological factors that govern distribution patterns of insects along altitudinal gradients (Jacobsen *et al.* 1997; Jacobsen 1998; Jacobsen *et al.* 2003; Jacobsen 2008a). A combination of empirical and experimental studies has shown that distribution patterns correspond to the respiratory physiology of individual species in relation

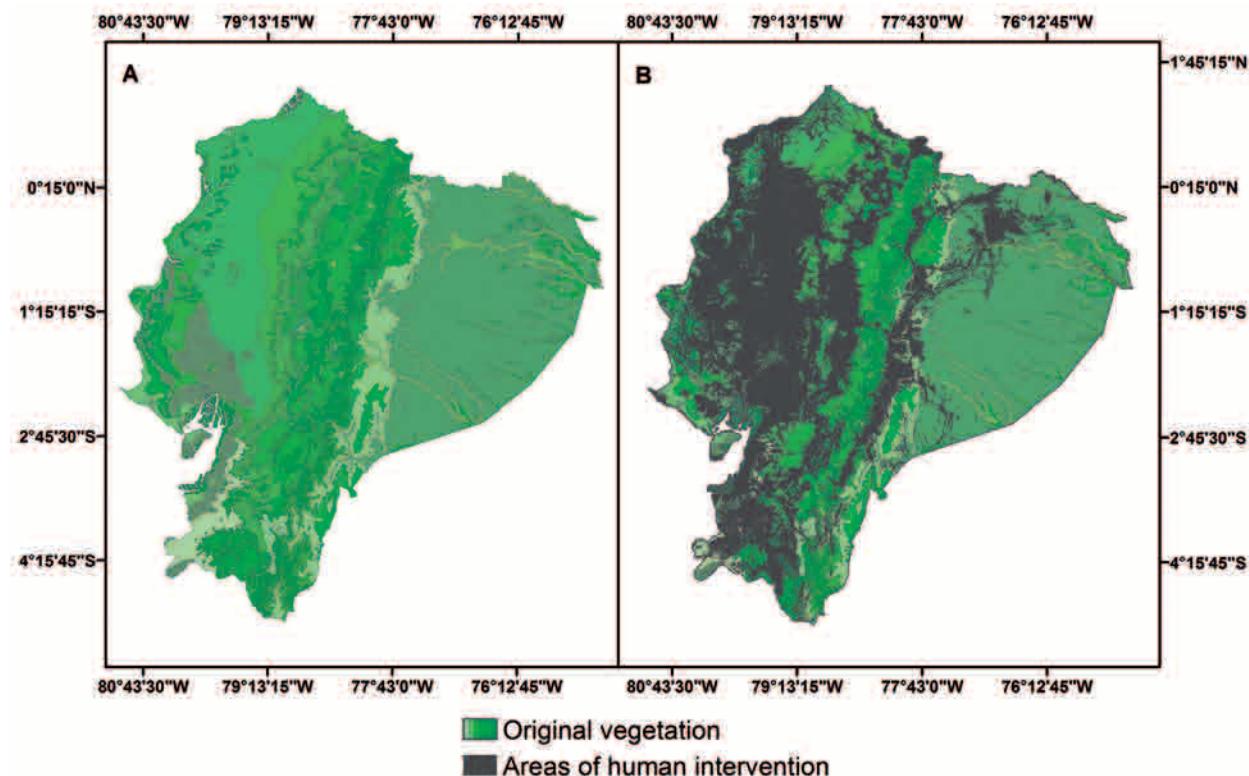
to the temperature and oxygen regime of the environment (Jacobsen & Brodersen 2008). Both temperature and oxygen saturation of stream water decrease with altitude. These two factors are highly correlated to the decrease in diversity of macroinvertebrates with altitude in Ecuadorian streams (Jacobsen 2008b). In addition, Rostgaard & Jacobsen (2005) showed that oxygen availability in streams is expected to decrease more with altitude than respiratory oxygen demand by macroinvertebrates, potentially affecting the composition of communities in streams at very high altitudes (Jacobsen *et al.* 2003). Orography of Ecuador should foster more studies on insect response to the changing environments experienced along altitudinal gradients, especially with regard to the growing awareness that these responses may serve as analogues for climate warming effects at a particular altitude over time.

### Future challenges: Ecuadorian entomology in a changing world

#### Habitat fragmentation

Ecuadorian civilizations, as well as the great

Peruvian empire of the Incas, have inhabited in the Ecuador for thousands of years. Since 1950, the population of Ecuador has experienced a five-fold increase. With 13,780,000 inhabitants (INEC 2008), Ecuador is one of the most densely populated country in South America (55 inhabitant/km<sup>2</sup>) resulting in strong pressure on many natural ecosystems (fig. 3). Because the coastal region and the inter-Andean valleys are the most hospitable to people, they are also the most degraded parts of the Ecuador, with less than 10 percent of their original natural habitat remaining (fig. 3, UICN & WWF 2000). Ecuador together with Honduras and El Salvador have suffered the highest rates of deforestation in Latin America between years 2000–2005 ( $\geq 1.5\%$  decrease in forest area /year *sensu* FAO 2007) principally due to changes in land use. In the montane forests, agriculture, dams, and road building are the most significant threats. At higher altitudes, seasonal burning, grazing, agriculture, mining, and fuel wood collection have degraded the grasslands and scrublands of páramos. In the Amazon, disturbances mainly originate from oil and gas companies that have constructed several roads for prospecting and



**Figure 3**

Maps of Ecuador showing (A) the original vegetation cover and (B) and the extent of habitat degradation in 2000, following Sierra (1999).

exploitation (Valencia *et al.* 2004). These roads have facilitated an extensive colonization by family farms and communities in previously unpopulated land. In the Galápagos, the introduction of domestic species such as goats, pigs, cats and rodents and the increase in bushfires frequency have deteriorated the natural vegetation of many islands. The clearing of native vegetation in the most humid zones for agriculture has significantly degraded the vegetation of the transition and scalesia zones on populated islands. This has been exacerbated by invasive plants such as raspberry (*Rubus niveus*), rose apple (*Syzygium jambos*), quinine (*Cinchona succirubra*), and Spanish flag (*Lantana camara*). Over 42.2% of the 438 exotic plant species are considered invasive (McMullen 1999).

Habitat fragmentation process implies habitat loss but also change in habitat configuration (Farhig 2003). While habitat loss has large, consistent negative effects on insect communities, habitat fragmentation *per se* has a much weaker effect, and may be negative but also often positive (Grez *et al.* 2004). In Ecuador, it has been shown that spatial scale affects significantly the response of insect communities to habitat fragmentation (e.g. Tylianakis *et al.* 2006 for cavity-nesting Hymenopterans on the Pacific Coast; Velasco 2008 for butterfly communities in the Chocó). The temporal component (time elapsed after disturbance) is also a crucial issue of habitat fragmentation (e.g. Abedrabbo 1988; Carpio *et al.* this issue). For example, Abredrabbo (1988) found a relatively fast recovery of terrestrial invertebrate fauna only 2 years after brush fires on Isabela Island, Galápagos. The rapid recolonization was facilitated by the presence of un-impacted isolated areas where the arthropod fauna was not altered. More studies separating the effect of habitat loss and fragmentation on insect communities, for example through manipulative experiments, are therefore urgently needed in Ecuador. Entomologists could also make good use of classical theories in community and population ecology such as the theory of island biogeography (McArthur & Wilson 1967), metapopulation dynamics (Levins 1969) and metacommunity dynamics (Holyoak *et al.* 2005) to predict the complex consequences of habitat fragmentation on the entomological fauna of Ecuador.

### Climate change

Potential impact of climate change on the Ecuadorian fauna has been poorly explored and has been restricted to only a few groups such as Amphibians (Pounds *et al.* 2006; Ron *et al.* in press) or plants (DeVries 2006). Obviously, as is the case for all ectothermic organisms

whose development time is temperature-dependent, insects are expected to respond strongly to changes in climate regimes, but this response may greatly differ depending on the region considered (Tewksbury *et al.* 2008). On the one hand, warming in the tropical Amazonian forest, although relatively small in magnitude, may have deleterious consequences because tropical insects are relatively sensitive to temperature change and may be living very close to their optimal temperature (Deutsch *et al.* 2008). On the other hand, effect of climate change on insect populations in the Andes is expected to be greater than in lowlands, reflecting the prediction of much larger proportional temperature rises in these areas (Hodkinson 2005). Warmer temperatures may affect population dynamics of some insect species (mainly agricultural pests), but also their altitudinal distribution. One of the few documented case in Ecuador is a study on the altitudinal distribution of the genus *Sphaenognathus* (Coleoptera: Lucanidae) (Onore & Bartolozzi 2008). Desiccated feces of lucanid larva were present in the soil at altitudes about 200 m lower than the lowest living populations of larvae at the time of their collections. This suggests an upward shift of these insects in the last 15–25 years. More studies on the impact of climate change on insects are definitely needed in Ecuador, especially because the small differences in elevation or vegetative cover over the country can create strong microclimatic differentials over short distances and allow development of persistent microclimatic refuges for insect populations to develop (see Dangles *et al.* 2008).

### Invasive species

Although Andean countries have recognized the problems associated with invasive insect species for several years (Ojasti 2001), a comprehensive approach to this issue is still to be developed, especially in Ecuador. Globalization with expanding trade and increased human movement is likely to increase the risk of invasive insect species in South America. In the Andean region, commercial exchanges at regional and local scales have been the main causes for the rapid expansion of the potato tuber moth *Tecia solanivora*, (Lepidoptera: Gelechiidae), an exotic pest originating from Guatemala. This pest now represents one of the most serious agricultural pest problems in Ecuador (Puillandre *et al.* 2008). In the Galápagos Islands, a one-year survey of arthropod communities associated with agricultural areas on the Santa Cruz Island collected 160 species, of which 76 were introduced (e.g. the pyralid *Diaphania hyalinata*, Oquendo 2002).

Insect invasions can also spread and become

established largely unnoticed as “tramp” species associated with human displacements. In a study of the drosophilid fly communities (Diptera: Drosophilidae) in Yasuni National park in the Amazonian rainforest, 7 of the 34 drosophilid species collected in habitats with various degrees of disturbance were exotic (Acurio *et al.*, pers. com.). A single study on Santa Cruz, Galápagos Islands, identified 17 ant species, of which only four were endemic and nearly all the rest were well-known tramp species (Clark *et al.* 1982).

New exotic host plants can also have indirect consequences for the native herbivorous insect fauna. Since its introduction in Ecuador in 1905, the Monterey pine (*Pinus radiata*) originating from California as well as the Mexican weeping pine *Pinus patula*, have been planted as large plantations (Woolfson 1987). The measuring worm (*Leuculopsis parvistrigata*, Lepidoptera: Geometridae), previously attacking *Hypericum laricifolium* and *Lupinus mutabilis*, was reported for the first time in 1980 attacking pine trees in Ecuador. Both direct and indirect consequences of invasion events for the structure and function of insect communities and the ecosystems they live in will be growing field of research for Ecuadorian entomologists.

## Strategies for development of entomology in Ecuador

### Priority research areas

To foster the development of entomology in Ecuador in the short term, it will be essential to support basic research while highlighting applied and demand-driven studies. We focus on three potential priority research areas although we are aware that many others could also be equally important.

#### Fostering the utility of entomological collections.

The collection of the QCAZ contains more than 2 million specimens belonging to at least 30,000 taxa (see Donoso *et al.* this issue). In addition to taxonomic studies, it is important to diversify the use of this material towards other disciplines such as genomics and phylogenetics, morphology and development, population genetics, evolutionary ecology, conservation biology or even more distant fields such as pharmacology or biomimetics. Another key challenge will be to increase the availability of taxonomic and biological data on these species combined with detailed environmental data (e.g. Babin-Fenske *et al.* 2008; Foley *et al.* 2008). This could be achieved through digitizing the collection and the creation of databases available over the Internet. This will facilitate connections with

foreign entomological collections and researchers. An effective collaboration of Ecuadorian entomological collections would significantly enhance their utility for international research programs and in return allow definition of new sampling strategies with regards to taxonomic groups and locations (see Graham *et al.* 2004). This process is currently underway but will demand continuous resources to be fully realized.

**Insect diversity for ecosystem functioning.** Decline of global insect diversity has recently focused attention on the implications of species losses for the maintenance of ecosystem functioning (Jonsson *et al.* 2002; Hoehn *et al.* 2008). In Ecuador, the functional relevance of the huge diversity of insects is virtually unknown. Functional diversity has been suggested to be the most important component of diversity (e.g. Tilman *et al.* 1997; Hulot *et al.* 2000) and a common approach to test the effects of biodiversity on ecosystem functioning is an experimental manipulation of functional guild diversity. This could be performed in Ecuador for a wide variety of groups and ecosystem processes such as butterflies and bees involved in pollination process or dung beetles and ants implicated in decomposition and nutrient cycling. Understanding the relationships between insect diversity and ecosystem functioning is crucial not only to predict the impact of the ongoing loss of Ecuadorian insects species but also to develop strategies to accelerate ecosystem restoration.

#### Entomology and the well-being of local people.

Insects, such as agricultural pests or vectors of diseases, also put severe pressure on the well-being of millions of people in Ecuador. Both agricultural and medical entomology should be prioritized. The study of the entomological fauna of agro-ecosystems is particularly relevant in Ecuador where national parks and private biosphere reserves currently protect only about 20% of the land area, while cultivated area occupy almost half of the country (ECOLAP 2007, fig. 2D). Moreover, although a large proportion of Ecuadorian people is under the risk of insect-borne diseases such as Chagas' disease (30,000 persons), malaria (up to 12,000 persons during epidemic phases), onchocerciasis (up to 1,200 persons during epidemic phases), or dengue (up to 23,000 persons during epidemic phases) medical entomology in Ecuador is still in its infancy. Our knowledge is limited to a handful of studies on few taxa: *Rhodnius* spp. (Hemiptera: Reduviidae, Aguilar *et al.* 1999; Abad-Franch *et al.* 2005; Suarez 2008), *Anopheles* spp. (Diptera: Culicidae, Birnberg 2008) and *Simulium* spp. (Diptera: Simuliidae, Vieira *et al.* 2007). The development of national investigations for both areas of research (agronomic and medical

entomology) is of major concern because many strategies for insect pest and insect vector management developed in other South American countries are not practical in Ecuador.

### **Increasing funding directed towards the study of insects**

At present, limited national funding is one of the major obstacles to the development of entomology, as well as other life science disciplines in Ecuador. To increase the interest of policy makers for entomological studies, one possible approach is to enhance the awareness of the importance of the link between ecosystem health and human well-being, expressed in the context of ecological services. In this context, there is a vast diversity of insects involved in complex interactions that allow natural systems to provide ecological services on which humans depend (Losey & Vaughan 2006). Decomposition of organic matter, pest control, pollination, and food resource for wildlife are among the major processes accomplished by insects, allowing the global functioning of both natural and cultivated ecosystems (Samways 2005). In Ecuador, as well as in many parts of the world, these service-providing insects are under increasing threat from a combination of factors, including habitat destruction, invasion of foreign species, and overuse of toxic chemicals. Once the benefits of insect-provided services are realized, we hope to realize increased funding directed toward the study of insects and the vital services they provide so that conservation efforts can be optimized (Losey & Vaughan 2006).

### **Establishing monitoring networks**

Monitoring is a fundamental part of environmental science and long-term data are particularly crucial for documenting key issues such as the spread of exotic species or the impact of climate change (Lovett *et al.* 2007). Monitoring networks also provide fundamental feedback for strengthening management and conservation programs and opportunities for increasing education and awareness (Martinez *et al.* 2006). In this context, insects have proven to be remarkable ecological sentinels for environmental changes in a wide range of tropical ecosystems such as forests (Basset *et al.* 2004), mountains (Moret 2005; Dangles *et al.* 2008) or rivers (Jacobsen 1998). Although the establishment of ecological networks with standardized, repeated, quantitative samplings faces limited funding and administrative capabilities in Ecuador, international initiatives could represent an opportunity for entomologists. For example, the Long-Term Ecological Research (LTER, <http://www.lternet.edu>)

networks that have been established mainly for plant studies in various Latin American countries including Ecuador (Myster 2007) could also focus on the study of insect assemblages (Bashford *et al.* 2001). Another example is the Global Observation Initiative in Alpine environments (GLORIA, <http://www.gloria.ac.at>) whose purpose is to establish and maintain world-wide long-term observation networks in Alpine environments. Several sites have already been established in the Andes (Peru, Colombia, and Bolivia). Some of these include insect community monitoring. The Entomology Department of PUCE is currently involved in the establishment of a GLORIA site in Ecuador (Yanacocha Reserve, Province of Pichincha, Ecuador). Insect monitoring networks would also be a necessary tool for the surveillance of the dynamics of vector insects, e.g. Reduviidae (Abad-Franch *et al.* 2001) and agricultural pests, e.g. potato moth (Dangles & Carpio 2008).

### **Strengthening training and collaborations**

Another important endeavor for the development of entomology in Ecuador will be to increase the small pool of trained entomologists. The lack of solid graduate programs in entomology and limited job opportunities push young professionals abroad, creating a serious “brain-drain” problem in the country. Efforts to develop local and regional entomological science should focus on retaining these valuable scientists, while continuing to foster international collaboration (see Martinez *et al.* 2006). To achieve this goal, it would be necessary to reduce the limitations that the bureaucracy of obtaining research and collection permits from the Ministry puts on researchers. This actually discourages many potential work and collaborations, with both national and foreigner scientists. Any type of partnerships with foreign countries should be strengthened and promoted not only to provide unavailable expertise and techniques (e.g. molecular systematics, modeling) but also to increase the overall funding available for entomological research. Such collaborations must encourage Ecuadorian entomologists to publish their results in international peer-reviewed and indexed journals, so that the greatest amount of reliable scientific information on the taxonomy, distribution, ecology and evolution of entomological fauna of Ecuador can be available. This will help to ensure that entomological knowledge participates in promoting the conservation and sustainable use of the highly threatened natural resources of Ecuador.

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# Diversity and distribution of type specimens deposited in the Invertebrate section of the Museum of Zoology QCAZ, Quito, Ecuador

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**Abstract.** The Invertebrate section of the Museum of Zoology QCAZ at the Pontifical Catholic University of Ecuador in Quito maintains nearly two million curated specimens, and comprises Ecuador's largest collection of native taxa. We review 1902 type specimens from 6 subspecies and 320 species in 121 genera and 42 families, currently kept in the Museum. The list includes 116 holotypes, 10 allotypes, 1774 paratypes and 2 neoparatypes. The collection of type specimens is particularly strong in the Coleoptera (family Carabidae and Staphylinidae) and Hymenoptera. However, other insect orders such as Diptera and Lepidoptera and non-insect arthropods such as Acari, Aranea and Scorpiones, are moderately represented in the collection. This report provides original data from labels of every type specimen record. An analysis of the geographic distribution of type localities showed that collection sites are clustered geographically with most of them found towards the northern region of Ecuador, in Pichincha, Cotopaxi and Napo provinces. Sites are mainly located in highly accessible areas near highways and towns. Localities with a high number of type species include the cloud forest reserve Bosque Integral Otonga and Parque Nacional Yasuní in the Amazon rainforest near PUCE's Yasuní Scientific Station. Type localities are not well represented in the Ecuadorian National System of Protected Areas. Future fieldwork should include localities in the southern region of Ecuador but also target less accessible areas not located near highways or towns. We discuss the value of the collection as a source of information for conservation and biodiversity policies in Ecuador.

**Résumé. Diversité et distribution des spécimens types déposés à la section Invertébrés du Musée de ZOOLOGY QCAZ, Quito, Equateur.** La section Invertébrés du Musée de Zoologie QCAZ héberge près de 2 millions de spécimens, ce qui en fait la plus grande collection de taxons natifs d'Equateur. Dans cet article, nous faisons la revue de 1902 spécimens types incluant 6 sous-espèces et 320 espèces dans 121 genres et 42 familles, actuellement conservés au Musée. La liste inclut 116 holotypes, 10 allotypes, 1774 paratypes et 2 neoparatypes. Au sein de l'embranchement Arthropoda, cette liste représente particulièrement bien les ordres d'insectes très diversifiés que sont les Coléoptères (familles Carabidae et Staphylinidae) et Hyménoptères. Toutefois, d'autres ordres d'insectes tels que les Diptères et Lépidoptères, ou encore les Arachnides (Acariens, araignées et scorpions) ne sont que modestement représentés dans la collection. Cette étude synthétise les données originales de chacun de ces spécimens. Une analyse de la distribution géographique des localités types montre que les sites de collection sont spatialement agrégés, la plupart d'entre eux étant trouvés dans la partie nord de l'Equateur, dans les provinces de Pichincha, Cotopaxi et Napo. Ces sites sont principalement situés dans des zones d'accès facile tels que près de routes et de villes. Les localités présentant un nombre de spécimens remarquablement élevés incluent la forêt de nuages *Bosque Integral Otonga* et le *Parque Nacional Yasuní* dans la forêt amazonienne, près de la station scientifique Yasuní de la PUCE. Les localités type ne sont pas bien représentées au sein du système équatorien des aires protégées. Nous suggérons que les futures études de terrain incluent des sites de collecte dans la partie sud de l'Equateur mais aussi qu'elles aient pour cible les zones ayant un accès plus limité, loin des routes et des villes. Nous discutons également la valeur de cette collection en tant que source d'information pour les stratégies politiques de conservation de la biodiversité en Equateur.

**Keywords:** QCAZ Museum, Invertebrates, Type specimens, Ecuador, Conservation.

Type collections are invaluable repositories of biological information and comprise unique and irreplaceable taxonomic and natural history reference material (Suarez & Tsutsui 2004; Wheeler *et al.* 2004). Type specimens, the “bearers of the scientific names of all nominal species-group taxa” (art. 72.10 of the ICZN 1999) are obvious objects of interest for systematics and taxonomists and studies in many other branches of scientific endeavor (Alberch 1993; Winston 2007). It is crucially important to catalogue and digitise this information, noting the site of deposition of type specimens and their state of conservation for wide dissemination (Garrett 1989; Michalski 1992).

The use of label data from natural history collections has improved our understanding of ecology, biogeography and evolutionary biology and conservation biology (Freitag *et al.* 1998; Soberón *et al.* 2000; Soberón *et al.* 2003; Reddy & Dávalos 2003; Meier & Dikow 2004, O’Connel *et al.* 2004). Museum specimens are evidence of the geographic location of a species at a given time. This information can be integrated in models exploring the geographic components of ecological processes, biodiversity and global change (Graham *et al.* 2004; Rahbek *et al.* 2007; but see Rowe 2005). Results from these studies attest to the benefits of modern database techniques, especially in terms of the dissemination of information from sources (museums) to users (scientists and policy makers) (Meier & Dikow 2004).

Our first objective was to review the type collection of the Invertebrate Section of the Museum of Zoology QCAZ (Quito, CAtólica, Zoología) at the Pontificia Universidad Católica del Ecuador (PUCE) in Quito. The museum was established in 1981 under the direction of Dr. Giovanni Onore as a unit of the School of Biological Sciences at PUCE. Additional information concerning the Museum’s history, structure, functions and challenges may be found in Barragán *et al.* (this issue) and Dangles *et al.* (this issue). From its start in the early 1980’s, PUCE scientists and students have collected invertebrates in mainland Ecuador, in the Galápagos Islands and associated shallow water marine habitats, a practice that continues today. These specimens comprise the bulk of the museum’s holdings and are stored in cabinets until they can be curated and identified by specialised taxonomists. These collections have motivated scientific research inside and outside Ecuador and have resulted in the description of several hundred new species to science. Vouchers of these new species are stored in the Museum as type specimens. For example, the collection holds the first records of several agricultural pests including several species of fruit flies *Anastrepha* spp. (Diptera: Tephritidae; Calles & Ponce

2003), *Eucalyptus* pests, *Phoracantha semipunctata* (Coleoptera: Cerambycidae) and the potato moth, *Tecia solanivora* (Lepidoptera: Gelechiidae; Barragán *et al.* 2004, Pollet *et al.* 2003). Collections of the insect vectors of human and veterinary disease such as the vectors of Chagas and other diseases caused by trypanosomes (Aguilar *et al.* 1999; Cárdenas & Vieira 2005; Palomeque *et al.* 2003; Pinto *et al.* 2003; Pinto *et al.* 2006;) are also housed in the Museum.

Our second objective was to examine spatial patterns in the collection and potential bias of the type material in documenting Ecuadorian invertebrate diversity, using geographical information systems (GIS) coupled to spatial analysis. Our goal is to provide to Ecuadorian authorities and policy makers basic information on the conservation status of the invertebrate fauna in Ecuador. This information can serve as a guide for conservation and biodiversity efforts (Shi *et al.* 2005).

## Materials and Methods

### Review of type specimens

From 2005–2008, an intensive search of the wet and dry collections of the Museum for specimens labeled or identified as “type” specimens (i.e. holotypes, paratypes, allotypes, neotypes, topotypes; but also specimens with a colored label) was done. These specimens were separated from the collection and their identity as type specimens was confirmed using original literature. When required, specimens were curated (i.e. change of alcohol, container, oxidized pins, addition of a restored label), but no original label, or other information, was removed from any specimen. Type specimens are maintained separately from the main collection and kept in designated locked cabinets under specific light and humidity conditions for long-term storage (Garrett 1989; Michalski 1992).

Type specimens were the initial focus of a current initiative of the Museum to digitise specimen label information for all museum specimens. Museum personnel established a strict digitisation protocol, which consists of the following steps. Label data from specimens stored in the museum cabinets (i.e. mainly country of origin, province, locality, altitude, geographic coordinates, date, collector, determination, and other ecological data) were recorded in a specially designed database (Apple Macintosh Filemaker Pro). The lowest taxonomic rank for each specimen was checked and recorded in the database up to Phylum (Triplehorn & Johnson 2005). This digitised information was linked to a unique accession number label (e.g. Tipos QCAZI 00001, for type specimens; QCAZI 00001, for other specimens), which was added to every specimen.

### Georeferencing

We used label data as the main source of information to georeference type specimens deposited in the Museum. Due to the age of these collections (mostly from 1980’s and 1990’s), a considerable number of data labels (72%) had no geographic coordinates. Before the widespread use of geographic information systems (GIS) products such as global positioning systems (GPS) and electronic gazetteers in the mid 1990’s, most

biological collections in the Museum did not have specific or complete geographic coordinates. We increased the number of known locations by submitting the label data information to a strict protocol of geo-referencing (Wieczorek *et al.* 2004). We divided the locality information from data labels into nine categories (Wieczorek *et al.* 2004). A locality description usually consists of several parts and could be assigned to more than one of the categories. These categories range from category 1 which refers to dubious localities with questionable information to category 9, which describes localities defined by a distance from a landmark (Table 1). The categories allowed us to estimate the geographical information content of each locality description. After the categorisation process, we used standard gazetteers for the country and publically available information GIS products such as digital Ecuadorian maps from the Almanaque Electrónico Ecuatoriano (2002) and UNEP-WCMC (2005) to provide geographic coordinates for those type localities with valid geographic information, but without coordinates.

### Spatial analyses

Basic collection tendencies and potential bias in the location of type specimens inside Ecuador were analysed using the following set of statistical analyses. First, we estimated the presence of clustering of the georeferenced localities using the nearest neighbor index (NNI) as calculated by the Spatial Statistics tool “average nearest neighbor distance” in ArcGIS 9.1 (ESRI 2005). Localities in our catalogue are assumed clustered if the nearest neighbor observed meandistance/expected mean distance ratio was less than 1 (i.e. NNI < 1). As a measure of statistical significance, we used the  $Z_{\text{score}}$  statistic to test for the null hypothesis that localities are not clustered in space (ArcGIS 9.1 Help, ESRI 2005).

If clustering was found, we analysed the degree of clustering using the nearest neighbor distance distribution function, G(r) (Diggle 1983). G(r) represents the accumulated frequency of the type localities as a function of the minimum distance separating them. We calculated distances between 165 type localities ( $n = 27,225$  entries) using the SpatStat package in R (v.2.4.1, R Development Core Team 2007). Distances were converted from geographic coordinates in degrees to km using the formula,  $1^\circ = 111.3$  km (Christopherson 2005). To obtain confidence intervals (CI) at 5% and 95%, we compared these distances with a null model generated by obtaining distances between 165 random-generated localities (100 simulations). Because

the simulated G(r) curves stabilised after approximately 500 entries, we used the first 500 entries for overall comparison.

We visualised the clustering pattern of type localities by generating a map of locality spatial densities. Geographic coordinates (x, y) of the 165 type localities and the corresponding number of collected species, z, were fitted to a surface of the form  $z(x, y)$ . We used the function, GRIDFIT written in MATLAB (D'Errico 2006), to smooth density values by nearest neighbor interpolation. The resulting GRIDFIT modeling surface, defined by values of a set of nodes forming a rectangular lattice, was then fitted to the profile map of Ecuador. The base polygon consisted of a vector shapefile of Ecuador divided into the main Ecuadorian geographic divisions: Coast (Costa), highlands (Sierra) and Amazon basin (Oriente).

### Conservation value of type specimens

We estimated the economic and social importance and conservation value of the type collections at the QCAZ by calculating the percentage of type localities located within the Ecuadorian Protected Areas National System (SNAP; UNEP-WCMC 2005). We used 30 protected areas located inside continental Ecuador, gathered in a polygon map (UNEP-WCMC 2005). The Galápagos Islands were excluded for this analysis. We calculated the percentage of type localities located inside the SNAP using the GIS tool “Count Points” in polygons defined using Hawth's Tools (Beyer 2004).

We quantified the overall accessibility (*sensu* Farrow & Nelson 2001) of type localities. Accessibility was defined as a physical access potential for moving from one place to the other, measured by travel hours. In ArcGIS 9.1, we extracted accessibility values from the accessibility layer presented in the Almanaque Electrónico Ecuatoriano (2002), which, is based on overall average trip time, in hours, to every type locality, with respect to the following features, topography, river navigability, first and second order roads and towns with more than 50,000 inhabitants. Areas with a high accessibility value are difficult to access and usually are seldom visited by humans (i.e. high value of conservation). Areas with a low accessibility value are associated with roads, navigable rivers and airports.

We further investigated the spatial distribution of type localities by counting the number of type localities within major Ecuadorian political divisions (i.e. provinces) and natural divisions or bioregions (Ron *et al.* in press).

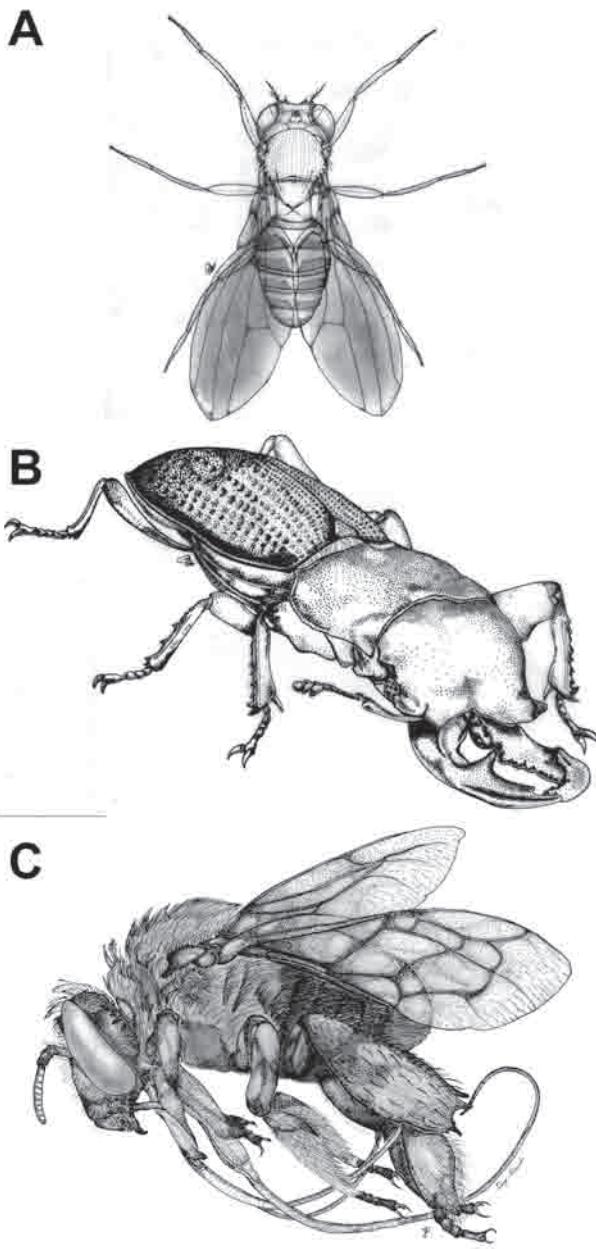
**Table 1.** Number of type localities for each of Wieczorek's definitions of localities (Wieczorek *et al.* 2004). Most localities ( $n = 156$ ) were assigned to Category 5 “Named place”. Examples of the type's data label are given for each locality.

	Definition	# Type Localities	Example of Type's Data Label
Category 1	Dubious	1	-
Category 2	Can not be located	49	Ecuador, Loja, Cord. Lag. Negra
Category 3	Demonstrably inaccurate	3	Ecuador, Azuay, Cuenca, Challuabamba, 11 km NE Cuenca
Category 4	Coordinates	41	Ecuador, Loja, Veracruz, 2000, -79.57302 -3.97709
Category 5	Named place	156	Ecuador, Cañar, Chocar
Category 6	Offset	0	-
Category 7	Offset along a path	8	Ecuador, Azuay, Km 100 Vía Cuenca-Loja
Category 8	Offsets in orthogonal directions	6	Ecuador, Pastaza, 1100m, Llandia, (17 km N. Puyo)
Category 9	Offset at a heading	11	Ecuador, Napo, 27 km NW Baeza, 2700 m

## Results

### Taxonomic content of the catalogue

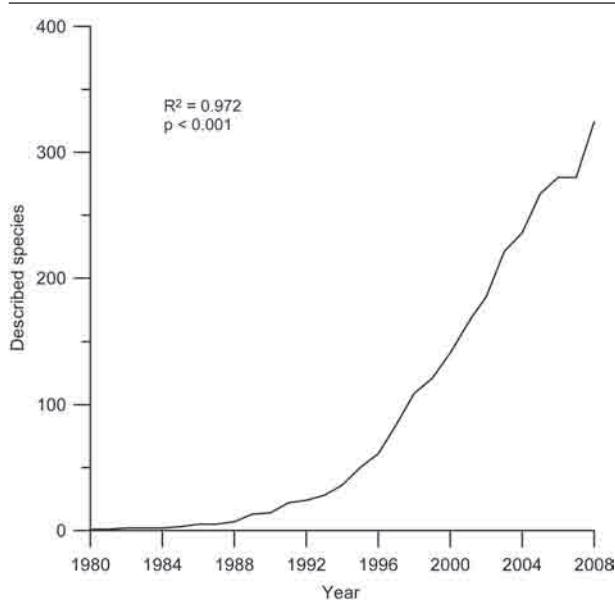
Our survey revealed 1,902 type specimens belonging to 6 subspecies and 320 species in 121 genera and 42 families currently stored in the QCAZ Museum



**Figure 1**

Drawings of emblematic type specimens deposited at the Invertebrate Section of the Museum of Zoology QCAZ, Quito, Ecuador. A, *Drosophila ecuatoriana* Vela & Rafael 2004, paratype; B, *Onorelucanus aequatorianus*, Bartolozzi & Bomans 1989, paratype; C, *Eulaema napensis* Oliveira 2006, holotype.

(Fig. 1). The catalogue (Appendix 1) contains 116 holotypes, 10 allotypes, 1,774 paratypes and 2 neoparatypes from two arthropod Classes: Insecta and Arachnida. Insecta type specimens are from 8 orders of which Coleoptera contains the majority with 16 families, 78 genera, and 199 species. Inside the Coleoptera, the Carabidae contains types from 23 genera and 91 species; the Staphylinidae contains types from 43 species in 19 genera and the Scarabaeidae has types from 20 species in 10 genera. Significant publications that describe Coleoptera type specimens from Ecuador include Cassola (1997), Smith (2003), and Moret (2005). The second greatest abundance of types is in the Hymenoptera with examples from 7 families and 22 species, followed by the Hemiptera with types from 5 families and 9 species and Diptera with types from 3 families and 58 species. Remarkably, there are 215 type specimens from 37 new species of *Drosophila* resulting from the work of Dr. Rafael at PUCE (Rafael & Arcos 1988, 1989; Vela & Rafael 2001; 2004a, b, c, 2005). Surprisingly, there are relatively few type specimens from the Lepidoptera with 14 new species reported from the Nymphalidae (Pyrcz & Viloria 1999) and just one type species (*Hemeroblemma laguerrei* Barbut & Lalanne-Cassou 2005) from the Noctuidae. There are 8 type specimens from the Class Arachnida all of which are spiders (Agnarsson 2006).



**Figure 2**

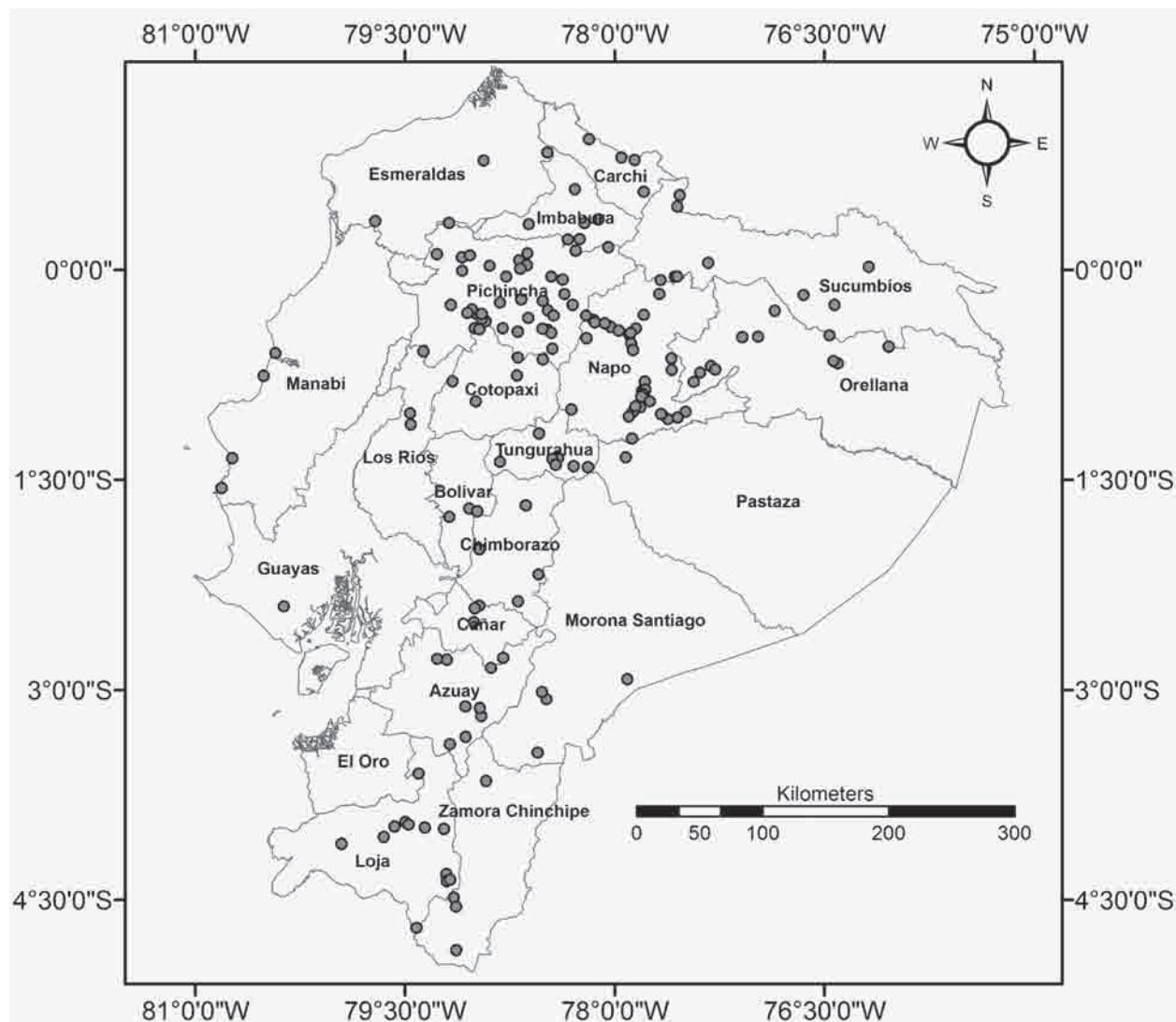
Accumulative number of Ecuadorian invertebrate species with types deposited in the Invertebrate Sector of the Museum of Zoology QCAZ since 1980.

The species accumulation curve (Fig. 2) describing the number of type species published per year since the creation of the Museum has a significant logarithmic trend through time ( $R^2 = 0.972$ ,  $p < 0.001$ ). This suggests a continuous increase in taxonomic interest in the poorly described invertebrate fauna of Ecuador. For example, 43 new type specimens from species described in 2008 in various articles and compiled by Giachino (2008) are currently kept at the Museum.

### Spatial analyses

Locality data from specimen labels were extracted from 1,902 type specimens in the collection. Due to similarities in collection sites, we reduced the number of

type localities in the type specimen database to 247. An analysis of this data set using the categorisation system proposed by Wieczorek *et al.* (2004) further reduced this to 165 unique type localities (Fig. 3). Fifty-two locality descriptions from Wieczorek's categories 1, 2 and 3 were eliminated from further analyses (Table 1) as being unreliable. A large proportion of invertebrate species and subspecies (28%) were collected in just five localities, Bosque Integral Otonga (35 species), Paschoa 1 (18 species), Paschoa 2 (16 species), Yasuní (14 species) and Las Pampas (8 species) (Fig. 4). We found that 22.4% of type localities are located in Pichincha province and 19.4% in Napo. No type specimens in the collection came from El Oro province, in the southern region of the country.



**Figure 3**

Geographic distribution of type localities in Ecuador. The political limits of Ecuadorian provinces as of 2007.

Type localities were significantly clustered geographically ( $NNI < 1$ ;  $Z_{\text{score}} = -7.101$ ;  $p < 0.01$ ). The analysis of the degree of clustering, by means of  $G(r)$  function analysis, further estimated that about 85% of the type localities were only 20 km or less from the nearest type locality (Fig. 5). The  $G(r)$  curve was above complete spatial randomness envelopes and confirmed a significant aggregation of type localities. Only 15% of type localities were separated by distances higher than 20 km.

A small percentage of type localities (10.3%) were located inside SNAP continental protected areas (Fig. 6). Furthermore, most type localities (>75 % of georeferenced localities) were situated in areas with easy access (e.g. trip time = 0–1 hours; Fig. 7). Based on the Ecuadorian bioregions proposed by Ron *et al.* (in press), type localities are more densely grouped in the Eastern Montane Forest (Baeza, Cosanga, El Chaco and El Reventador), followed by the Amazonian Tropical Rain Forest (Yasuní), the Western Foothills Montane Forest (Calacalí, Nanegalito, Chiriboga, Otongachi, Otonga), Andean Scrub Forest (Loja, Cuenca) and Parámo (Paschoa, Volcán Atacazo, Parque Nacional

El Cajas). Bioregions with few or no type localities include the Chocoan Tropical Forest, the Deciduous Forest and the Dry Forest, with just 20 species between them.

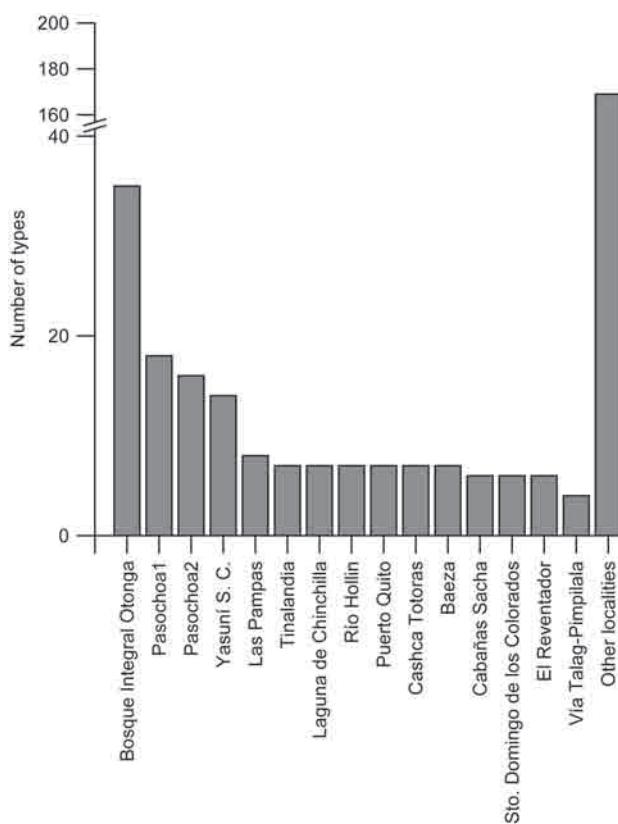
## Discussion

This is the first catalogue of type specimens kept in the Invertebrate Section of the Museum of Zoology QCAZ in Quito. This collection contains a significant number of type specimens, 1,902 type specimens from 320 species and 6 subspecies, which provide a measure of the importance of the museum in a national and international context.

Most type specimens in the Museum (62.6%) belong to the Coleoptera, which is in accordance to the taxonomic diversity of the order on a global scale. However, perhaps more important than the total diversity of the group, species descriptions were related to the number of taxonomists working on the group (Wheeler 2007). For example, butterflies (Lepidoptera), flies (Diptera), social insects (Hymenoptera) and spiders (Class Arachnida), which are also highly diverse insect groups in Ecuador and worldwide, were relatively rare in our catalogue of types. This is perhaps related to difficulties of doing taxonomy in tropical regions (Balakrishnan 2005), rather than specimen availability in the collection (Checa *et al.*, this issue).

Most type localities were clustered towards the northern region of the country, in Pichincha, Cotopaxi and Napo provinces and in areas of easy accessibility. Several reasons may account for these biases. First, the main airport servicing the country is located in the capital city, Quito, in Pichincha province. Foreign scientists, usually constrained by time, tend to collect in places near main airports and with good logistical support (Soberón *et al.* 2000). Second, the main campus of PUCE is also located at Quito. Collections from PUCE students and researchers, the main sources of specimens for the museum, also tend to represent nearby, accessible areas around Quito. The logistical support of the Bosque Integral Otonga in Cotopaxi Province and the Yasuní Scientific Station in Amazonia has facilitated the growth of the collection from these areas as well.

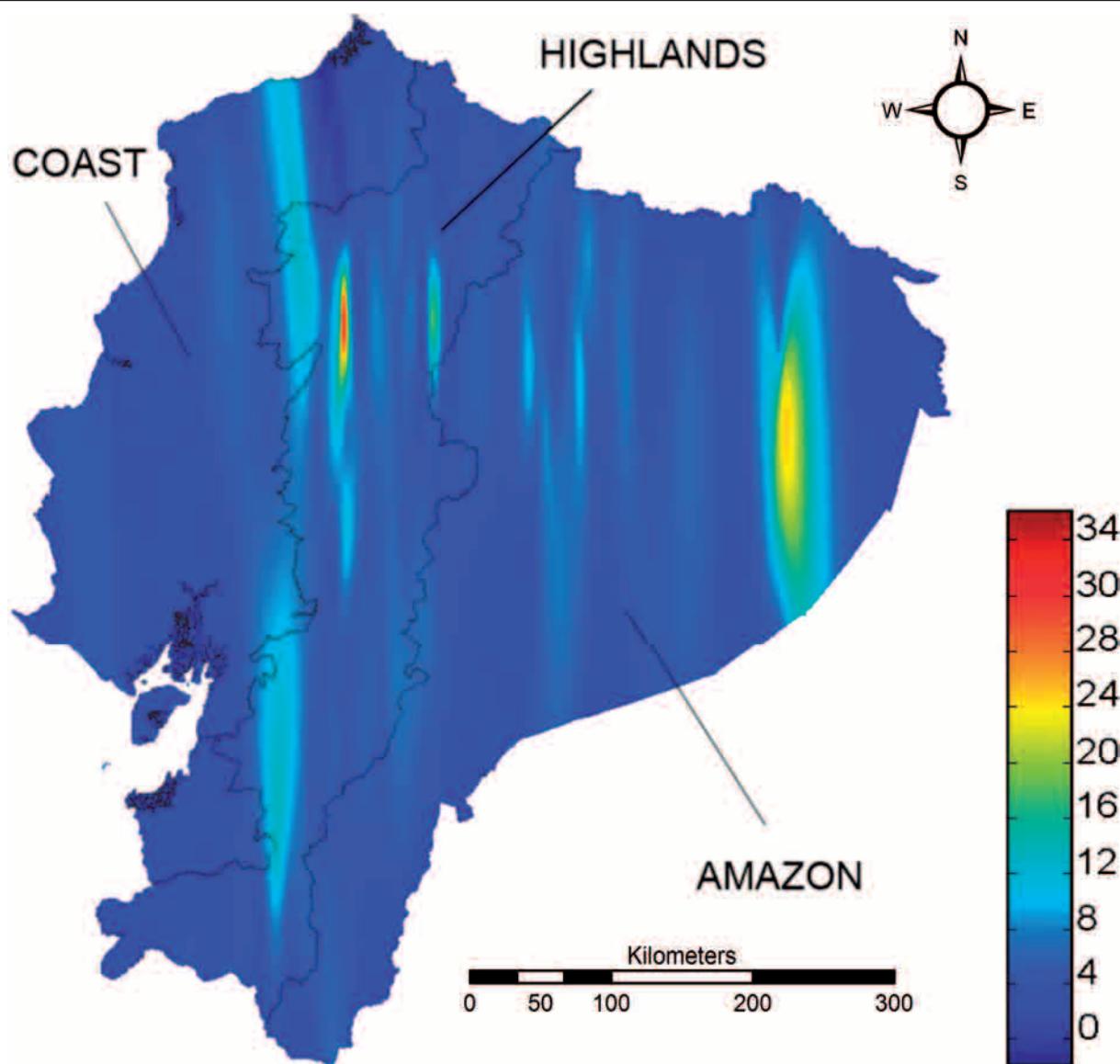
Similar to patterns in African conservation studies (Reddy & Dávalos 2003), our study demonstrated a relationship between type localities and areas of high biological diversity, hotspots *sensu* Myers *et al.* (2000). There has been a bias of researchers to collect in high rated biodiversity areas such as the Ecuadorian bioregions Tropical Andes and the southern limits of the Chocó-Darién. Accessibility indexes of type



**Figure 4**  
Number of type specimens in the fifteen richest localities in Ecuador.

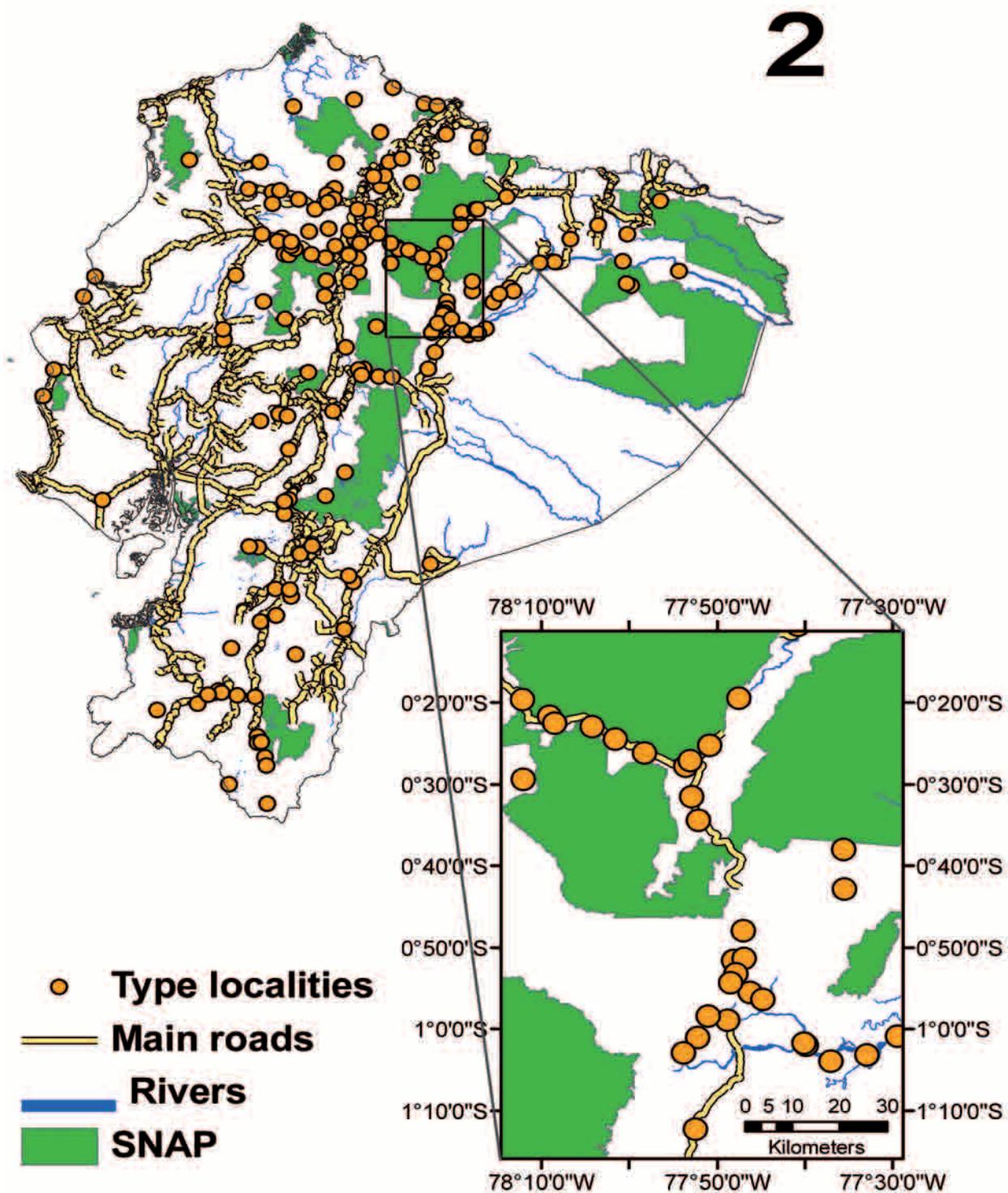
localities were also positively related to areas with oil company facilities. Biologists in Ecuador have taken advantage of oil industry infrastructure and logistics for biodiversity surveys (e.g. Carpio *et al.* this issue). This is also evident in Yasuní National Park, located in the Amazonian Tropical Rain Forest hotspot (Myers *et al.* 2000) that contains oil exploration block 31, managed by Petrobras Oil Company (Brazil) and block 16, managed by Repsol Oil Company (Spain). These areas have been the sites for extensive, although still incomplete, inventories of the local invertebrate fauna.

Collection activities were also related to biological hotspots near important agriculture zones, such as the Chocó-Darién Western Ecuador hotspot (Myers *et al.* 2000). In the southern limits of the Chocó-Darién there were several type localities, such as Otonga and Otongachi, easily accessed by scientists through off-roads created after the Ecuadorian agricultural reformation in the 1960's (Acosta 1999). It is unclear the degree to which collection bias (such as scientists fondness for easily accessible biodiversity hotspots with good infrastructure) may influence our perception of



**Figure 5**

Type locality density extrapolations in the three main ecological regions of Ecuador (coast, highlands, Amazon). Areas with more type localities are presented with reddish colors, while areas with few or no localities are in blue.

**Figure 6**

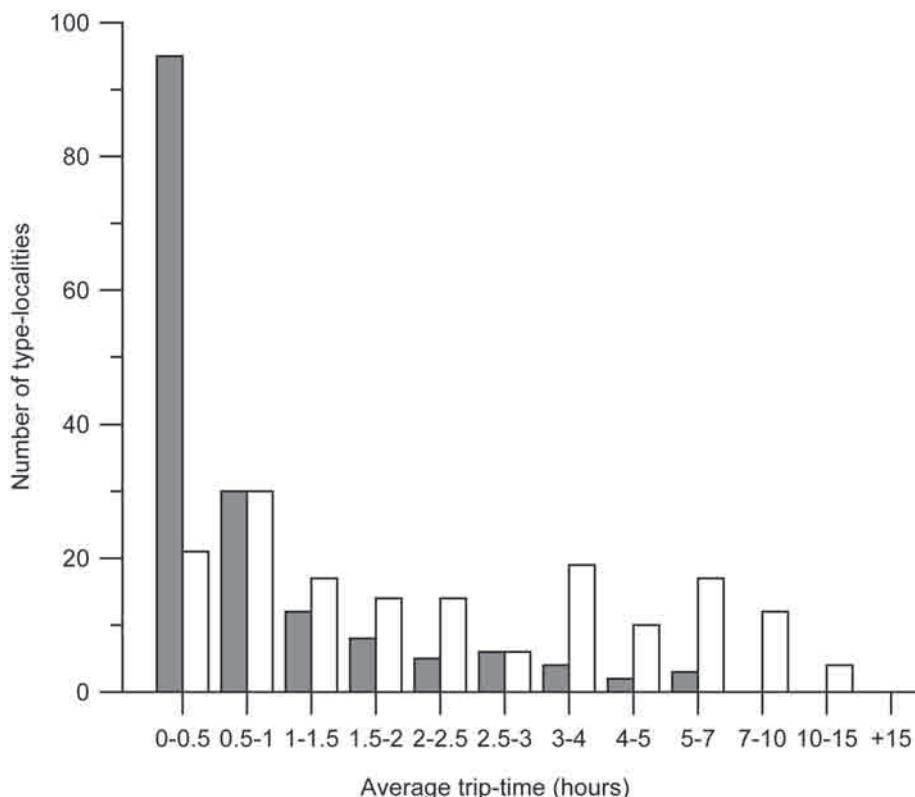
Unique type-localities and relationship with Protected Areas National System (SNAP) with highways and river accessibility features.

biodiversity patterns in Ecuador.

Geographic clustering of type localities is a strong warning about the completeness of the Museum collection. It also reduces its usefulness as a source of information on the invertebrates in under-sampled areas of the country (Soberón *et al.* 2000). Perhaps most dangerous for conservation planning, type localities tended to be close to easily accessed areas. This may devalue the apparent value of more remote areas for conservation when actually they have simply not been adequately sampled. It is unclear what the consequences are of these biases in the collection. Clearly, at the present, the collection does not adequately represent Ecuador's biodiversity and provide baseline data for effective conservation planning (Soberón *et al.* 2000, Reddy & Dávalos 2003). We hope that future collection efforts address this problem, targeting collection sites located toward southern and less accessible regions of the country. We also suggest that collection activity should move toward more pristine areas, which may consequently provide better chances of collecting rare or new biological material. These collections should

begin to address patterns of speciation of various groups in Ecuador. Collection activity should also be planned to examine potential barriers to gene flow leading to speciation such as altitude, phytogeographic regions, biogeographic regions and major physiographic features of the landscape. We argue that in doing so, researchers may increase both the amount and quality of invertebrate material in museum, and the significance of their own work.

The Merriam Webster dictionary defines conservation as "planned management of a natural resource to prevent exploitation, destruction, or neglect". Priority setting is an elemental step towards biological conservation (Shi *et al.* 2002). However, it is a complex task to set priorities for conservation and to put in place the mechanisms for effective conservation practice in small countries such as Ecuador. Difficulties arise from different sources. First, the role and leadership of the government in priority setting and enforcement of laws and programs for conservation is not clear. The recent constitution of Ecuador provides for rights of the environment, however, the mechanism



**Figure 7**

Number of type-localities (filled bars) and random localities (empty bars) in relation to the average trip-time ( $N=165$ ) it takes to arrive to such localities. The average trip time is a measure of the physical access capacity of mobility from a given point to another (trip average hours), determined by logistic and infrastructure facilities of both (UNEP-WCMC 2005).

to realise these rights in balance with development and exploitation of natural resources is not defined. Second, the current state of taxonomic expertise represented as both the number of people working and the amount of published information make conservation based on invertebrates difficult. We are probably loosing species to habitat destruction faster than they can be described or even discovered. As a result, the extent to which effective conservation agendas can be set up over taxonomically poorly known groups such as insects is debatable. However, the importance of the invertebrate fauna as a measure of biodiversity and ecosystem functioning cannot be ignored.

We conclude that invertebrate collections in Ecuador, represented by type specimens at the Museum, are diverse but skewed towards few taxonomic groups and areas of high accessibility and recognised diversity. We challenge current and future researchers to direct their collection efforts to locations and taxonomic groups other than the ones reported in this work. It is important to work collaboratively with scientists and institutions around the world in this effort. It will be impossible for Ecuador to develop sufficient scientific resources to catalogue, much less study in any depth, the country's biodiversity. Ecuadorian students should pursue postgraduate opportunities abroad. We must develop collaborative relationships with major natural history museums around the world to understand our fauna yet still protect the biological patrimony of the country.

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## APPENDIX 1. Catalogue of type specimens deposited at the Invertebrate Section of QCAZ Museum.

The list is organized alphabetically following classes, orders, families and ultimately genera and species. Complete and original label information are available as **appendix 2** to download on the *Annales de la Société entomologique de France* web site.

### Class Insecta

#### Order Coleoptera

##### Family Buprestidae

*Halecia onorei* Cobos 1989. Holotype.

*Hylaeogena onorei* Cobos 1989. Holotype, paratype.

*Pachyschelus sabatratus* Cobos 1989. Holotype.

*Policesta excavate episcopalalis* Cobos 1989. Holotype.

##### Family Carabidae

*Abaris napoensis* Will 2002. Paratype.

*Bembidion (Ecudion) achipungui* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) camposi* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) camposi* Moret & Toledano 2002. Paratype.

*Bembidion caoduroi* L. Toledano 2008. Paratype.

*Bembidion (Ecudion) chilei* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) cotopaxi* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) giselae* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) humboldti* Moret & Toledano 2002. Paratype.

*Bembidion illuchi* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) mathani* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) onorei* Moret & Toledano 2002. Paratype.

*Bembidion (Ecudion) saragurensis* Moret & Toledano 2002. Holotype, paratype.

*Bembidion walterrossii* Toledano 2008. Paratype.

*Blennidus (Agraphoderus) chinchillanus* Moret 2005. Holotype, paratype.

*Blennidus (Agraphoderus) ecuadorianus viduus* Moret 1996. Holotype, paratype.

*Blennidus (Agraphoderus) gregarius* Moret 1996. Paratype.

*Blennidus (Agraphoderus) gregarius montivagus* Moret 1996. Paratype.

*Blennidus marlenae* Moret 1995. Holotype, paratype.

*Blennidus (Agraphoderus) mucronatus* Moret 1996. Holotype, paratype.

- Blennidus (Sierrobius) viridans* Moret 1995. Holotype.  
*Blennidus (Sierrobius) thoracatus* Moret 2005. Paratype.  
*Bradycellus aequatorius* Moret 2001. Paratype.  
*Bradycellus martinezii* Moret 2001. Paratype.  
*Bradycellus youngi* Moret 2001. Paratype.  
*Coptodera apicalis* Shpeley & Ball 1993. Paratype.  
*Dercylus (Licinodercylus) onorei* Moret 1995. Paratype.  
*Dercylus (Licinodercylus) orbiculatus* Moret 1995. Paratype.  
*Dercylus (Licinodercylus) praepilatus* Moret 1995. Paratype.  
*Dercylus (Licinodercylus) granifer* Moret 1995. Paratype.  
*Dercylus (Licinodercylus) gibber* Moret 1995. Paratype.  
*Diploharpus rossii* Moret 2008. Paratype.  
*Dyscolus (s. str.) algidus* Moret 2005. Paratype.  
*Dyscolus (s. str.) araneus* Moret 2005. Holotype, paratype.  
*Dyscolus (s. str.) arvalis* Moret 2005. Paratype.  
*Dyscolus (s. str.) atkinsi* Moret 2001. Paratype.  
*Dyscolus (s. str.) bliteus* Moret 2005. Paratype.  
*Dyscolus (s. str.) bordoni* Moret 1993. Paratype.  
*Dyscolus (s. str.) breviculus* Moret 2001. Paratype.  
*Dyscolus (s. str.) capsarius* Moret 2005. Paratype.  
*Dyscolus (s. str.) carbonescens* Moret 2005. Holotype, paratype.  
*Dyscolus (s. str.) cephalotes* spp. *sirinae* Moret 2005. Paratype.  
*Dyscolus (s. str.) desultor* Moret 2005. Paratype.  
*Dyscolus (s. str.) exsul* Moret 2005. Paratype.  
*Dyscolus (s. str.) fartilis* Moret 2005. Paratype.  
*Dyscolus (s. str.) fucatus* Moret 2005. Paratype.  
*Dyscolus immodicus* Moret 2005. Paratype.  
*Dyscolus involucer* Moret 1994. Paratype.  
*Dyscolus involucer geodesicus* Moret 1994. Paratype.  
*Dyscolus (s. str.) lignicola* Moret 1994. Paratype.  
*Dyscolus (s. str.) lubricus* Moret 2001. Holotype.  
*Dyscolus (s. str.) maleodoratus* Moret 2005. Paratype.  
*Dyscolus (s. str.) montivagus* Moret 1998. Paratype.  
*Dyscolus (s. str.) montrufari* Moret 2005. Paratype.  
*Dyscolus (s. str.) nubilus* Moret 2001. Paratype.  
*Dyscolus onorei* Moret 1993. Paratype.  
*Dyscolus (s. str.) palatus* Moret 1998. Paratype.  
*Dyscolus (s. str.) pullatus* Moret 2005. Paratype.  
*Dyscolus (s. str.) rivetti* Moret 2001. Paratype.  
*Dyscolus segnipes* Moret 1990. Paratype.  
*Dyscolus (s. str.) tapiarius* Moret 2005. Holotype, paratype.  
*Dyscolus (s. str.) trossulus* Moret 2005. Paratype.  
*Dyscolus (s. str.) verecundus* Moret 1998. Paratype.  
*Dyscolus (Hydrodyscolus) hirsutus* Moret 2005. Paratype.  
*Dyscolus (Hydrodyscolus) imbaburae* Moret 2005. Paratype.  
*Dyscolus (Hydrodyscolus) nocticolor* Moret 2005. Paratype.  
*Dyscolus (Hydrodyscolus) smithersi* Moret 2001. Paratype.  
*Euchella kiplingi* Shpeley & Ball 2000. Paratype.  
*Glyptolenoides balli* Moret 2005. Paratype.  
*Incastichus aequidianus* Moret 1996. Paratype.  
*Loxandrus ecuadoricus* Straneo 1991. Paratype.  
*Loxandrus photophilus* Straneo 1991. Paratype.  
*Ogmopleura (Agraphoderus) colomai* Straneo 1991. Paratype.  
*Ogmopleura balli* Straneo 1991. Paratype.  
*Ogmopleura ecuadoriana* Straneo 1991. Paratype.  
*Ogmopleura (Agraphoderus) liodes planoculis* Straneo 1991. Paratype.  
*Oxytrechus onorei* Allegro et al. 2008. Paratype.  
*Oxytrechus pierremoreti* Allegro et al. 2008. Paratype.  
*Oxytrechus revertadori* Moret 2005. Holotype.  
*Oxytrechus zoiai* Casale & Sciaky 1986. Paratype.  
*Pelmatellus gracilis* Moret 2000. Paratype.  
*Pelmatellus inca* Moret 2000. Paratype.  
*Pelmatellus polylepis* Moret 2000. Paratype.  
*Pelmatellus caerulescens* Moret 2005. Holotype, paratype.  
*Perigona belloii* Giachino, Moret & Picciau 2008. Paratype.  
*Sierrobius onorei* Straneo 1991. Paratype.  
*Stenognathus (Prostenognathus) onorei* Shpeley & Ball 2000. Paratype.  
*Stolonis tapiai* Will 2005. Paratype.  
*Stolonis spinosus* Will 2005. Paratype.  
*Stolonis catenarius* Will 2005. Paratype.  
*Stolonis yasuni* Will 2005. Paratype.  
*Trechisibus (Ecuadoritrechus) tapiai* Deuve 2002. Holotype.

### Family Cerambycidae

- Apteraleidion lapierrei* Hovore 1992. Paratype.  
*Eburia frankei* Noguera 2002. Paratype.  
*Neseuterpia couturieri* Tavakilian 2001. Paratype.

### Family Chrysomelidae

- Aslamidium (s. str.) ecuadoricum* Borowiec 1998. Holotype.  
*Cyclocassis secunda* Borowiec 1998. Paratype.  
*Discomorpha onorei* Borowiec 1998. Holotype, paratype.  
*Eugenisa jasinskii* Borowiec & Dłbrowska 1997. Paratype.  
*Eugenisa unicolor* Borowiec & Dłbrowska 1997. Paratype.  
*Stolas napoensis* Borowiec 1998. Holotype, paratype.  
*Stolas perezi* Borowiec 1998. Holotype.  
*Stolas stolida jadwiszczaki* Borowiec 1998. Paratype.  
*Stolas zumbaensis* Borowiec 1998. Paratype.

### Family Cicindelidae

- Ctenostoma (Neoprocephalus) cassolai* Naviaux 1998. Paratype.  
*Ctenostoma (Procephalus) ecuadoriensis* Naviaux 1998. Holotype.  
*Ctenostoma (Procephalus) onorei* Naviaux 1998. Holotype.  
*Oxycheila brzoskai* Wiesner 1999. Holotype, paratype.  
*Oxygonia nigrovenator* Kippenhan 1997. Holotype.  
*Pseudoxycheila atahualpa* Cassola 1997. Holotype, paratype.  
*Pseudoxycheila caribe* Cassola 1997. Paratype.  
*Pseudoxycheila inca* Cassola 1997. Paratype.  
*Pseudoxycheila nitidicollis* Cassola 1997. Holotype, paratype.  
*Pseudoxycheila onorei* Cassola 1997. Holotype, paratype.  
*Pseudoxycheila pearsoni* Cassola 1997. Holotype, paratype.  
*Pseudoxycheila pseudotarsalis* Cassola 1997. Holotype, paratype.  
*Pseudoxycheila quechua* Cassola 1997. Paratype.

**Family Curculionidae***Baillytes bartolozzi* Voinin 1996. Paratype.*Melchus onorei* Anderson 2003. Paratype.**Family Elateridae***Achrestus onorei* Golbach, Zamudio & Guzmán de Tomé 1988. Holotype, paratype.**Family Heteroceridae***Tropicus bartolozzii* Mascagni 1994. Paratype.**Family Languriidae***Lepidotoramus grouvellei* Leschen 1997. Paratype.**Family Leiodidae***Adelopsis aloecuatoriana* Salgado 2008. Paratype.*Adelopsis (Adelopsis) bioforestae* Salgado 2002. Holotype, paratype.*Adelopsis (Adelopsis) ecuatoriana* Salgado 2002. Holotype, paratype.*Adelopsis (Lutururuca) debiscentis* Salgado 2002. Holotype, paratype.*Adelopsis onorei* Salgado 2002. Holotype, paratype.*Adelopsis (Lutururuca) tuberculata* Salgado 2002. Holotype, paratype.*Dissochaetus anseriformis* Salgado 2001. Holotype, paratype.*Dissochaetus napoensis pallipes* Salgado 2008. Paratype.*Eucatops (Eucatops) incognitus* Salgado 2003. Holotype, paratype.*Eucatops (Sphaerotops) granuliformis* Salgado 2003. Holotype.*Eucatops (Eucatops) onorei* Salgado 2008. Paratype.**Family Lucanidae***Onorelucanus aequatorianus* Bartolozzi & Bomans 1989. Paratype.*Sphaenognathus (Chiasognathinus) xerophilus* Bartolozzi & Onore 2006. Holotype, paratype.**Family Passalidae***Passalus kaupi* Boucher 2004. Paratype.*Verres onorei* Boucher & Pardo-Locarno 1997. Paratype.**Family Rhysodidae***Stereodermus jonathanii* Mantilleri 2004. Paratype.**Family Scarabaeidae***Aequatoria aenigmatica* Soula 2002. Paratype.*Ataenius cristobalensis* Cook & Peck 2000. Paratype.*Ataenius floreanae* Cook & Peck 2000. Paratype.*Bdelyrus grandis* Cook 1998. Paratype.*Bdelyrus parvoculus* Cook 1998. Holotype.*Bdelyrus pecki* Cook 1998. Paratype.*Bdelyrus triangulus* Cook 1998. Holotype.*Callosides genieri* Howden 2001. Paratype.*Coprophanaeus morenoi* Arnaud 1982. Paratype.*Cryptocanthon otonga* Cook 2002. Holotype, paratype.**Family Dynastidae***Cyclocephala pseudomelanoccephala* Dupuis 1996. Paratype.*Neoathyreus brasiliensis* Howden 1985. Paratype.*Ontherus diabolicus* Génier 1996. Paratype.*Ontherus politus* Genier 1996. Paratype.*Ontherus pubens* Genier 1996. Paratype.*Platycoelia furva* Smith 2003. Holotype, paratype.*Platycoelia galerana* Smith 2003. Paratype.*Platycoelia hiporum* Smith 2003. Paratype.*Platycoelia paucarae* Smith 2003. Paratype.*Ptenomela giovannii* Soula 2003. Paratype.*Scatimus onorei* Genier & Kohlmann 2003. Holotype, paratype.**Family Staphilinidae***Apalonia archidonensis* Pace 2008. Paratype.*Apalonia pampeana* Pace 1997. Paratype.*Apalonia sigchosensis* Pace 2008. Holotype, paratype.*Apalonia vicina* Pace 2008. Holotype, paratype.*Atheta altocotopaxicola* Pace 2008. Paratype.*Atheta annularina* Pace 2008. Holotype.*Atheta cayambensis* Pace 2008. Paratype.*Atheta cioccai* Pace 2008. Paratype.*Atheta ecumaculata* Pace 2008. Holotype.*Atheta eucastaneipennis* Pace 2008. Holotype.*Atheta hollinensis* Pace 2008. Holotype.*Atheta neasuspiciose* Pace 2008. Paratype.*Atheta pseudoclaudiensis* Klimaszewski & Peck 1998. Paratype.*Atheta toachiensis* Pace 2008. Holotype.*Cajachana carltoni* Ashe & Leschen 1995. Paratype.*Diestota simplex* Pace 2008. Holotype.*Falagria ecuapallida* Pace 2008. Holotype.*Gyrophaena cotopaxiensis* Pace 1996. Paratype.*Gyrophaena otongensis* Pace 2008. Holotype.*Gyrophaena rossii* Pace 2008. Holotype, paratype.*Gyrophaena spatulata* Pace 1996. Paratype.*Heterostiba rossii* Pace 2008. Paratype.*Homalota cotopaxiensis* Pace 2008. Holotype.*Leptandria ecitophila* Hanley, 2003. Paratype.*Leptandria tishechkini* Hanley, 2003. Paratype.*Meronera ecuadorica* Pace 2008. Holotype.*Meronera otongicola* Pace 2008. Holotype, paratype.*Myllaena pichinchaensis* Pace 2008. Paratype.*Orphnebius curticornis* Pace 2008. Holotype.*Orphnebius ecuadorensis* Pace 1997. Paratype.*Orphnebius otongensis* Pace 2008. Holotype, paratype.*Paraplandria caraorum* Pace 2008. Holotype, paratype.*Paraplandria ecuadoricola* Pace 2008. Holotype.*Parasilusa otongensis* Pace 2008. Holotype.*Plesiomalota giachinoi* Pace 2008. Paratype.*Plesiomalota paschoensis* Pace 2008. Paratype.*Plesiomalota ruficollis* Pace 2008. Holotype.*Plesiomalota ruficornis* Pace 2008. Holotype.*Plesiomalota squalida* Pace 2008. Holotype.

*Plesiomalota varicornis* Pace 2008. Holotype, paratype.  
*Pseudoleptonia ecuadorica* Pace 2008. Holotype, paratype.  
*Pseudomniophila cotopaxiensis* Pace 2008. Holotype, paratype.  
*Pseudomyllaena ecuadorensis* Pace 2008. Holotype, paratype.

### Family Tenebrionidae

*Opatriinus ecuadorensis* Iwan 1995. Paratype.

## Order Diptera

### Family Drosophilidae

*Drosophila amaguana* Vela & Rafael 2004. Holotype, paratype.  
*Drosophila apag* Vela & Rafael 2005. Holotype.  
*Drosophila arcosae* Vela & Rafael 2001. Holotype.  
*Drosophila asiri* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila carlosvilelai* Vela & Rafael 2001. Holotype, paratype.  
*Drosophila condormachay* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila cuscungu* Vela & Rafael 2005. Holotype.  
*Drosophila ecuatoriana* Vela & Rafael 2004. Holotype, paratype.  
*Drosophila fontdevilai* Vela & Rafael 2001. Holotype, paratype.  
*Drosophila guayllabambae* Rafael & Arcos 1988. Holotype, paratype.  
*Drosophila huancavilcae* Rafael & Arcos 1989. Holotype, paratype.  
*Drosophila ichubamba* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila korefae* Vela & Rafael 2004. Holotype, paratype.  
*Drosophila machachensis* Vela & Rafael 2001. Holotype, paratype.  
*Drosophila ninarumi* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila ogradi* Vela & Rafael 2004. Holotype, paratype.  
*Drosophila paschoensis* Vela & Rafael 2001. Holotype, paratype.  
*Drosophila patacornia* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila pichinchana* Vela & Rafael 2004. Holotype, paratype.  
*Drosophila pilaresae* Vela & Rafael 2001. Paratype.  
*Drosophila pugyu* Vela & Rafael 2005. Holotype.  
*Drosophila quillu* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila quitensis* Vela & Rafael 2004. Holotype, paratype.  
*Drosophila ruminabuui* Vela & Rafael 2004. Holotype.  
*Drosophila rumipamba* Vela & Rafael 2005. Holotype.  
*Drosophila rundoloma* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila shuyu* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila shyri* Vela & Rafael 2004. Holotype.  
*Drosophila sisa* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila suni* Vela & Rafael 2005. Holotype.  
*Drosophila surucucho* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila taxohuaycu* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila tomasi* Vela & Rafael 2001. Holotype, paratype.  
*Drosophila urcu* Vela & Rafael 2005. Holotype.  
*Drosophila valenciae* Vela & Rafael 2001. Holotype, paratype.  
*Drosophila yana* Vela & Rafael 2005. Holotype, paratype.  
*Drosophila yangana* Rafael & Vela 2003. Holotype, paratype.

### Family Phoridae

*Apocephalus ancylus* Brown 1997. Paratype.

*Apocephalus asyndetus* Brown 2000. Paratype.  
*Apocephalus catholicus* Brown 2000. Paratype.  
*Apocephalus comosus* Brown 2000. Paratype.  
*Apocephalus extraneus* Brown 1997. Paratype.  
*Apocephalus funditus* Brown 2000. Paratype.  
*Apocephalus melinus* Brown 2000. Paratype.  
*Apocephalus onorei* Brown 1997. Paratype.  
*Apocephalus quadratus* Brown 1997. Paratype.  
*Apocephalus roeschardae* Brown 2000. Paratype.  
*Apocephalus securis* Brown 1997. Paratype.  
*Apocephalus tanyurus* Brown 2000. Paratype.  
*Apocephalus torulus* Brown 2000. Paratype.  
*Apocephalus trifidus* Brown 2000. Paratype.

### Family Sphaeroceridae

*Druciatus tricetus* Marshall 1995. Paratype.  
*Opacifrons triloba* Marshall & Langstaff 1998. Paratype.  
*Opacifrons redunda* Marshall & Langstaff 1998. Paratype.  
*Palaeocorprina equiseta* Marshall 1998. Paratype.  
*Phthitia merida* Marshall 1992. Paratype.  
*Rachispoda justini* Wheeler 1995. Paratype.  
*Rachispoda praealta* Wheeler 1995. Paratype.

## Order Hemiptera

### Family Coreidae

*Anasa scitula* Brailovsky & Barrera 2000. Holotype, paratype.  
*Salapia onorei* Brailovsky 1999. Holotype.  
*Sephina faceta* Brailovsky 2001. Paratype.

### Family Gerridae

*Potamobates shuar* Buzzetti 2006. Paratype.

### Family Miridae

*Anomalocornis peyreti* Couturier & Costa 2002. Paratype.  
*Parafulvius henryi* Costa & Couturier 2000. Paratype.

### Family Pentatomidae

*Thyanta xerotica* Rider & Chapin 1991. Paratype.

### Family Membracidae

*Metcalfiella jaramillorum* McKamey 1991. Paratype.  
*Metcalfiella nigribumera* McKamey 1991. Paratype.

## Order Hymenoptera

### Family Apidae

*Euglossa lugubris* Roubick 2004. Paratype.  
*Euglossa occidentalis* Roubick 2004. Holotype, paratype.  
*Euglossa orellana* Roubick 2004. Holotype, paratype.  
*Euglossa samperi* Ramirez 2006. Holotype.  
*Euglossa tiputini* Roubick 2004. Paratypes.  
*Eulaema napensis* Oliveira 2006. Holotype.  
*Paratrigona onorei* Camargo & Moure 1994. Paratype.

**Family Diapriidae***Mimopria campbellorum* Masner 1976. Paratype.**Family Formicidae***Leptanilloides nomada* Donoso, Vieira & Wild 2006. Holotype, paratype.*Leptanilloides nubecula* Donoso, Vieira & Wild 2006. Holotype, paratype.*Linepithema aztecoides* Wild 2006. Paratype.*Linepithema neotropicum* Wild 2006. Paratype.*Linepithema tsachila* Wild 2006. Holotype.*Pheidole alpestris* Wilson 2003. Paratype.*Pseudomyrmex eculeus* Ward 1999. Paratype.*Pseudomyrmex insuavis* Ward 1999. Paratype.*Pseudomyrmex ultririx* Ward 1999. Paratype.**Family Pompilidae***Pepsis multichroma* Vardy 2002. Paratype.*Pepsis onorei* Vardy 2002. Paratype.**Family Scelionidae***Thoron gaciai* Johnson & Masner 2004. Paratype.**Family Vespidae***Agelaia silvatica* Cooper 2000. Paratype.**Order Lepidoptera****Family Noctuiidae***Hemeroblemma laguerrei* Barbut & Lalanne-Cassou 2005. Paratype.**Family Nymphalidae***Altoperdaliodes tena nucea* Pyrcz & Viloria 1999. Paratype.*Manerebia golondrina* Pyrcz & Willmott 2006. Paratype.*Manerebia satra pauperata* Pyrcz & Willmott 2006. Paratype.*Manerebia germaniae* Pyrcz & Hall 2006. Paratype.*Manerebia undulata undulata* Pyrcz & Hall 2006. Paratype.*Manerebia inderena similis* Pyrcz & Willmott 2006. Paratype.*Manerebia inderena clara* Pyrcz & Willmott 2006. Paratype.*Manerebia inderena laeniva* Pyrcz & Willmott 2006. Paratype.*Manerebia inderena mirena* Pyrcz & Willmott 2006. Paratype.*Pedaliodes rumba* Pyrcz & Viloria 1999. Paratype.*Pedaliodes morenoi pilaloensis* Pyrcz & Viloria 1999. Paratype.*Pedaliodes arturi* Pyrcz & Viloria 1999. Paratype.*Pedaliodes balnearia* Pyrcz & Viloria 1999. Paratype.*Pedaliodes peuvestas restricta* Pyrcz & Viloria 1999. Paratype.**Order Megaloptera****Family Corydalidae***Chloronia convergens* Contreras 1995. Paratype.*Corydalus clauseni* Contreras 1998. Paratype.**Order Odonata****Family Lestidae***Lestes jerrelli* Tennessean 1997. Paratype.**Family Coenagrionidae***Oxyagrion tennesseanum* Mauffray 1999. Paratype.**Family Aeshnidae***Aeshna (Marmaraeschna) brevicercia* Muzón & Von Ellenrieder 2001. Holotype, paratype.**Order Orthoptera****Family Grillidae***Gryllus abditus* Otte & Peck 1997. Paratype.*Gryllus isabela* Otte & Peck 1997. Paratype.**Family Acrididae***Aphanolampis aberrans* Descamps 1978. Neoparatype.*Hyalinacris diaphana* Amédégnato & Poulin 1998. Paratype.*Hyalinacris onorei* Amédégnato & Poulin 1998. Paratype.**Class Arachnida****Order Scorpionida****Family Buthidae***Tityus jussarae* Lourenço 1988. Paratype.**Family Chactidae***Chactas mahneri* Lourenço 1995. Paratype.**Order Araneae****Family Theridiidae***Anelosimus guacamayos* Agnarsson 2006. Paratype.*Anelosimus oritoyacu* Agnarsson 2006. Paratype.*Anelosimus baeza* Agnarsson 2006. Paratype.*Anelosimus elegans* Agnarsson 2006. Paratype.**Order Acari****Family Lohmaniidae***Heptacarus encantadae* Schatz 1994. Paratype.*Torpacarus omittens galapagensis* Schatz 1994. Paratype.

## APPENDIX 2.

### Catalogue of type specimens deposited at the Invertebrate Section of QCAZ Museum

The list is organized alphabetically following classes, orders, families and ultimately genera and species. Complete and original label information (i.e. as it appeared) is provided for each record, except when labels provided duplicate information. Red labels indicating the status of the specimens (e.g. holotype, paratype) were omitted from the catalog. References are provided at the end of each record.

#### CLASS INSECTA

#### ORDER COLEOPTERA

#### FAMILY BUPRESTIDAE

*Halecia onorei* Cobos 1989. Holotype QCAZI 603. Ecuador, Napo, Coca, I. 85, Legit: G. Onore. Ref. Cobos 1989.

*Hylaeogena onorei* Cobos 1989. Holotype QCAZI 605. Ecuador, Napo, Sacha, VII.84, Legit: G. Onore. Paratypes QCAZI 606 and QCAZI 607 (Allotype) with the same label as the holotype. Ref. Cobos 1989.

*Pachyschelus sabatratus* Cobos 1989. Holotype QCAZI 608. Ecuador, Pichincha, Los Bancos, 28-I-84, Log: M. Larrea. Ref. Cobos 1989.

*Policesta excavate episcopalis* Cobos 1989. Holotype QCAZI 604. Ecuador, Manabí, Bahía de Caraquez, III-1983, Lg. Gómez P. Ref. Cobos 1989.

#### FAMILY CARABIDAE

*Abaris napoensis* Will 2002. Paratype QCAZI 1965 \$. Label 1: Ecuador, Napo, Onkone Gare Camp 00°39'10"S, 76°26'00"W; 220 m. Terra firma forest; Label 2: flowerfall-leaf litter; at night 5&8.X.1995 07-95; Label 3: T. L. ERWIN ECUADOR EXPEDITON 1995. G.E. Ball and D. Shpeley colls. Ref. Will 2002.

*Bembidion (Ecuadion) achipungi* Moret & Toledano 2002. Paratype QCAZI 81. Ecuador, Chimborazo, Achipungo, (Atillo), 4250 m, 7Jan1995, G. Zapata. Ref. Moret & Toledano 2002.

*Bembidion (Ecuadion) camposi* Moret & Toledano 2002. Paratypes QCAZI 89 and QCAZI 90. Ecuador, Salcedo, vía Napo km 40, XII. 87, leg.G. Onore. Ref. Moret & Toledano 2002.

*Bembidion caoduroi* L. Toledano 2008. Paratypes QCAZI 1832 and QCAZI 1833. Ecuador, Pichincha, Lloa, Río Blanco, m 2410, S 00°12'37.1", W 78°40'01.9", 1.VIII.2006, P. M. Giachino. Ref. Toledano 2008.

*Bembidion (Ecuadion) chilesi* Moret & Toledano 2002. Paratype QCAZI 98. Chiles, 4050 m, 10. VIII .1997, n285, N. Atkins. Ref. Moret & Toledano 2002.

*Bembidion (Ecuadion) cotopaxi* Moret & Toledano 2002. Paratypes QCAZI 91 to QCAZI

97. Ecuador, Cotopaxi, Parque Nacional Cotopaxi, Control Norte, 3755 m,  
10Feb2001, I. G. Tapia. Ref. Moret & Toledano 2002.

*Bembidion (Ecuadion) giselae* Moret & Toledano 2002. Paratype QCAZI 103. Ecuador,  
Loja, Valladolid, Límite del Parque Jocotoco y Podocarpus, 6Jan2001, I. G. Tapia.  
Ref. Moret & Toledano 2002.

*Bembidion (Ecuadion) humboldti* Moret & Toledano 2002. Paratypes QCAZI 99 and  
QCAZI 100. Ecuador, Chimborazo, Ozogoche, alrededor de la Laguna,  
27Dec1994, GOnore. Ref. Moret & Toledano 2002.

*Bembidion illuchi*, Moret & Toledano 2002. Paratype QCAZI 101. Ecuador, Cotopaxi,  
Salcedo, Vía a Tena Pass, 3800 m, 15Jan1995, GOnore. Ref. Moret & Toledano  
2002.

*Bembidion (Ecuadion) mathani*, Moret & Toledano 2002. Paratype QCAZI 102. Ecuador,  
Chimborazo, Achipungo, (Atillo), 4250 m, 7Jan1995, GZapata. Ref. Moret &  
Toledano 2002.

*Bembidion (Ecuadion) onorei* Moret & Toledano 2002. Paratypes QCAZI 104 and QCAZI  
105. Ecuador, 7.VIII.90, Volcán Cotopaxi, 3800 - 4800 m, leg. Sciaki. Ref. Moret  
& Toledano 2002.

*Bembidion (Ecuadion) saragurensis* Moret & Toledano 2002. Holotype QCAZI 108. Label  
1: Ecuador, Loja, Saraguro, Paraíso de Celen, Laguna de Chinchilla, 3660 m.,  
20Dec1998, E. Tapia; Label 2: EX: Dry season. Paratypes QCAZI 109 to QCAZI  
113, with the same label as the holotype. Ref. Moret & Toledano 2002.

*Bembidion walterrossii* Toledano 2008. Paratype QCAZI 499. Ecuador, Cotopaxi, Cantón  
Sigchos, Las Pampas, Otonga Natural Reserve, 25-28 VII 2005, W. Rossi. Ref.  
Toledano 2008.

*Blennidus (Agraphoderus) chinchillanus* Moret 2005. Holotype QCAZI 136. Label 1:  
Ecuador, Loja, Saraguro, Paraíso de Celen, Laguna de Chinchilla, 3660 m.,  
20Dec1998, E. Tapia; Label 2: Ex: dry season. Paratypes QCAZI 137 to QCAZI  
144, with the same label as the holotype. Ref. Moret 2005.

*Blennidus (Agraphoderus) ecuadorianus viduus* Moret 1996. Holotype QCAZI 128.  
Ecuador, Chimborazo, Ozogoche, alrededor de la Laguna, 27Dec1994, G.Onore. 6  
paratypes with the same label as the holotype. Ref. Moret 1996a.

*Blennidus (Agraphoderus) gregarius* Moret, 1996. Paratype QCAZI 134. Ecuador, Prov.  
Azuay, Nudo de Azuay, 3980 m, Paredones sous pierre, P. Moret leg., 14. VII. 88.  
Ref. Moret 1996a.

*Blennidus (Agraphoderus) gregarius montivagus* Moret 1996. Paratype QCAZI 135.  
Ecuador, Chimborazo, km 28 Guamote-Macas, 4000 m, –sous pierre, P. Moret leg.,  
7. I. 95. Ref. Moret 1996a.

*Blennidus marlenae* Moret 1995. Holotype QCAZI 2. Ecuador, Cañar, Chocar, 3300 m,  
Nov1990, Legit: G. Onore. Paratype QCAZI 3 with the same label as the holotype.  
Ref. Moret 1995

*Blennidus (Agraphoderus) mucronatus* Moret 1996. Holotype QCAZI 8. Ecuador, Pichincha, Atacazo volcano, 3800-4000 m, 18Dec1994. 17 paratypes with the same label as the holotype. Ref. Moret 1996a.

*Blennidus (Sierrobius) viridans* Moret 1995. Holotype QCAZI 22. Ecuador, Azuay, Nabón, 3200 m, Nov1990, Legit. G. Onore. Ref. Moret 1995.

*Blennidus (Sierrobius) thoracatus* Moret 2005. Paratypes QCAZI 23. Label 1: Ecuador, Loja, Saraguro, Paraíso de Celén, Laguna de Chinchilla, 3660 m, 20Dec1998, E. Tapia; Label 2: Ex: dry season. QCAZI 24. Ecuador, Loja, Saraguro, Laguna de Chinchilla, 3665 m, 79°24'W 03°36'S, 20Dec1998, E. Tapia. Ref. Moret 2005

*Bradyceillus aequatorius* Moret 2001. Paratypes QCAZI 34. Ecuador, Bolívar, Cashca Totoras, XII/87, Legit: L. Coloma. QCAZI 36. Ecuador, Bolívar, Cashca Totoras, 87-12-29, Legit S. Paredes. QCAZI 35. Ecuador, El Oro/Loja, 6 km ESE Guanazán, Pass, 3040 m, 7 Nov1987, C. Young, R. Davidson, J. Rawlins. Grassland. QCAZI 37. Ecuador, Bolívar, Guaranda, San Miguel, Santuario Lourdes, 3100 m, 4 Nov1995, GOnore. QCAZI 38. Ecuador, Bolívar, Totoras, 24-VI-87, Legit F. Campos. Ref. Moret 2001b.

*Bradyceillus martinezii* Moret 2001. Paratypes QCAZI 25 and QCAZI 29. Ecuador, Cotopaxi, Parque N. Cotopaxi, 4000 m, 14-V-1983, Col: D. Bastidas. QCAZI 26 and QCAZI 31. Ecuador, Cotopaxi –Volcán, m. 4000, 19. VI-1983, Lg. L. Coloma. QCAZI 27. Label 1: Ecuador, Pichincha, Quito, 8-V-85, Leg: R. León; Label 2: Ex: *Solanum tuberosum* roots. QCAZI 28. Ecuador, Cotopaxi –Volcán, m. 4000, 25-V-1983, Lg. Ernesto Martínez. QCAZI 30. Ecuador, Cotopaxi, (4500), 04-05-1983, Lg. Valle, C. QCAZI 32. Ecuador, Cotopaxi, Mishia Huayco, 3200 m., 17SEP1995, Zapata. QCAZI 33. Ecuador, Cotopaxi, Planchaloma, 3100 m, 2 APR1995, G. Zapata. Ref. Moret 2001b.

*Bradyceillus youngi* Moret 2001. Paratype QCAZI 39. Ecuador, El Oro/Loja, 6 km ESE Guanazán pass, 3040 m., 7Nov1987, C. Young, R. Davidson J. Rawlins. Grassland. Ref. Moret 2001b.

*Coptodera apicalis* Shpeley & Ball 1993. Paratype QCAZI 42. Ecuador, Esm. Pr., Zapallo Grande, 4February1988, Mike Huybensz. Ref. Shpeley & Ball 1993.

*Dercylus (Licinodercylus) onorei* Moret 1995. Paratypes QCAZI 168 to QCAZI 170. Ecuador, Cañar, Shical, 3200 m, Nov1990, Legit: G. Onore. Ref. Moret & Bousquet 1995.

*Dercylus (Licinodercylus) orbiculatus* Moret 1995. Paratype QCAZI 171. Ecuador, XI 83, Azuay, Cajas, Legit: G. Onore. Ref. Moret & Bousquet 1995.

*Dercylus (Licinodercylus) praepilatus* Moret 1995. Paratypes QCAZI 172. Ecuador, Bolívar, Totoras, II-87, Legit: L. Coloma. QCAZI 173. Ecuador, Chimborazo, Guangopud- Chimbo pass, 14Aug1993, 4200 m, C. W. Young, G. Onore & E. Tapia. Ref. Moret & Bousquet 1995.

*Dercylus (Licinodercylus) granifer* Moret 1995. Paratype QCAZI 179. Ecuador, Morona – Santiago/Azuay Pass, 21 km SE Gualaceo, 3720 m, 21Oct1987, C. Young, R. Davidson, J. Rawling. Wet paramo. Ref. Moret & Bousquet 1995.

*Dercylus (Licinodercylus) gibber* Moret 1995. Paratype QCAZI 167. Ecuador, Loja, 2800 m, 12Marzo1991, Legit: G. Onore. Ref. Moret & Bousquet 1995.

*Diploharpus rossii* Moret 2008. Paratypes QCAZI 502, QCAZI 1826 and QCAZI 1827. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Bosque Integral de Otonga, 11-12 VII 2007, W. Rossi. Ref. Moret 2008

*Dyscolus (s. str.) algidus* Moret 2005. Paratype QCAZI 56. Ecuador, Napo, Quilindaña, 4000 m, 12 MAY1995, G.Zapata. QCAZI 57. Ecuador, Cotopaxi, vía Salcedo-Tena, Etribación Oriental, 2800-3800 m, 15JAN1995, G. Onore. Ref. Moret 2005

*Dyscolus (s. str.) araneus* Moret 2005. Holotype QCAZI 70. Ecuador, Azuay, Patacocha, 3500 m, 31DEC1995, G.Onore. Paratypes QCAZI 71 to QCAZI 76, with the same label as the holotype. QCAZI 77. Ecuador, Azuay, Paute, Antena, 3000 m, 17MAR1996, F.Salazar. Ref. Moret 2005.

*Dyscolus (s. str.) arvalis* Moret 2005. Paratype QCAZI 58. Label 1: Rio-bamba, m-3500 m, Aoñt 77; Label 2: Equateur, Coll. J. Negre. Ref. Moret 2005

*Dyscolus (s. str.) atkinsi* Moret 2001. Paratypes QCAZI 49 to QCAZI 51. Carchi, Volcán Chiles, 3850 m., páramo, 11. VII. 1997, n°289, N. Atkins leg. Ref. Moret 2001a.

*Dyscolus (s. str.) bliteus* Moret 2005. Paratypes QCAZI 79. Ecuador, Chimborazo, Lag. Negra (Atollo), 3600 m., 6JAN1995, G.Zapata. QCAZI 80. Ecuador, Chimborazo, Hacienda Cubillin, 3650 m, ruisseau, 5.8.1998, P. Moret. Ref. Moret 2005.

*Dyscolus (s. str.) bordoni* Moret 1993. Paratype QCAZI 78. Ecuador, 16-IX-84, Prov. Pichincha, Cayambe, NE lag. San Marcos, Pierre Moret legit, 3600 m. Ref. Moret 1993.

*Dyscolus (s. str.) breviculus* Moret 2001. Paratype QCAZI 81. Carchi, Volcán Chiles, 3850 m, paramo, 11.VIII.1997, n°290, N. Atkins leg. Ref. Moret 2001a.

*Dyscolus (s. str.) capsarius* Moret 2005. Paratypes QCAZI 82 and QCAZI 83. Label 1: Ecuador, Azuay, Las Cajas, 35 km WNW Cuenca, 3950 m, 9November1987; Label 2: R. Davidson, J. Rawlins, C. Young, páramo habitat, QCAZI 84. Ecuador, Azuay, Nudo de Cajas pass, 4150 m, 17.V.1997, A. Cassale leg. Ref. Moret 2005.

*Dyscolus (s. str.) carbonescens* Moret 2005. Holotype QCAZI 60. Ecuador, Cañar, La Carbonería, 2850 m, 18JAN1996, FSalazar & G.Onore. Paratypes QCAZI 61 to QCAZI 66, with the same label as the holotype. Ref. Moret 2005.

*Dyscolus (s. str.) cephalotes spp. sirinae* Moret 2005. Paratype QCAZI 67. Ecuador - Chimborazo, Cerro Achipungu, (N) 4230 m, –sous pierre, P. Moret leg. 7.I.95. Ref. Moret 2005

*Dyscolus (s. str.) desultor* Moret 2005. Paratypes QCAZI 68 and QCAZI 69. Ecuador, Chimborazo, Ozogoche, alrededor de la Laguna, 27DEC1994, G.Onore. Ref. Moret 2005.

*Dyscolus (s. str.) exsul* Moret 2005. Paratypes QCAZI 198 to QCAZI 210. Ecuador, Azuay, Patacocha, 3500 m, 30Dec1995, GOnore. Ref. Moret 2005.

*Dyscolus (s. str.) fartilis* Moret 2005. Paratype QCAZI 197. Ecuador -Chimborazo, Hacienda Cubillin, 3400-3520 m, foret, 5.8.1998, P. Moret. Ref. Moret 2005

*Dyscolus (s. str.) fucatus* Moret 2005. Paratype QCAZI 211. Ecuador, Chimborazo, Shangay volcan, 3300 m, 14.VI.1991, Craie Downer. Ref. Moret 2005.

*Dyscolus immodicus* Moret 2005. Paratypes QCAZI 213 to QCAZI 216. Ecuador, Pich, Antisana, VI-85, Legit: J. Coloma. QCAZI 217. Label 1: Ecuador, Pich, Antisana, VI-85, legit: A. Velasco, M. Larrea, 23 VII 1984; Label 2: Ex: excremento. Ref. Moret 2005.

*Dyscolus involucer* Moret 1994. Paratype QCAZI 220. Label 1: W. Otavalo, (Ecuador), 3100 m., 5Sept.77; Label 2: Collection J. Négre. Ref. Moret 1994.

*Dyscolus involucer geodesicus* Moret 1994. Paratypes QCAZI 218 and QCAZI 219. Ecuador, Carchi, San Gabriel, Monte Verde, Bosque de Arrayanes, 2800 m, C. Young, G. Onore. Ref. Moret 1994.

*Dyscolus (s. str.) lignicola* Moret 1994. Paratypes QCAZI 238. Ecuador, Pichincha, Vía Chiriboga Guarumal, I-84, Leg. Yépez. QCAZI 239 and QCAZI 240. Label 1: Ecuador, Pichincha, Pasocha, V-85, Legit: A. Salazar; Label 2: Hunting on *Polylepis* sp. QCAZI 241. Ecuador, XII -87, Otavalo, m 3000, leg. G. Onore. Ref. Moret 1994.

*Dyscolus (s. str.) lubricus* Moret 2001. Holotype QCAZI 231. Ecuador, VIII-86, Carchi, Tufino, Legit: G. Onore. Ref. Moret 2001a.

*Dyscolus (s. str.) maleodoratus* Moret 2005. Paratypes QCAZI 222 to QCAZI 225. Ecuador, Pichincha, Páramo de Guamaní, 20-10-84, Legit: V. Zak. Ref. Moret 2005.

*Dyscolus (s. str.) montivagus* Moret 1998. Paratype QCAZI 227. Ecuador, Carchi, 23 km W Tufino, pass, Volcán Chiles, 4070 m, 18Nov1987, R. Davidson, C. Young. Paramo. Ref. Moret 1998.

*Dyscolus (s. str.) montufari* Moret 2005. Paratype QCAZI 226. Label 1: Ecuador, Bolívar, Chimborazo Pass, 23 km SSW Chimborazo, 4040 m, 17Oct1987; Label 2: C. Young, R. Davidson, J. Rawlins. Dry paramo. Ref. Moret 2005.

*Dyscolus (s. str.) nubilus* Moret 2001. Paratypes QCAZI 229 and QCAZI 230. Ecuador, VIII-86, Carchi, Tufiño, Legit: G. Onore. Ref. Moret 2001a.

*Dyscolus onorei* Moret 1993. Paratype QCAZI 242. Ecuador, II-86, Carchi, Chiles, 3900 m., Legit: P. Ponce. Ref. Moret 1993.

*Dyscolus (s. str.) palatus* Moret 1998. 7 paratypes with the following label: Ecuador, Pichincha, Atacazo volcan, 3800-4000 m 18Dec1994, GOnore. Ref. Moret 1998.

*Dyscolus (s. str.) pullatus* Moret 2005. Paratypes QCAZI 153. Ecuador, Bolívar, XII.81, Totoras, 3000 m, Legit: J. Naranjo. QCAZI 155, QCAZI 156, QCAZI 160. Ecuador, Bolívar, XII-87, Totoras, Legit: R. Puebla. QCAZI 158, QCAZI 159, QCAZI 163. Ecuador, Bolívar, 28.XII.81, Totoras, 3000 m, Legit: J. Naranjo.

QCAZI 162. Ecuador, XII-86, Bolívar, Totoras, Legit: L. Coloma. QCAZI 164 and QCAZI 165. Ecuador, VI-86 Bolívar, Totoras, Legit: L. Coloma. QCAZI 154. Ecuador, Bolívar, Cashca Totoras, XII-87, Legit: L. Coloma. QCAZI 161. Ecuador, Bolívar, Cashca Totoras, 28-XII-1987, Legit: P. Coral. QCAZI 157. Ecuador, VIII - 86, Pallatanga, Legit: G. Onore. Ref. Moret 2005.

*Dyscolus (s. str.) riveti* Moret 2001. Paratypes QCAZI 145 to QCAZI 152. Carchi, Volcán Chiles, 4050 m, paramo, 10. VIII.1997, n 285, N. Atkins Leg. Ref. Moret 2001a.

*Dyscolus segnipes* Moret 1990. Paratype QCAZI 166. Label 1: Ecuador, Napo, Paso de Guamaní; e. Quito under stones; road-side, 3810-3962 m, May 13, 1982, #51-3; Label 2: Ecuador, exp. 1982, H. E. Frania & F. A. H. Sperling collectors. Ref. Moret 1990.

*Dyscolus (s. str.) tapiarius* Moret 2005. Holotype QCAZI 232. Ecuador, Loja, Saraguro, Paraíso de Celen, Laguna de Chinchilla, 3660 m, 20Dec1998, E. Tapia. Paratypes QCAZI 233 to QCAZI 235 with the same label as the holotype. Ref. Moret 2005

*Dyscolus (s. str.) trossulus* Moret 2005. Paratype QCAZI 246. Ecuador, Azuay, S. José de Raranga, 3300 m, 16Nov1990, Legit: G. Onore. Ref. Moret 2005

*Dyscolus (s. str.) verecundus* Moret 1998. Paratype QCAZI 247. Ecuador, Pichincha, Atacazo volcan, 3800-4000 m, 18Dec1994, G. Onore. Ref. Moret 1998.

*Dyscolus (Hydrodyscolus) hirsutus* Moret 2005. Paratype QCAZI 221. Ecuador, XI. 85, Napo, Papallacta, Legit: G. Onore. Ref. Moret 2005.

*Dyscolus (Hydrodyscolus) imbaburae* Moret 2005. Paratype QCAZI 212. Ecuador, Imbabura, road Cahuasqui to Buenos Aires, 3500 m, 10Mar1993, G. Onore. Ref. Moret 2005

*Dyscolus (Hydrodyscolus) nocticolor* Moret 2005. Paratype QCAZI 228. Ecuador, Imbabura, Mojanda, 4-Dic-89, Legit Mónica Coello. Ref. Moret 2005.

*Dyscolus (Hydrodyscolus) smithersi* Moret 2001. Paratype QCAZI 174. Carchi, Volcán Chiles, 3400 m., stream side, VIII-1997, IDSPO8, P. Smithers leg. Ref. Moret 2001a.

*Euchella kiplingi* Shpeley& Ball 2000. Paratype QCAZI 40 and QCAZI 41. 01°02'03"S, 77°39'49"W, Ecuador, Napo Prov., Puerto Misahualli, 11:IX:1997, Col. K. Will. Ref. Shpeley & Ball 2000.

*Glyptolenoides balli* Moret 2005. Paratype QCAZI 180. Ecuador, Pichincha, Pifo-Baeza km 45, 29-XI-85, Legit: A. Izurieta. Ref. Moret 2005.

*Incastichus aequidianus* Moret 1996. Paratype QCAZI 177. Label 1: Ecuador, Pichincha; Label 2: Palmeras, 24/01/93, E. Pichilingue. Ref. Moret 1996b.

*Loxandrus ecuadoricus* Straneo 1991. Paratype QCAZI 176. Label 1: Ecuador: Carchi, Chical, 1250 m, 0 56'N, 78 11'W, Coll. R. Davidson. VII.11-20.1983; Label 2: ex: *Eleacharis elegans* swamp. Ref. Straneo 1991a.

*Loxandrus photophilus* Straneo 1991. Paratype QCAZI 175. Paraguay, Dept. Central, San Lorenzo, 18-19 Nov 1986, J. A. Kochalka. Uv light trap. Ref. Straneo 1991a.

*Ogmopleura (Agraphoderus) colomai* Straneo 1991. Paratypes QCAZI 114 to QCAZI 121. Ecuador, Pichincha, Antisana, 4200 m, 4-II-1984, Lg. G. Onore. Comments: Labeled as *Blennidus antisanae* (Bates) by P. Moret in 2001. Ref. Straneo 1991b

*Ogmopleura balli* Straneo 1991. Paratype QCAZI 122. Label 1: Ecuador, Azuay, Las Cajas, 35 km WNW Cuenca, 3950 m, 9 November 1987; Label 2: R. Davidson, J. Rawlins; C. Young, Paramo habitat. Comments: Labeled as *Blennidus balli* Straneo by P. Moret in 2001. Ref. Straneo 1991b.

*Ogmopleura ecuadoriana* Straneo 1991. Paratype QCAZI 133. Label 1: Ecuador, Bolívar, Chimborazo, Pass, 23 km SSW Chimborazo, 4040 m, 17 Oct 1987; Label 2: C. Young, R. Davidson, J. Rawlins, Dry paramo. Comments: Labeled as *Blennidus ecuadorianus* (Straneo) by P. Moret in 2001. Ref. Straneo 1991b.

*Ogmopleura (Agraphoderus) liodes planoculis* Straneo 1991. Paratype QCAZI 1. Ecuador, Tungurahua, 7 km NW Chimbacazo, 3960 m., 15 Oct 1987, R. Davidson, J. Rawlins, C. Young. Dry subparamo. Ref. Straneo 1991b, but see Moret 1996a.

*Oxytrechus onorei* Allegro et al. 2008. Paratype QCAZI 500. Ecuador, Pichincha, Volcán Cayambe, m. 4500, 14.VIII.1990, Sciaky. Ref. Allegro et al. 2008.

*Oxytrechus pierremoreti* Allegro et al. 2008. Paratype QCAZI 501. Ecuador, Pichincha, Atacazo volcán, 3800-4000 m., 18 Dec 1994, G. Onore. Ref. Allegro et al. 2008.

*Oxytrechus reventadori* Moret 2005. Holotype QCAZI 195. Ecuador, Sucumbios, Volcan Reventador, 3530 m, Mayo 1999, E. Tapia. Ref. Moret 2005.

*Oxytrechus zoiae* Casale & Sciaky 1986. Paratype QCAZI 196. Ecuador, M. Cotopaxi, m 4800, 3.IV.86, Leg. A. Casale. Ref. Casale & Sciaky 1986.

*Pelmatellus gracilis* Moret 2000. Paratypes QCAZI 189. Ecuador, Pichincha, Puembo, 2450 m, 25-I-85, Legit: J. Coloma. QCAZI 190. Ecuador, Pichincha, Pomasaqui, 20-8-85, Legit: L. Torres. QCAZI 191. Ecuador, Tungurahua, Píllaro, 22-I-89, Legit: R. Puebla A. Ref. Moret 2000.

*Pelmatellus inca* Moret 2000. Paratype QCAZI 192. Ecuador, 14.VIII.88, Prov. Cañar, Nudo de Azuay, Paredones, 3980 m, Pierre Moret legit. Ref. Moret 2000.

*Pelmatellus polylepis* Moret 2000. Paratype QCAZI 193. Label 1: Ecuador, Azuay, Las Cajas, 35 km WNW Cuenca, 3950 m, 9 November 1987; Label 2: R. Davidson, J. Rawlins, C. Young. Paramo habitat. Ref. Moret 2000.

*Pelmatellus caerulescens* Moret 2005. Holotype QCAZI 181. Label 1: Ecuador, Loja, Saraguro, Paraíso de Celen, Laguna de Chinchilla, 3660 m, 20 Dec 1998, E. Tapia; Label 2: Ex: Dry season. Paratypes QCAZI 182 to QCAZI 188 with the same labels data as the holotype. Ref. Moret 2005.

*Perigona belloii* Giachino, Moret & Picciau 2008. Paratype QCAZI 1831 f. Ecuador, Pichincha, m 3150, S. José de Minas, Cerro Blanco, S 00°12'37.3", W

78°21'03.0", 7.VIII.2006, C. Bellδ. Ref. Giachino *et al.* 2008.

*Sierrobius onorei* Straneo 1991. Paratypes QCAZI 106. Ecuador, VI-86, Bolívar, Totoras, Legit: L. Coloma. QCAZI 107. Ecuador, Bolívar, Totoras, Legit: L. Coloma, XII/86. Comments: Synonymized as *Blennidus onorei* (Straneo) by P. Moret 2001. Ref. Straneo 1991b.

*Stenognathus (Prostenognathus) onorei* Shpeley & Ball 2000. Paratype QCAZI 178. Ecuador, Napo, II-89, Cosanga, Legit: G. Onore. Ref. Shpeley & Ball 2000.

*Stolonis tapiai* Will 2005. Paratype QCAZI 1971 \$. 00°40'36" S, 76°24'02" W, ECUADOR, Napo Prov., Yasuni Scientific Station, 20:IV:1998, 210m, Col. K. Will, Headlamp. QCAZI 1972 , with the same label as QCAZI 1971 except for: 19:IV:1998 £. Ref. Will 2005.

*Stolonis spinosus* Will 2005. Paratype QCAZI 1968 \$. 00°40'36" S, 76°24'02" W, ECUADOR, Napo Prov., Yasuni Scientific Station, 22:IV:1998, 210m, Col. K. Will, Headlamp. Ref. Will 2005.

*Stolonis catenarius* Will 2005. Paratype QCAZI 1966 \$. 00°40'36"S 76°24'02"W ECUADOR, Napo Prov., Yasuni Scientific Station, 22:IV:1998, 210m, Col. K. Will, Headlamp. QCAZI 1967, with the same label as QCAZI 1966 except for: 21:IV:1998, £. Ref. Will 2005.

*Stolonis yasuni* Will 2005. Paratypes QCAZI 1969 \$, QCAZI 1970 £. 00°40'36"S 76°24'02"W ECUADOR, Napo Prov., Yasuni Scientific Station 21:IV:1998, 210m, Col. K. Will. Ref. Will 2005.

*Trechisibus (Ecuadoritrechus) tapiai* Deuve 2002. Holotype QCAZI 194. Ecuador, Loja, Saraguro, Paraíso de Celen, Laguna de Chinchilla, 3660 m, 20DEC1998, E. Tapia. Figura 6 Pronotum. Ref. Deuve 2002.

#### FAMILY CERAMBYCIDAE

*Apteraleidion lapierrei* Hovore 1992. Paratype QCAZI 616. Costa Rica, Cartago Pr., Cerro de la Muerte, 3450 m, 11/13June1987, F. T. Hovore coll. Ref. Hovore 1992.

*Eburia frankei* Noguera 2002. Paratype QCAZI 615. Costa Rica, Guan. Pr., Santa Rosa N. P., 31May/01 June 2002, F. Hovore, I. Swift coll. Ref. Noguera 2002.

*Neseuterpiacouturieri* Tavakilian 2001. Paratypes QCAZI 613 \$ and QCAZI 614 \$. Label 1: Ecuador, (Puyo), Santa Clara-San José vía Puyo-Cena (522 m), 6novembre2000, Thomas Peyret leg.; Label 2: 01°17'07"S, 77°47'18"O, sur inflorescence en anthése *Astrocaryum urostachys* Burret (ASTERACEAE). Ref. Tavakilian 2001.

#### FAMILIA CHRYSOMELIDAE

*Aslamidium* (s. str.) *ecuadoricum* Borowiec 1998. Holotype QCAZI 730. Ecuador, Napo, Misahualli, 450 m, MAY28 1994, C. Boada. Ref. Borowiec 1998a.

*Cyclocassis secunda* Borowiec 1998. Paratype QCAZI 731. Ecuador, 2000 m, Loja, Veracruz 12 Aug1994, F. Maza. Ref. Borowiec 1998b.

*Discomorpha onorei* Borowiec 1998. Holotype QCAZI 732. Ecuador, Napo, X-87, Loreto, Legit: G. Onore. Paratype QCAZI 733. Ecuador, Napo, Río Hollin, 6/12/91, P. Delgado. Ref. Borowiec 1998b.

*Eugenisa jasinskii* Borowiec & Dšbrowska 1997. Paratypes QCAZI 734. Ecuador, kupiony Baños, V-1996. QCAZI 735. Ecuador, Jatun Sacha, 6-09-89, Legit Martin Steer. Ref. Borowiec & Dšbrowska 1997.

*Eugenisa unicolor* Borowiec & Dšbrowska 1997. Paratypes QCAZI 736. Ecuador, Napo, Puyuyacu, 27-V-1996, leg. A. Jasinski. QCAZI 737. Ecuador, Pichincha, Puerto Quito, 720 mts, 3-XII-1982, Lg. M. Chieruzzi. QCAZI 738. Ecuador, Napo, Lumbaqui, 850 m, 28II 1976, Coll Vénédictoff. QCAZI 739. Ecuador, Napo, Talag, Pimpilala, 5 Nov1999. QCAZI 740. Ecuador, Napo, Misahualli, 480 m, 28Dec1995, X. Salazar. Ref. Borowiec & Dšbrowska 1997.

*Stolas napoensis* Borowiec 1998. Holotype QCAZI 741. Ecuador, Napo, SC Station Yasuní PUCE, 400 m, 11-23Sep1995, E. Baquero, F. Maza. Paratypes QCAZI 744, with the same label as the holotype. QCAZI 742 and QCAZI 745 with the same label as the holotype except for: 12APR1996, G. Cañas; 16Nov1996, M. Torres. QCAZI 743. Ecuador, Napo, Talag, 700 m, 10Jun1994, G. Onore. QCAZI 746. Label 1: Ecuador, Napo, SC Yasuní, 250 m, 28-30May1997, E. Baus; Label 2: Ex: Trampa de luz. Ref. Borowiec 1998b.

*Stolas perezi* Borowiec 1998. Holotype QCAZI 747. Ecuador, Napo, Campanococha, 431 m, 15/Jan/1994, Legit. C. Pérez. Ref. Borowiec 1998b.

*Stolas stolida jadwiszczaki* Borowiec 1998 . Paratypes QCAZI 748 and QCAZI 749. Label 1: Ecuador, Napo, Archidona, 705 m, 8-VI-91, Leg. Lee Sehel; Label 2: Jumandi, (Baeza-Archidona). QCAZI 750. Ecuador, Napo, Archidona, 1 May1992, J. Lussio. QCAZI 751. Ecuador, Napo, Tena, 500 m, 26Dic1996, I. Olmedo. Ref. Borowiec 1998b.

*Stolas zumbaensis* Borowiec 1998. Paratype QCAZI 752. Ecuador, Zamora Chinchipe, Zumba, 19.04.97, K. Los. Ref. Borowiec 1998b.

#### FAMILY CICINDELIDAE

*Ctenostoma (Neoprocephalus) cassolai* Naviaux 1998. Paratype QCAZI 248. Ecuador, Pichincha, La Unión del Toachi, (Cuesta del Gallinazo), 950 m, 78°57'10"W, 00°21'05"S, 6Mar1997, G. Onore. Ref. Naviaux 1998 [not reviewed].

*Ctenostoma (Procephalus) ecuadoriensis* Naviaux 1998. Holotype QCAZI 249. Ecuador, Pichincha, Chiriboga, 1800 m, 78°45'54"W, 00°13'42"S, 2 Nov1983, Leg. Comments: Labeled as *CTENOSTOMA dormei* Horn by F. Cassola in 1987. Ref. Naviaux 1998 [not reviewed].

*Ctenostoma (Procephalus) onorei* Naviaux 1998. Holotype QCAZI 250. Ecuador, Esmeraldas, Rocafuerte, 50 m, 79°24'00"W, 01°01'00"N, APR1987, E. E. Briones; Comments: Labeled as *CTENOSTOMA nigrum* CHAUDOIR by F. Cassola. Ref. Naviaux 1998 [not reviewed].

*Oxycheila brzoskai* Wiesner 1999. Holotype QCAZI 252. Label 1: Ecuador, Pichincha,

Tinalandia, (525m), 22March1995, D. W. Brzoska; Label 2: Nocturnal- rocks of Mountain stream. Paratype QCAZI 257 with the same label as the holotype. QCAZI 253. Ecuador, Pichincha, Tinalandia, 650 m, 79°02'57 W, 00°18'21 S, 23Dec1973, N. Venedictoff. QCAZI 254 and QCAZI 256 with the same label as QCAZI 253 except for: 800 m, 3JAN1997, D. Guevara; 5JAN1997, C. Pérez. QCAZI 255. Ecuador, Pichincha, Santo Domingo De Los Colorados, 500 m, 79°10'11" W; 00°15'08"S, 29APR1973, N. Venedictoff. Comments: QCAZI 255 was labeled as *OXYCHILA nigroaenea* by F. Cassola in 1987 and *Oxycheila chestertoni* Bates by R. L. Huber in 1995. Ref. Wiesner 1999.

*Oxygonia nigrovenator* Kippenhan 1997. Holotype QCAZI 251. Label 1: Ecuador, Napo, 20 km e. Tena-Baeza Rd., 22 Sept.1994, (1,100 m), D. L. Pearson, et al.; Label 2: DIURNAL –ON ROCKS IN SMALL STREAM. Ref. Kippenhan 1997.

*Pseudoxycheila atahualpa* Cassola 1997. Holotype QCAZI 258. Ecuador, Napo, Río Hollin, 1100 m, 77°40'W, 00°42'S, 6Dec1987, M. Mena. Paratypes QCAZI 260 (Allotype). Ecuador, Napo, San Rafael, 1400 m, 77°34'W, 00°03'S, 03Dec1988, C. Ayala. 3 paratypes with the same label as QCAZI 260 except for: E. Trujillo; V. Cachago; M. Pallares; 2 paratypes with the same label as QCAZI 260 except for: Nov1984, C. Josse; M. Ferro; QCAZI 270. Ecuador, Napo, San Rafael, 1500 m, 77°34'W, 00°03'S, 2Nov1984, X. Pazmiño. QCAZI 290. Ecuador, Sucumbios, San Rafael, 1480 m, 77°33'W, 00°03'S, 20Nov1993, M. Montalvo. QCAZI 292. Ecuador, Napo, San Rafael, 1500 m, 77°33'W, 00°03'S, 1Nov1984, M. Ferro. QCAZI 259, with the same label as the holotype except for: S. Gutierrez. QCAZI 261, QCAZI 334. Ecuador, Napo, Río Hollin, 1100 m, 77°40'W, 00°42'S, 6Dec1987, J. Gómez. QCAZI 274 and QCAZI 275, Ecuador, Napo, Río Hollin, 1100 m, 77°40'W, 00°42'S, 6Dec1987, H. Freire. 6 paratypes with the same label as the holotype except for: S. Gutierrez; R. Boada; F. Arellano; Hernández; M. Peñaherrera; R. Manosalvas. 6 paratypes with the same label as the holotype except for: 6DEC1991, P. Ramón; 5 Dec1987, Espinosa; 6DEC1981, M. Endara; 7DEC1991, F. Cáceres; Nov1994, J. Chávez; 5DEC1996. M. Bustamante. QCAZI 300 and QCAZI 301. Ecuador, Napo, Río Hollin, 1100 m, 77°40'W 00°42'S 9DEC1995, D. Prado. QCAZI 308 to QCAZI 310; QCAZI 312. Ecuador, Napo, Río Hollin, 1100 m, 77°40'W 00°42'S 8DEC1996, F. Maza. QCAZI 327 and QCAZI 328. Ecuador, Napo, Río Hollin, 1100 m, 77°40'W 00°42'S 5DEC1987, N. L. Granda. 2 paratypes with the same label as the holotype except for: 07DEC1996, M. Avila; E. Gortaire. 7 paratypes with the same label as the holotype except for: 6DEC1996, R. Ramírez; J. Gil. J. Lecaro; V. Barragán; G. Castañeda; F. Villalva; G. Granda. QCAZI 263. Ecuador, Napo, Vía Baeza- Lago Agrio, JAN1976, F. I. Ortiz. QCAZI 264. Ecuador, Napo, El Reventador, 77°33'W, 00°02'S, May1988, G. Onore. QCAZI 289 and QCAZI 325. Ecuador, Napo, El Reventador, 77°33'W, 00°02'S, 1400 m, 9JAN1984, S. Sandoval. 2 paratypes with the same label as QCAZI 289 except for: 03DEC1988, P. Jiménez; M. Pallares. QCAZI 265 and QCAZI 272. Ecuador, Napo, El Reventador, 77°33'W, 00°02'S, 1400 m, 3Dec1988, F. Haro. QCAZI 276. Ecuador, Napo, Reventador, 77°33'W, 00°02'S, 1400 m, 9JAN1984, S. Sandoval. QCAZI 279. Ecuador, Napo, El Reventador, 77°33'W, 00°02'S, 1400 m, 4DEC1993, K. Proaño; QCAZI 266. Ecuador, Napo, Jumandi, 700 m, 00°52'S, 77°47'W, 18APR1992, R. Bernal. QCAZI 281. Ecuador, Napo, Jumandi, 400 m, 77°09'W, 00°29'S, 18APR1992, R. Bernal. QCAZI 271. Ecuador, Napo, Loreto, 350 m, 77°16'45"W, 00°42'42"S, Oct1987, G. Onore. QCAZI 273. Ecuador, Pichincha, Vía Puerto Quito, 300 m, 79°16'10"W,

00°06'42"N, 26Dec1985, F. Albán. QCAZI 282. Ecuador, Pichincha, Nanegalito, 1600 m, 78°41'00"W, 00°08'00"N, 23JAN1994, H. Romero. QCAZI 283. Ecuador, Pichincha, Nanegalito, 1600 m, 78°41'00"W, 00°08'00"N, 1JAN1993, D. Villagómez. QCAZI 284. Ecuador, Pichincha, Mindo, 1200 m, 78°48'00"W, 00°03'00"S, 20Jun1993, M. Gamboa. QCAZI 316. Label 1: Ecuador, Pichincha, Mindo, 1200m, 78°48'00"W, 00°03'00"S, 17JAN1997, R. Oliva; Label 2: LOCALITY DOUBTFUL! F. Cassola, 1997. QCAZI 285. Ecuador, Pichincha, Tandapi, 1460 m, 78°49'34"W, 00°25'05"S, 13JAN1992, B. Elizalde. QCAZI 288. Ecuador, Napo, Baeza, 1400 m, 77°53'W, 00°27'S, 19JAN1992, V. Yánez. QCAZI 289. Ecuador, Napo, Archidona, 610 m, 77°48'09"W, 00°54'13"S, 18JAN1992, P. Fernández. QCAZI 295, QCAZI 297, with the same label as QCAZI 289 except for: 21 May1993, T. Santander; 1MAY1992, L. Vinueza. QCAZI 296. Ecuador, Pichincha, Sto. Domingo, 650 m, 79°10'11"W, 00°15'08"S, 18DEC1992, J. Herbas. QCAZI 302. Ecuador, Napo, Papallacta, 3500 m, 78°08'00"W, 00°22'00"S, 6MAY1995, N. Marchán. QCAZI 303. Ecuador, Napo, El Chaco, 1000 m, 77°47'26"W, 00°19'27"S, 30MAY1995, X. Cisneros. 2 paratypes with the same label as QCAZI 303 except for: 6MAY1995, M. Rodríguez. 2 paratypes with the same label as QCAZI 303 except for: 6JUN1995, V. Quitiguña; 6MAY1995, R. Paredes. QCAZI 311. Ecuador, Tungurahua, Río Blanco, 1500 m, 78°20'00"W, 01°22'00"S, AUG1994, F. Maza. QCAZI 313. Ecuador, Napo, San Francisco de Borja, 77°49'W, 00°25'S, 18APR1992, V. Utreras. QCAZI 314 and QCAZI 315, with the same label as QCAZI 313 except for: 8APR1992. Comments: QCAZI 259, QCAZI 263, QCAZI 264 and QCAZI 271 labeled as *PSEUDOXYCHILA bipustulata* Latr. by F. Cassola in 1987. Ref. Cassola 1997.

*Pseudoxycheila caribe* Cassola 1997. Paratypes QCAZI 336. Venezuela, Táchira, Carr. Cordero- Michelena, Casa del Padre, 2350 m, 24-25.VI.95, F. Cassola. QCAZI 337. Venezuela, Táchira, Casa del Padre, m 2300. tra Cordero e Michelena, 16.V.1993, leg. A. Bandinelli. Ref. Cassola 1997.

*Pseudoxycheila inca* Cassola 1997. Paratypes QCAZI 338. Label 1: Ecuador: Loja, 9 km al s. Yangana, 15Mar.1996, 4°22's, 79°12'w, (2090), D. L. Pearson; Label 2: Road cut. QCAZI 339 to QCAZI 340. Ecuador, Zamora Ch., Valladolid, 2000 m, 79°08'W, 0433'S, 20APR1997, A. Jasinski. Ref. Cassola 1997.

*Pseudoxycheila nitidicollis* Cassola 1997. Holotype QCAZI 341. Label 1: Ecuador, Napo, 15 km w. Cosanga, 29Sept.1994, (2,200 m), D. L. Pearson et.al; Label 2: FORESTED CATTLE PASTURE. Paratypes (Allotype) QCAZI 347, with the same labels data as the holotype. QCAZI 369, with the same labels data as the holotype except for: 16 km w instead of 15 km w. QCAZI 368. Ecuador: Napo, 6.6 km n. Cosanga, 22Sept.1994 (1,875m), D. L. Pearson et al. BRUSHY ROAD CUT. QCAZI 342, QCAZI 343, QCAZI 346. Ecuador, Napo, San Rafael, 1100 m, 00°04'S, 77°34'W, 09AUG1991, G. Onore. QCAZI 350. Ecuador, Napo, San Rafael, 1100 m, 00°04'S, 77°34'W, 6DEC1992, Mtroya. QCAZI 361. Ecuador, Sucumbios, San Rafael, 1400 m, 00°04'S, 77°34'W, Nov1984, M. Ferro. QCAZI 344. Ecuador, Napo, Cosanga, 2000 m, 77°55'00"W, 00°34'00" S, 23AUG1992, R. Bernal. QCAZI 367. Label 1: Ecuador, Napo, Cosanga, 2000 m, 77°55'00"W, 00°34'00" S, 20NOV1991, L. Suárez; Label 2: PASTURE EDGE. 6 paratypes with the same label as QCAZI 344 except for: Feb1989, G. Onore. QCAZI 359. Ecuador, Napo, Cosanga, 2000 m, 77°55'00"W, 00°34'00"S, 27APR1992, K. Paredes. QCAZI 388 and QCAZI 390. Ecuador, Napo, Cosanga, 2000 m,

77°55'00" W, 00°34'00" S, 24 May1996, M. Vallejo. 3 paratypes with the same label as QCAZI 388 except for: 24 May1996, B. Yangari; 25May1996, V. Troya; 26May1996, J. Chávez. QCAZI 348, QCAZI 389, QCAZI 397. Ecuador, Tungurahua, Viscaya, 2100-2300 m, 7 MAY1996, K. Los. QCAZI 349, QCAZI 394. Ecuador, Napo, San Francisco de Borja, 1300m, 77°49'W, 00°25'S, 18APR1992, V. Utrereras. QCAZI 352. Ecuador, Napo, Baeza, 1450 m, 77°53'06" W, 00°27'35" S, 19JAN1992, R. Bernal. QCAZI 372. Label 1: Ecuador, Napo, Baeza, 1450 m, 77°53'06" W, 00°27'35" S, 31NOV1985; Label 2: P. González. Habitus figured F. Cassola, 1995. 3 paratypes with the same label as QCAZI 352 except for: 30NOV1985, S. M. Paz; 4MAY1995, D. Villagómez; 30Nov1985, P. Vega. Ex: UNDER STONE. QCAZI 364. Ecuador, Sucumbios, El Reventador, 1400 m, 00°03'S, 77°34'W, 5DEC1992, I. de la Torre. 3 paratypes with the same label as QCAZI 364 except for: X. Carrillo; J. Arellano; 06DEC1992, E. Barahona. Habitus and aedeagus figured F. Cassola, 1995. QCAZI 356, QCAZI 385. Ecuador, Napo, Cuyuja, 2200m, 78°00'48" W, 00°29'12" S, 16JAN1988, M. Ponce. QCAZI 357. Ecuador, Pichincha, Sto. Domingo de los Colorados, 500 m, 79°10'11" W, 00°15'08" S, AUG1974, N. Venedictoff. QCAZI 358. Ecuador, Sucumbíos, Vía La Bonita-La Fama, 00°32'N, 77°32'W, 2200 m, 01JAN1994, G. Onore. QCAZI 377, QCAZI 380 and QCAZI 381. Ecuador, Sucumbios, La Bonita, 1800 m, 77°33'00" W, 00°27'00" N, 22FEB1996, G. Onore. QCAZI 360. Ecuador, Napo, Misahualli, 431 m, 77°34'00" W, 01°03'00" S, 14JAN1994, M. Montalvo. QCAZI 370. Ecuador, Napo, Río Pano, 500 m, 00°59'S, 77°49'W, 3OCT1991, M. C. Erazo. QCAZI 373, QCAZI 374. Ecuador, Morona S., Vía Gualaceo-Limón, 78°31'W, 03°01'S, 2050 m, 19OCT1995, D. L. Pearson. QCAZI 375. Label 1: Ecuador, Morona S., Indaza, Vía Sigsig, 78°27'W, 03°05'S, 1050 m, 28DEC1995, G. Onore; Label 2: Ex: adult associated with larva. Same data. QCAZI 376, QCAZI 378. Ecuador, Napo, vía Salcedo-Tena, 10Jul1995, E. Tapia. QCAZI 382. Ecuador, Pichincha, Río San Rimas, 25 Mar1996, I. Aldaz. QCAZI 383. Ecuador, Pichincha, Nanegalito, 1500 m, 78°41'00" W, 00°08'00" N, 8JUL1995. J. Freile. QCAZI 384. Ecuador, Napo, Río Hollín, Vía Loreto, 77°40'W, 00°42'S, 1100 m, 9DEC1995, P. Muriel. QCAZI 386. Ecuador, Napo, Cuyabeno, 250 m, 76°10'49" W, 00°01'05" N, Mar1984, E. Asanza. QCAZI 395, QCAZI 398 and QCAZI 399. Ecuador, Río Blanco. QCAZI 396. Ecuador, Sucumbios, Sucumbíos, 300 m, 77°12'W, 00°10'N, JAN1996, I. Villafuerte. Ref. Cassola 1997.

*Pseudoxycheila onorei* Cassola 1997. Holotype QCAZI 400. Ecuador, Loja, Catacocha, 2500 m, 79°39'W, 04°03'S, 30DEC1994, G. Onore. Paratypes QCAZI 401 (Allotype) to QCAZI 403, with the same label as the holotype. QCAZI 404 to 412. Ecuador, Loja, Las Chinchas, 2200 m, 79°28'W, 03°59'S, 27DEC1996, G. Onore. Ref. Cassola 1997.

*Pseudoxycheila pearsoni* Cassola 1997. Holotype QCAZI 413. Ecuador, Zamora Ch., 16 km SE de Zamora, 04°05'S, 78°55'W, 18Mar1996, D. L. Pearson. Paratypes QCAZI 414. Ecuador, Zamora Ch., Vía 28 Mayo- Guadalupe, 78°55'W, 03°40'S, 1600 m, 23May1996, A. Jasinski. QCAZI 415, QCAZI 416; QCAZI 419. Ecuador, Zamora Ch., Veintiocho de Mayo, 78°55'W, 03°38'S, 1400 m, 23May1996, K. Los. QCAZI 420. Ecuador, Zamora Ch., 8 km al Sur de 28 de Mayo, 78°55'W, 03°39'S, 1500 m, 30APR1997, K. Los. QCAZI 417 and 418. Ecuador, Zamora Ch., Cordillera del Cónedor, 1300 m, 29APR1997, A. Jasinski. Ref. Cassola 1997.

*Pseudoxyccheila pseudotarsalis* Cassola 1997. Holotype QCAZI 421 \$. Ecuador, Pichincha, Puerto Quito, 300 m, 79°16'10" W, 00°06'42" N, JAN 1984, P. Ponce. Paratypes QCAZI 427 (Allotype). Label 1: Ecuador, Esmeraldas, Río Pitzará, 400-500 m, 00°20' N, 79°11' W, APR1984, G. Onore; Label 2: Habitus figured F. Cassola, 1995. QCAZI 422, QCAZI 428 and 429, with the same label as QCAZI 427 except for: MAR1985. QCAZI 423, QCAZI 425, with the same label as the holotype except for: 17Mar1985, S. Struve; 09JUN 1985, A. Sancho. QCAZI 424. Ecuador, Pichincha, Maquipucuna, 78°37' W, 00°15' S, 26 Mar1988, I. Lippke. QCAZI 426. Ecuador, Pichincha, San Bernabé, May 1986, L. Coloma. Ref. Cassola 1997.

*Pseudoxyccheila quechua* Cassola 1997. Paratypes QCAZI 430. Bolivia, Cochabamba, Yungas del Chaparé, 30-31.I.76, Leg. C. Lopreiato. Ref. Cassola 1997.

#### FAMILY CURCULIONIDAE

*Baillytes Bartolozzi* Voisin 1996. Paratypes QCAZI 619. Ecuador, Cotopaxi, S. Francisco de Las Pampas, (1300-1500 m), II.1993, L. Bartolozzi (N.Mag.1406). QCAZI 620. Ecuador, Cotopaxi, Las Pampas, V/1985, G. Onorel. Ref. Voisin 1996.

*Melchus onorei* Anderson 2003. Paratype QCAZI 621. Ecuador, Sto. Domingo de los Colorados, I-1982, Lg. G. Onore. Ref. Anderson 2003.

#### FAMILY ELATERIDAE

*Achrestus onorei* Golbach, Zamudio & Guzmán de Tomé 1988. Holotype QCAZI 601. Label 1: Ecuador, Napo, Coca, XII-83, G. Onoré col.; Label 2: On oil- palm. Paratype QCAZI 600 (Allotype). Ecuador, Napo, Coca, V. 84, Legit: G. Onore. Ref. Golbach *et al.* 1988.

#### FAMILY HETEROCERIDAE

*Tropicus bartolozzii* Mascagni 1994. Paratype QCAZI 431. Ecuador, Manabí, dint. Puerto López, 20.II.1993, L. Bartolozzi, (Numero Magazz. 1406). Ref. Mascagni 1994.

#### FAMILY LANGURIIDAE

*Lepidotoramus grouvellei* Leschen 1997. Paratypes QCAZI 432 to QCAZI 435. Ecuador, Napo, Cuyabeno, Legit: E. Corriazo. Comments: altitude and date of collection differ between paratypes. Ref. Leshen 1997.

#### FAMILY LEIODIDAE

*Adelopsis aloecuatoriana* Salgado 2008. Paratypes QCAZI 1828 £, QCAZI 1829 \$ and QCAZI 1830 \$. Ecuador, Cotopaxi, Otonga, m 2065, S 00°25'01.2", W79°00'14.0", 21.III.2003 G. Onore. Ref. Salgado 2008.

*Adelopsis (Adelopsis) bioforestae* Salgado 2002. Holotype QCAZI 589. Label 1: Ecuador, Cotopaxi, Otonga, 2000 m, 00°25'S, 79°00'W, 22Jul1999, I. G. Tapia & P. Ponce; Label 2: Ex: monte bajo CH2. Paratypes QCAZI 590, with the same label as the holotype except for: 24Jul1997. QCAZI 588. Ecuador, Cotopaxi, Otonga, 2000 m, 78°57'00" W, 00°19'11" S 30Jun1997, I. G. Tapia, P. Ponce. Ref. Salgado 2002.

*Adelopsis (Adelopsis) ecuatoriana* Salgado 2002. Holotype QCAZI 591. Ecuador, Cotopaxi, 2000 m, 00°25'S, 79°00'W, 22Jul1999, I. Tapia & P. Ponce. Paratype QCAZI 592, with the same label as the holotype except for: 24Jul1999. Ref. Salgado 2002.

*Adelopsis (lultururuca) dehiscentis* Salgado 2002. Holotype QCAZI 583. Ecuador, Los Ríos, CCRP, 4JAN1981, S. Sandoval. Paratypes QCAZI 582 and QCAZI 586. Ecuador, Los Ríos, CCRP, 10JAN1981, S. Sandoval; 6 paratypes with the same label as the holotype except for: 29Dec1980; 11JAN1981; 8JAN1981, £; 4JAN1980; 4JAN1981; 20DEC1980. QCAZI 577. Ecuador, Pichincha, CCRP, 10JAN1981, S. Sandoval. QCAZI 578. Ecuador, Pichincha, CCRP, 23DEC1981, S. Sandoval. Ref. Salgado 2002.

*Adelopsis onorei* Salgado 2002. Holotype QCAZI 536. Ecuador, Morona, Río Yaupi, 260 m, Cueva Achikianas, 2°55'24"LS, 77°54'21"O, 20JAN2001, M. Vallejo. Paratypes 12 paratypes with the same label as the holotype. QCAZI 545, QCAZI 547- QCAZI 549 and QCAZI 554. Ecuador, Napo, Tena, 850 m, Lagarto Cave, LW77°46'79, LS00°49'55, 16JAN1999, Olmedo. QCAZI 552 \$. Ecuador, Napo, Archidona, 850 m, 00°49'33" S, 77°46'47 W, 2 Nov1998, M. Avila & F. Sáenz. Ref. Salgado 2002.

*Adelopsis (lultururuca) tuberculata* Salgado 2002. Holotype QCAZI 561. Ecuador, Napo, Archidona, 850 m, LS00°49'55, LW79°46'79, 16JAN1999, F. Ayala. Ex: Lagarto cave in guano. Paratypes 5 paratypes with the same label as the holotype. QCAZI 565, QCAZI 566, QCAZI 573 and QCAZI 576. Ecuador, Napo, Tena, 850 m, Lagarto cave, LW 77°46'79, LS00°49'55, 16JAN1999, Olmedo. QCAZI 558, QCAZI 569. Label 1: Ecuador, Napo, Archidona, 850 m, S00°49'33,W77°46'47. 2Nov1998, M. Avila; Label 2: Ex: Lagarto cave. QCAZI 555, QCAZI 568. Ecuador, Napo, Archidona, 750 m, Cave Kamatoa, 00°54' S, 76°56'W, 10Dec2000, P. Piedrahita. QCAZI 564, QCAZI 575, with the same label as QCAZI 555 except for: 13JAN2001, J. Rodríguez. QCAZI 557. Ecuador, Napo, Archidona, Cueva Kamatoa, 750 m, LS 0°54' 55", LW 76°46'38", 20JAN2001, F. Villamaría. QCAZI 556. Label 1: Ecuador, Napo, Tena, 750 m, 00°53'18"S, 77°47'49"W, 27Dec1998, A. Lara; Label 2: Ex: Jumandi cave on the wall. QCAZI 559, QCAZI 572. Ecuador, Napo, Archidona, 780 m, 00°50'54"S, 77°46'73"W, 16JAN1999, D. Paucar. Ex: Piña cave in guano. QCAZI 567 and QCAZI 574. Ecuador, Napo, Archidona, 750 m, Cueva del Cacique, 77°48'09"W, 00°54'13"S, 13JAN2001, J. Rodríguez. Ref. Salgado 2002.

*Dissochaetus anseriformis* Salgado 2001. Holotype QCAZI 524. Label 1: Ecuador, Bolívar, Cashcatotoras, 2800 m, 77°36'38.9"W, 00°05'53.2"S, 3 -6Oct2000, F. Maza, L. Coloma; Label 2: Ex: Berlese. Paratypes 14 paratypes £ and 10 paratypes \$ with the same labels data as the holotype. QCAZI 531. Ecuador, Pichincha, Mte. Paschooa, 3000 m, 15-XI-1987, Leg Rodríguez. QCAZI 533. Ecuador, Napo, Baeza, 30-XI-85, Sara M. Paz. QCAZI 534 to QCAZI 535. Ecuador, Cotopaxi (entrada Machachi-Latacunga), m 3440, Land. W Cotopaxi, 2.IX.1984, S. Zoia. Ref. Salgado 2001.

*Dissochaetus napoensis pallipes* Salgado 2008. Paratype. QCAZI 498. Ecuador, Cotopaxi prov., Otonga, 13-VII-2007, Rossi leg. Ref. Salgado 2008.

*Eucatops (Eucatops) incognitus* Salgado 2003. Holotype QCAZI 593. Ecuador, Cotopaxi, Las Pampas, 1500 m, 78°57'04" W, 00°25'16" S, 02Jul1997, I. G. Tapia, P. Ponce. Paratype QCAZI 594. Ecuador, Imbabura, Barcelona, 12-20Sep1995, A. Endara. Ref. Salgado 2003.

*Eucatops (Sphaerotops) granuliformis* Salgado 2003. Holotype QCAZI 595. Label 1: Ecuador, Napo, SC Yasuní, 250 m, 7-14Sept1997, F. Maza; Label 2: Ex: intercepcion trap. Ref. Salgado 2003.

*Eucatops (Eucatops) onorei* Salgado 2008. Paratypes QCAZI 1834, QCAZI 1835 and QCAZI 1836. Ecuador, Napo via Jondachi-Loreto km 59, ex cave m 700, 13.VIII.2006, G. Onore leg. Ref. Salgado 2008.

#### FAMILY LUCANIDAE

*Onorelucanus aequatorianus* Bartolozzi & Bomans 1989. Paratype QCAZI 599 \$. Ecuador, Cotopaxi, Palo Quemado, XII-1988, G. Onore. Ref. Bartolozzi & Bomans 1989.

*Sphaenognathus (Chiasognathinus) xerophilus* Bartolozzi & Onore 2006. Holotype QCAZI 1520 £. Perú, Huancabamba, Huancabamba, 2860 m, 02JAN2005, G. Onore. Paratypes 55 paratypes \$ with the same label as the holotype. Bartolozzi & Onore 2006

#### FAMILY PASSALIDAE

*Passalus kaupi* Boucher 2004. Paratypes QCAZI 466, QCAZI 469. Ecuador, Pichincha, Las Pampas Argentinas, 1300 m, 04.88. Lg. A. Rodríguez. 5 paratypes with the same label as QCAZI 466 except for: 04.88 Lg. Bustamante. 3 paratypes with the same label as QCAZI 466 except for: IV/88, 1500 m. Leg. M. Grijalva. 4 paratypes with the same label as QCAZI 466 except for: 04.88, Lg. S. Cazar. QCAZI 468. Ecuador, Pichincha, Las Pampas Argentinas, 1300 m, 16.04.88, Lg. Galarza. QCAZI 472. Ecuador, Pichincha, Las Pampas Argentinas, 15-16Abr-88, Ilenka von Lippke. QCAZI 474. Ecuador, Pichincha, Las Pampas Argentinas, 1300 m, 04.88, Lg. J. Córdova. QCAZI 477. Ecuador, Pichincha, Pamp. Argentin, IV/88, 1500 m, Leg. P. Casares. QCAZI 467. Ecuador, Pichincha, Puerto Quito, 7-I-84, Leg: R. León. 6 paratypes with the same label as QCAZI 467 except for: 28-I-84, Leg: M. Larrea; XII-1983, Leg. G. Paz y Miño; 27-I-84, Col. M. Paz García ; 4-XII-83, Leg. L. Santamaría; 3-XII-83, Leg: C. Fiallo; 28-V-83, Lg. J. Woolfson. QCAZI 492. Ecuador, Pichincha, km 113 Vía Pto. Quito, 4XII83, col. Granizo. QCAZI 485. Ecuador, Pichicha, Sto. Domingo, 550 m, 17JAN1993, M. Troya. QCAZI 486 and QCAZI 487, with the same label as QCAZI 485 except for: A. Quiñones; I. Pallares. QCAZI 488. Ecuador, Pichincha, 10 km W Nanegalito, 1700 m, 16Jan1992, L. de la Torre. QCAZI 496. Ecuador, Pichincha, Nanegalito, 1400 m, 23JAN1993, C. Segovia. QCAZI 497. Ecuador, Pichincha, Nanegalito, 1300 m, 1Jan1993, D. Villagómez. QCAZI 489. Ecuador, Pichincha, Tandapi, alt: 900 m, 29-06-91, Legit Pérez V. QCAZI 493. Ecuador, Pichincha, S. Dom. Tinalandia, 650 m, 1972, Coll Venédicoff. 2 paratypes with the same label as QCAZI 493 except for: 7-IV-1973; 30-III-1972. Ref. Boucher 2004.

*Verres onorei* Boucher & Pardo-Locarno 1997. Paratypes QCAZI 459. Ecuador,

Pichincha, S. Dom. Tinalandia, 650 m, 1972, Coll Vénédictoff, QCAZI 460.  
Ecuador, Napo, Reventador, V-1984, Legit: G. Onore. QCAZI 461. Ecuador, Prov.  
Pichincha, Puerto Quito, 5-XII-1983, Leg. M. Iturralde. QCAZI 462. Ecuador,  
Pichincha, Pto. Quito, 4-XII-82, lg. H. Bustos. QCAZI 463. Ecuador, Sucumbíos,  
Reventador, 1500 m, 5, 6Dec1992, P. Salvador. QCAZI 464. Ecuador, Pichincha,  
Alluriquín, 15JUA1983, H. Bustos. QCAZI 465. Ecuador, Cotopaxi, Guasagunda,  
27 12 94, L. Salazar. Ref. Boucher & Pardo-Locarno 1997.

#### FAMILY RHYSODIDAE

*Stereodermus jonathani* Mantilleri 2004. Paratype QCAZI 610. Ecuador, Pichincha,  
Tandayapa, IV-1983, leg. G. Onore. Comments: Genitalia separated. Ref.  
Mantilleri 2004.

#### FAMILY SCARABAEIDAE

*Aequatoria aenigmatica* Soula 2002. Paratypes QCAZI 719 to QCAZI 721. Ecuador,  
Cotopaxi, Las Pampas, May1984, G. Onore. Ref. Soula 2002 [not reviewed].

*Ataenius cristobalensis* Cook & Peck 2000. Paratypes QCAZI 694 and QCAZI 695. Ecu:,  
Galápagos, S. Cristobal, 4 km E Baquerizo, 150 m, trans. z., 12-23.II.89, Fit Peck  
& Sinclair, 89-53. QCAZI 696 and QCAZI 697. Ecu: Galapagos, San Cristobal,  
pampas, 500-700 m, 15-23. II. 1989, S. Peck, general collecting. QCAZI 698. Ecu.,  
Galapagos, S Cristobal, El Junco 1kmE, Miconia Ravine, 14.II.89, siftinglitter, 500  
m, S. Peck 89-61. Ref. Cook & Peck 2000.

*Ataenius floreanae* Cook & Peck 2000. Paratypes QCAZI 699 to QCAZI 701. Ecu.,  
Galapagos, Floreana, 6 km E Black Beach, Scalesia z. cowdung, 360 m, 28. III. 89,  
S. Peck, 89-166. Ref. Cook & Peck 2000.

*Bdelyrus grandis* Cook 1998. Paratype QCAZI 59. Ecuador, Napo, Cuyabeno, IV-1986,  
Legit G. Onore. Ref. Cook 1998.

*Bdelyrus parvulus* Cook 1998. Holotype QCAZI 86. Ecuador, Napo, El Reventador, II  
88, Legit G. Onore. Ref. Cook 1998.

*Bdelyrus pecki* Cook 1998. Paratype QCAZI 85. Ecuador, Napo, Hollin, 1100 m, 7-XII-91,  
F. Caceres. Ref. Cook 1998.

*Bdelyrus triangulus* Cook 1998. Holotype QCAZI 87. Label 1: Ecuador, Napo, Sunka, 29-  
I-89, Legit Sandoval; Label 2: Ex: Hojarasca Bosque Alto. Ref. Cook 1998.

*Callosides genieri* Howden 2001. Paratypes QCAZI 643 and QCAZI 644. Ecuador,  
Carchi, Bosque de Arrayanes, 6.1 km E San Gabriel, 2830 m, 00°32'33"N,  
77°47'26" W, 2.XI.1999-221, R. Anderson arrayan forest litter. Ref. Howden 2001.

*Coprophanaeus morenoi* Arnaud 1982. Paratypes QCAZI 625 \$, QCAZI 626 £, QCAZI  
627 \$ and QCAZI 628 £. Ecuador, (Pich), Tinalandia, I. 1982, 850 m, P & L.  
Arnaud leg. Ref. Arnaud 1982

*Cryptocanthon otonga* Cook 2002. Holotype QCAZI 648. Label 1: Cotopaxi, Ecuador,  
Otonga, 2000 m, 0°25'S, 79°0'W, 4Mar1999, T. Enríquez; Label 2: Ex: Primary

forest Pitfall Trap Human dung. Paratypes 5 paratypes with the same label as QCAZI 648 except for: 24Mar1999; Label 2: Pitfall Trap, all same data Label, types of bait and type of forest. 17 paratypes with the same label as QCAZI 648 except for: 22Mar1999. 7 paratypes with the same label as QCAZI 648 except for: 19Abr1999. 7 paratypes with the same label as QCAZI 648 except for: 16Mar1999. QCAZI 663, QCAZI 676. Label 1: Ecuador, Cotopaxi, Otonga, 2000 m, 0°25'S, 79°0'W, 20 May1999, L. Torres; Label 2: Thubert Primary forest NTP80 Trap Fish. QCAZI 669, QCAZI 674. Ecuador, Cotopaxi, Otonga, 2000 m, 0°25'S, 79°0'W, 23Apr1999, T. Enríquez Primary forest NTP80 Trap Fish. QCAZI 668 with the same labels data as QCAZI 669 except for: 27Aug1999. QCAZI 688. Label 1: Ecuador, Cotopaxi, Otonga, 2000 m, 0°25'S, 79°0'W, 21Apr1999, T. Enríquez; Label 2: Ex: secondary forest NTP80 Trap Fish. Cook 2002.

#### FAMILIA DYNASTIDAE

*Cyclocephala pseudomelanocephala* Dupuis 1996. Paratype QCAZI 729. Ecuador, Pv. Loja, Masanamaca, III-85, Lg. L. Coloma. Ref. Dupuis 1996.

*Neoathyreus brasiliensis* Howden 1985. Paratype QCAZI 647. S. Paulo, Sorocova, Mendes leg. X-35. Ref. Howden 1985.

*Ontherus diabolicus* Génier 1996. Paratypes QCAZI 633 and QCAZI 634. Ecuador, Past., 1100m, Llandia, (17 km N. Puyo), 19.VII.1994, F. Génier, remnant rain for. feces tp. Ref. Génier 1996.

*Ontherus politus* Genier 1996. Paratype QCAZI 635 \$. Ecuador: Napo, 6600, 15km NW Baeza, 2-6. iii. 76, S. Peck cloud forest dung trap 12. Ref. Génier 1996.

*Ontherus pubens* Genier 1996. Paratypes QCAZI 636 and QCAZI 637. Ecuador, Napo Prov., Tena, 400 m., 15-21.II.1986, human feces trap, Francois Génier. Ref. Génier 1996.

*Platycoelia furva* Smith 2003. Holotype QCAZI 705 \$. Ecuador, XII-86, Bolivar, Totoras, Legit: L. Coloma. Paratype QCAZI 706 £. Ecuador, XII/86, Bolivar, Totoras, Legit: L. Coloma. Ref. Smith 2003.

*Platycoelia galerana* Smith 2003. Paratypes QCAZI 707 \$ to QCAZI 715 \$. Ecuador, Napo, Sumaco, 10-20Nov1995, A. Barragán. QCAZI 716 \$. Ecuador, Loja, La Toma, 1800 m, 22May1996, P. Salvador. QCAZI 717 £. Ecuador, Napo, Las Palmas, 1858 m, 78°42'W, 0°33'S, 13Sep1996, M. Vallejo. Ref. Smith 2003.

*Platycoelia hiporum* Smith 2003. Paratype QCAZI 718. Ecuador, Esmeraldas, Cristal, 1500 m, 6Dec1985, Legit: M. Vallejo. Ref. Smith 2003.

*Platycoelia paucarae* Smith 2003. Paratypes QCAZI 702 \$. Ecuador, Pichincha, Tandapi, 1550 m, 3 En1997, D. Guevara. QCAZI 703 \$. Ecuador, Cotopaxi, La Otonga, 2000 M, 10JAN1998, G. Onore. QCAZI 704 \$. Ecuador, Loja, Chinchas/Piñas km7, 1950 m, 17 I 1975, Coll Vénédicoff. Ref. Smith 2003.

*Ptenomela giovannii* Soula 2003 . Paratypes QCAZI 724, QCAZI 726, QCAZI 727. Ecuador, Cotopaxi, La Otonga, 2000 m, Sep1996, I. Tapia. QCAZI 725. Ecuador, Cotopaxi, La Otonga, 2000 m, 79°5'W, 00°27'S, 2May1997, T. Romero. QCAZI

728. Ecuador, Pichincha, P V Maldonado, 760 m, 30Apr 1995, N. Marchán. Ref. Soula 2003 [not reviewed].  
*Scatimus onorei* Genier & Kohlmann 2003. Holotype QCAZI 645. Ecuador, III.90, Loja, Celica, Legit: G. Onore. QCAZI 646 ♂ (Allotype). Ecuador, III.90, Loja, Celica, Legit: G. Onore. Ref. Genier & Kohlmann 2003.

#### FAMILY STAPHILINIDAE

*Apalonia archidonensis* Pace 2008. Paratype QCAZI 1920. Ecuador, Napo, Archidona, S. Domingo, m 680, S 00°57'33.3", W 77°45'11.9", 28-31.VII.2006, P. M. Giachino. Ref. Pace 2008

*Apalonia pampeana* Pace 1997. Paratypes QCAZI 436 to QCAZI 440. Ecuador, Cotopaxi, S. Francisco de Las Pampas, (1300-1500 m), II.1993, L. Bartolozzi (N. Mag. 1406). Ref. Pace 1997.

*Apalonia sigchosensis* Pace 2008. Holotype QCAZI 1960. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi.  
Paratypes QCAZI 1923 and QCAZI 1924 with the same label as the holotype. Ref. Pace 2008

*Apalonia vicina* Pace 2008. Holotype QCAZI 1959. Ecuador, Pichincha La Union del Toachi Otongachi Natural Reserve 21-30.VII.2005 W. Rossi. Paratype QCAZI 1925, with the same label as the holotype. Ref. Pace 2008.

*Atheta altocotopaxicola* Pace 2008. Paratype QCAZI 1927. Ecuador, Cotopaxi, m 3500, Volcan Cotopaxi, El Pedregal, 3.VIII.2006, P.M. Giachino. Ref. Pace 2008

*Atheta annularina* Pace 2008. Holotype QCAZI 1953. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008.

*Atheta cayambensis* Pace 2008. Paratype QCAZI 1867 and QCAZI 1868. Ecuador, Cotopaxi, m 3500, Volcan Cotopaxi, El Pedregal, 3.VII.2006, G. Coaduro. Ref. Pace 2008.

*Atheta cioccai* Pace 2008. Paratype QCAZI 1928. Ecuador, Cotopaxi, Otongachi, m 820, pitfall, 23.VI-2.VII.2006, S. Ciocca leg. Ref. Pace 2008.

*Atheta ecumaculata* Pace 2008. Holotype QCAZI 1954. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008

*Atheta ecucastaneipennis* Pace 2008. Holotype QCAZI 1955. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008

*Atheta hollinensis* Pace 2008. Holotype QCAZI 1952. Ecuador, Napo, Jondachi Loreto rd., Rio Hollin, m 1100, 1.VIII.2005, W. Rossi leg. Ref. Pace 2008.

*Atheta neasuspiciosa* Pace 2008. Paratypes QCAZI 1921. Ecuador, Pichincha, m 3900, Los Ilinizas, La Virgen, S 00°37'45.3", W 78°41'18.6", 6.VIII.2006, G. Coaduro.  
QCAZI 1865. Ecuador, Pichincha, Paschooa, m 3000, S 00°25'19.5", W

78°30'57.9", 26.VII.2006, P.M. Giachino. Ref. Pace 2008.

*Atheta pseudoclaudiensis* Klimaszewski & Peck 1998. Paratypes QCAZI 446 to QCAZI 448. Label 1: Ecu. Galap. St Cruz CDRS, 10 m, 7.III.89; Label 2: old tortoise droppings & hay, S. Peck 89-36. QCAZI 449 and QCAZI 450. Label 1: Ecu. Galap. San Cristobal, 600 m, El Junco, pampas; Label 2: horsemanure, 14.II.89 S. Peck 89-60. QCAZI 451. Label 1: Ecu., Galap., Floreana, 6 km E Black Beach; Label 2: 28. III.89, 89-166 S. Peck, Scalesia z. cowdung, 360 m. QCAZI 452 and QCAZI 453. Label 1: Ecu. Galap. Floreana, 8 km E Black Beach; Label 2: Peck & Sinclair, 360m, 22-28. III.89, 89-147 Scalesia, FIT. QCAZI 454. Ecu., Galap., Isabela, 9kmNE Tagus Cove, 1100 m, V. Darwin, 18-20.V.92, arid zone, dung traps, S. Peck 92-192. Ref. Klimaszewski & Peck 1998.

*Atheta toachiensis* Pace 2008. Holotype QCAZI 1951. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 21-30.VII.2005, W. Rossi. Ref. Pace 2008.

*Cajachara carltoni* Ashe & Leschen 1995. Paratypes QCAZI 442, QCAZI 443. Label 1: Ecuador, Azuay, Reserva Río Mazán, 25 km NW Cuenca, Lago Toreadora, 3800 m; Label 2: 31DEC1991, C. Carlton R. Leschen, #81 ex: Polylepis berlasale. Ref. Ashe & Leschen 1995.

*Diestota simplex* Pace 2008. Holotype QCAZI 1946. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008.

*Falagria ecuapallida* Pace 2008. Holotype QCAZI 1947. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005 W. Rossi. Ref. Pace 2008.

*Gyrophaena cotopaxiensis* Pace 1996. Paratype QCAZI 455. Ecuador: Cotopaxi prov., dint. di S. Francisco de Las Pampas, (1300 -1500 m), II.1993 (num. Mag.1406), legit L. Bartolozzi. Ref. Pace 1996.

*Gyrophaena otongensis* Pace 2008. Holotype QCAZI 1939. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008.

*Gyrophaena rossii* Pace 2008. Holotype QCAZI 1938 Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Paratypes QCAZI 1843- QCAZI 1853, QCAZI 1900-1905. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008.

*Gyrophaena spatulata* Pace 1996. Paratype QCAZI 456. Ecuador: Cotopaxi prov., dint. di S. Francisco de Las Pampas, (1300 -1500 m), II.1993 (num. Mag.1406) legit L. Bartolozzi. Ref. Pace 1996.

*Heterostiba rossii* Pace 2008. Paratypes QCAZI 1919. Label 1: Ecuador, Tungurahua, Volcán Chimborazo, m 4058, S 01°22'20.3", W 78°49'06.2", 5.VIII.2006, G. Coaduro Label 2: Laboulbeniales n 2977 Walter Rossi. QCAZI 1926. Ecuador, Pichincha, m 3900, Los Ilinizas, La Virgen, S 00°37'45.3", W 78°41'18.6", 6.VIII.2006, G. Coaduro. Ref. Pace 2008.

*Homalota cotopaxiensis* Pace 2008. Holotype QCAZI 1940. Ecuador, Cotopaxi, Cantón

Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref.  
Pace 2008.

*Leptandria ecitophila* Hanley, 2003. Paratype QCAZI 445 \$. Label 1: Ecuador: Napo, mid.  
Río Tiputini, Yasuni res. Stn. 0°40.5'S, 76°24'W, 22July 1999, AKT#091; Label 2:  
*Ectiton burchelli* colony EC#21. Nomadic bivouac site just after emigration A.  
Tishechkin. Ref. Hanley 2003.

*Leptandria tishechkini* Hanley, 2003. Paratype QCAZI 444 \$. Label 1: Ecuador, Napo,  
mid. Río Tiputini, Yasuni res. Stn. 0°40.5'S, 76°24'W, 26July 1999, AKT#111;  
Label 2: *Ectiton hamatum* colony EC #28. Total bivouac sampling. A. Tishechkin.  
Ref. Hanley 2003.

*Meronera ecuadorica* Pace 2008. Holotype QCAZI 1948. Label 1: Ecuador, Cotopaxi,  
Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 7-10.VII.2006, W. Rossi;  
Label 2: Laboulbeniales n 2979 Walter Rossi. Ref. Pace 2008.

*Meronera otongicola* Pace 2008. Holotype QCAZI 1956. Ecuador, Cotopaxi, Cantón  
Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Ross. Paratype  
QCAZI 1936, with the same label as the holotype. Ref. Pace 2008.

*Myllaena pichinchaensis* Pace 2008. Paratype QCAZI 1837. Ecuador, Cotopaxi, Cantón  
Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref.  
Pace 2008.

*Orphnebius curticornis* Pace 2008. Holotype QCAZI 1958. Label 1: Ecuador, Cotopaxi,  
Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi.  
Ref. Pace 2008.

*Orphnebius ecuadorensis* Pace 1997. Paratypes QCAZI 457 and QCAZI 458. Ecuador,  
Manabí dint., Puerto Cayo, 21.II.1993, L. Bartolozzi alle luci (N. Mag. 1406). Ref.  
Pace 1997.

*Orphnebius otongensis* Pace 2008. Holotype QCAZI 1957. Ecuador, Pichincha, La Union  
del Toachi Otongachi, Natural Reserve, 21-30.VII.2005, W. Rossi. Paratype  
QCAZI 1922 with the same label as the holotype. Ref. Pace 2008.

*Paraplandria caraorum* Pace 2008. Holotype QCAZI 1950. Ecuador, Cotopaxi, Cantón  
Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi.  
Paratypes QCAZI 1934 and QCAZI 1935 with the same label as the holotype. Ref.  
Pace 2008.

*Paraplandria ecuadoricola* Pace 2008. Holotype QCAZI 1962. Ecuador, Napo, Jondachi  
Loreto rd., Rio Hollin, m 1100, 1.VIII.2005, W. Rossi leg. Pace 2008.

*Parasilusa otongensis* Pace 2008. Holotype QCAZI 1941. Ecuador, Cotopaxi, Cantón  
Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref.  
Pace 2008.

*Plesiomalota giachinoi* Pace 2008. Paratype QCAZI 1861. Ecuador, Pichincha, Lloa, Rio  
Blanco, m 2650, (under bark), 1.VIII.2006, P.M. Giachino. Ref. Pace 2008.

*Plesiomalota paschoensis* Pace 2008. Paratypes QCAZI 1862-QCAZI 1864. Ecuador, Pichincha, Paschoa, m 3000, S 00°25'19.5", W 78°30'57.9", 26.VII.2006, G. Caoduro. Ref. Pace 2008.

*Plesiomalota ruficollis* Pace 2008. Holotype QCAZI 1942. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008.

*Plesiomalota ruficornis* Pace 2008. Holotype QCAZI 1943. Label 1: Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi; Label 2: HOLOTYPE *Plesiomalota ruficornis* mihi det. R. Pace 2007. Ref. Pace 2008.

*Plesiomalota squalida* Pace 2008. Holotype QCAZI 1943. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Ref. Pace 2008.

*Plesiomalota varicornis* Pace 2008. Holotype QCAZI 1944. Ecuador, Pichincha, La Union del Toachi, Otongachi Natural Reserve, 21-30.VII.2005, W. Rossi. Paratype QCAZI 1860, with the same label as the holotype. Ref. Pace 2008.

*Pseudoleptonia ecuadorica* Pace 2008. Holotype QCAZI 1949. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Paratype QCAZI 1866, with the same label as the holotype. Ref. Pace 2008.

*Pseudomniophila cotopaxiensis* Pace 2008. Holotype QCAZI 1937. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Paratypes QCAZI 1854- QCAZI 1859. Ecuador, Pichincha, La Union del Toachi, Otongachi Natural Reserve, 21-30.VII.2005, W. Rossi. Ref. Pace 2008.

*Pseudomyllaena ecuadorensis* Pace 2008. Holotype QCAZI 1961. Ecuador, Cotopaxi, Cantón Sigchos, Las Pampas, Otonga Natural Reserve, 25-28.VII.2005, W. Rossi. Paratypes QCAZI 1907 and QCAZI 1913, with the same label as the holotype. Ref. Pace 2008.

#### FAMILY TENEBRIONIDAE

*Opatriinus ecuadorensis* Iwan 1995. Paratypes QCAZI 611. Label 1: Pichilingue, Ecuador 16.XI.1977; Label 2: Black light 79.443. QCAZI 612. Ecuador, Los Ríos, Quevedo, VII.1977, Iwan 1995.

#### ORDER DIPTERA

#### FAMILIA DROSOPHILIDAE

*Drosophila amaguana* Vela & Rafael 2004. Holotype QCAZI 1665 \$. Ecuador, Pichincha, Volcán Paschoa, Jul 1996, D. Vela col. Paratypes QCAZI 1666 \$ and QCAZI 1667 \$. Ecuador, Pichincha, Volcán Paschoa, Jul 1997, D. Vela col. Ref. Vela & Rafael 2004.

*Drosophila apag* Vela & Rafael 2005. Holotype QCAZI 1756 \$. Ecuador, Pichincha, Volcán Paschoa, Jul 1996, D. Vela col. Ref. Vela & Rafael 2005.

*Drosophila arcosae* Vela & Rafael 2001. Holotype QCAZI 1686 \$. Ecuador, Pichincha, Volcán Paschoa, Ago1996, DVela col. Ref. Vela & Rafael 2001.

*Drosophila asiri* Vela & Rafael 2005. Holotype QCAZI 1704 \$. Ecuador, Pichincha, Volcán Paschoa, Jun 1996, DVela col. Paratype QCAZI 1705 \$. Ecuador, Pichincha, Volcán Paschoa, 20Oct 2001, DVela col. Ref. Vela & Rafael 2005.

*Drosophila carlosvilelai* Vela & Rafael 2001. Holotype QCAZI 1629 \$. Ecuador, Pichincha, Volcán Paschoa, 3200 m, LW 78°29', LS 0°28', 30Ago1996, DVela. Paratypes \$: 3 paratypes with the same label as holotype except for: Jun 1997 DVela col. 3 paratypes with the same label dat as holotype except for: Jul 1997. 11 paratypes with the same label as the holotype except for: Jul 1996. 4 paratypes with the same label as the holotype except for: Ago 1996. QCAZI 1651 with the same label as the holotype except for: Jun 1997. Ref. Vela & Rafael 2001.

*Drosophila condormachay* Vela & Rafael 2005. Holotype QCAZI 1739 \$. Ecuador, Pichincha, Paschoa, 16Jun2001, V. Rafael, DVela. Paratypes \$: QCAZI 1740 with the same label as the holotype except for: 18Ago2001. 2 paratypes with the same label as the holotype except for: 29Sep2001. QCAZI 1743 with the same label as the holotype except for: 28Oct2001. QCAZI 1744 with the same label as the holotype except for: 20Oct2001. Ref. Vela & Rafael 2005.

*Drosophila cuscungu* Vela & Rafael 2005. Holotype QCAZI 1774 \$. Ecuador, Pichincha, Paschoa, 16Jun2001, V. Rafael, D. Vela. Ref. Vela & Rafael 2005.

*Drosophila ecuatoriana* Vela & Rafael 2004. Holotype QCAZI 1609 \$. Ecuador, Pichincha, Volcán Paschoa, 16Jul1996, D. Vela. Paratypes 5 paratypes with the same label as the holotype except for: Jul 1996. 4 paratypes with the same label as the holotype except for: Jul 1997. 3 partypes with the same label as the holotype except for: Ago1996. Ref. Vela & Rafael 2004.

*Drosophila fontdevilai* Vela & Rafael 2001. Holotype QCAZI 1655 \$. Ecuador, Pichincha, Paschoa, 3200 m, LW 78°29', LS 0°28', 30Jul1996, DVela. Paratypes \$: QCAZI 1656 to QCAZI 1663. Ecuador, Pichincha, Volcán Paschoa, Jul 1996, DVela col. Ref. Vela & Rafael 2001.

*Drosophila guayllabambae* Rafael & Arcos 1988. Holotype QCAZI 1775 \$. Label 1: Ex: Isolínea 1P. N° 1; Label 2: Ecuador, Pichincha, Guayllabamba, Estación 1; Label 3: 30 Km. Al NE de Quito, margen derecha del Río Guayllabamba, 2200 m.s.n.m.; Label 4: VII/86, Leg: G. Arcos & V. Rafael. Paratypes 9\$ paratypes and 9 £ with the same labels data as the holotype. Ref. Rafael & Arcos 1989.

*Drosophila huancavilcae* Rafael & Arcos 1989. Holotype QCAZI 1760. Ecuador, Guayas, Progreso, NO de Guayaquil, 300 m.s.n.m., XI/86, Leg: G. Arcos y M. Rivera. Paratype QCAZI 1761 (Allotype) with the same label as the holotype. Ref. Rafael & Arcos 1989.

*Drosophila ichubamba* Vela & Rafael 2005. Holotype QCAZI 1735 \$. Ecuador, Pichincha, Volcán Paschoa, DVela col. 5May. 2001. Paratypes QCAZI 1736 with the same label as the holotype. QCAZI 1737 and QCAZI 1738 with the same label as the holotype except for: 01Abr2002. Ref. Vela & Rafael 2005.

*Drosophila korefae* Vela & Rafael 2004. Holotype QCAZI 1717 \$. Ecuador, Pichincha, Volcán Paschoa, D. Vela col., Jun. 1996. Paratypes 2 paratypes with the same label as the holotype. Ref. Vela & Rafael 2004.

*Drosophila machachensis* Vela & Rafael 2001. Holotype QCAZI 1652. Ecuador, Pichincha, Volcán Paschoa, DVela col., Ago1996. Paratypes \$: 2 paratypes with the same label as the holotype except for: Jul1996. Ref. Vela & Rafael 2001.

*Drosophila ninarumi* Vela & Rafael 2005. Holotype QCAZI 1765 \$. Ecuador, Pichincha, Volcán Paschoa, D. Vela col., Abr. 2001. Paratypes \$: QCAZI 1766 with the same label as holotype except for: 16Jun2001. QCAZI 1767 with the same label as holotype except for: 14Jull2001. QCAZI 1768 with the same label as holotype except for: 26Jan2002. 2 paratypes with the same label as the holotype except for: 02Feb2002. Ref. Vela & Rafael 2005.

*Drosophila ogradi* Vela & Rafael 2004. Holotype QCAZI 1719 \$. Ecuador, Pichincha, Paschoa, DVela col., Jun. 1996. Paratypes \$: 6 paratypes with the same label as the holotype except for: Ago96; 2 paratypes with the same label as the holotype except for: Jul96. 3 paratypes with the same label as the holotype except for: Jul1997. 4 paratypes with the same label as the holotype except for: Jun1997. Ref. Vela & Rafael 2004.

*Drosophila paschoensis* Vela & Rafael 2001. Holotype QCAZI 1626 \$. Ecuador, Pichincha, Volcán Paschoa, DVela 07Jul97. Paratypes \$: 13 paratypes with the same label as the holotype. 7 paratypes with the same label as the holotype except for: Jul1996. 9 paratypes with the same label as the holotype except for: Ago1997. Ref. Vela & Rafael 2001.

*Drosophila patacornia* Vela & Rafael 2005. Holotype \$: QCAZI 1694. Ecuador, Pichincha, Volcán Paschoa, D. Vela col., Mar. 2001. Paratype \$: QCAZI 1695 with the same label as the holotype except for: 04Abr 2001. Ref. Vela & Rafael 2005.

*Drosophila pichinchana* Vela & Rafael 2004. Holotype \$: QCAZI 1622. Ecuador, Pichincha, Volcán Paschoa, DVela col., Jul. 1996. Paratype \$: QCAZI 1623 with the same label as the holotype. Ref. Vela & Rafael 2004.

*Drosophila pilaresae* Vela & Rafael 2001. Paratypes \$: QCAZI 1687 to QCAZI 1689. Ecuador, Pichincha, Volcán Paschoa, Jul1997. Ref. Vela & Rafael 2001.

*Drosophila pugyu* Vela & Rafael 2005. Holotype \$: QCAZI 1764. Ecuador, Pichincha, Volcán Paschoa, 17Oct2001, DVela col. Ref. Vela & Rafael 2005.

*Drosophila quillu* Vela & Rafael 2005. Holotype \$: QCAZI 1706. Ecuador, Pichincha, Paschoa, Mar2001, DVela col. Paratypes \$: QCAZI 1707 with the same label as the holotype except for: 30Jun2001. QCAZI 1708 with the same label as holotype except for: 04Abr2001. 8 paratypes with the same label as the holotype except for: 01Abr2002. 2 paratypes with the same label as the holotype except for: 14Jul2001. Ref. Vela & Rafael 2005.

*Drosophila quitensis* Vela & Rafael 2004. Holotype \$: QCAZI 1624. Ecuador, Pichincha, Volcán Paschoa, Jul 1996, D. Vela col. Paratype \$: QCAZI 1625 with the same label as the holotype except for: Ago1996. Ref. Vela & Rafael 2004.

*Drosophila ruminahuii* Vela & Rafael 2004. Holotype \$: QCAZI 1690. Ecuador,  
Pichincha, Volcán Pasocha, Jul. 1997, DVela col. Ref. Vela & Rafael 2004.

*Drosophila rumipamba* Vela & Rafael 2005. Holotype \$: QCAZI 1703. Ecuador,  
Pichincha, Volcán Pasocha, Jul. 1996, DVela. Ref. Vela & Rafael 2005.

*Drosophila rundoloma* Vela & Rafael 2005. Holotype \$: QCAZI 1699. Ecuador,  
Pichincha, Volcán Pasocha, Jun. 1997, DVela col. Paratypes \$: 3 paratypes with the  
same label as the holotype except for: Jul 1996. Ref. Vela & Rafael 2005.

*Drosophila shuyu* Vela & Rafael 2005. Holotype \$: QCAZI 1696. Ecuador, Pichincha,  
Volcán Pasocha, 30Jun 2001, DVela col. Paratypes \$: QCAZI 1697 with the same  
label as the holotype except for: 10Nov2001; QCAZI 1698 with the same label as  
the holotype except for: 01Abr2002. Ref. Vela & Rafael 2005.

*Drosophila shyri* Vela & Rafael 2004. Holotype \$: QCAZI 1664. Ecuador, Pichincha,  
Volcán Pasocha, 23Jul1996, DVela col. Ref. Vela & Rafael 2004.

*Drosophila sisa* Vela & Rafael 2005. Holotype \$: QCAZI 1772. Ecuador, Pichincha,  
Volcán Pasocha, 01Abr2002, DVela col. Paratype \$: QCAZI 1773 with the same  
label as the holotype. Ref. Vela & Rafael 2005.

*Drosophila suni* Vela & Rafael 2005. Holotype \$: QCAZI 1771. Ecuador, Pichincha,  
Volcán Pasocha, Mar2001, DVela col. Ref. Vela & Rafael 2005.

*Drosophila surucucho* Vela & Rafael 2005. Holotype \$: QCAZI 1747. Ecuador, Pichincha,  
Volcán Pasocha, 21Abr2001, DVela col. Paratypes \$: 2 paratypes with the same  
label as the holotype except for: 04Abr2001. 2 paratypes with the same label as the  
holotype except for: 05May2001. QCAZI 1752 with the same label as the holotype  
except for: 16Jun 2001. QCAZI 1753 with the same label as the holotype except  
for: 09Jun 2001; QCAZI 1754 with the same label as the holotype except for:  
14Jul2001; 2 paratypes with the same label as the holotype except for: 16Jul2001.  
Ref. Vela & Rafael 2005.

*Drosophila taxohuaycu* Vela & Rafael 2005. Holotype \$: QCAZI 1745. Ecuador,  
Pichincha, Volcán Pasocha, Mar2001, DVela col. Paratype \$: QCAZI 1746 with  
the same label as the holotype except for: 05May2001. Ref. Vela & Rafael 2005.

*Drosophila tomasi* Vela & Rafael 2001. Holotype \$: QCAZI 1668. Ecuador, Pichincha,  
Volcán Pasocha, Jul1997, DVela col. Paratypes \$: 5 paratypes with the same label  
as the holotype except for: Ago 1997; 10 paratypes with the same label as the  
holotype except for: Jul1997. Ref. Vela & Rafael 2001.

*Drosophila urcu* Vela & Rafael 2005. Holotype \$: QCAZI 1755. Ecuador, Pichincha,  
Volcán Pasocha, 01Abr2002, DVela col. Ref. Vela & Rafael 2005.

*Drosophila valenciae* Vela & Rafael 2001. Holotype \$: QCAZI 1684. Ecuador, Pichincha,  
Volcán Pasocha, Jul1996, DVela col. Paratype \$: QCAZI 1685 with the same  
label as the holotype except for: Jul1997. Ref. Vela & Rafael 2001.

*Drosophila yana* Vela & Rafael 2005. Holotype \$: QCAZI 1691. Ecuador, Pichincha,  
Volcán Pasocha, Mar 2001, DVela col. Paratypes \$: QCAZI 1692 with the same

label as the holotype except for: 05May2001. QCAZI 1693 with the same label as the holotype except for: 10Nov2001. Ref. Vela & Rafael 2005.

*Drosophila yangana* Rafael & Vela 2003. Holotype \$: QCAZI 1757. Ecuador, Loja, Yangana, 1800 m, LW $79^{\circ}10'28''$ , LS  $4^{\circ}21'24''$ , D. Vela col., Sep. 2001. Paratypes £: 2 paratypes with the same label as the holotype. Ref. Vela & Rafael 2005.

#### FAMILY PHORIDAE

*Apocephalus aenylus* Brown 1997. Paratype QCAZI 1362 £. Ecuador, Napo, Jatun Sacha,  $1.07^{\circ}$ S,  $77.6^{\circ}$ W, 17.ix.1996, J. Röschard, raid *Eciton burchelli*. Ref. Brown 1997.

*Apocephalus asyndetus* Brown 2000. Paratype QCAZI 1368. Ecuador, Sucumbíos, Sacha Lodge,  $0.5^{\circ}$ S,  $76.5^{\circ}$ W, 24.v-3.vi.1994, P. Hibbs MT., 270 m. Ref. Brown 2000.

*Apocephalus catholicus* Brown 2000. Paratypes QCAZI 1373 £. Ecuador, Esmeraldas, Bilsa Biol. Stn., 500 m,  $0.34^{\circ}$  N,  $79.71^{\circ}$  W, 8.v.1996, B. Brown. Inj. *Pachycondyla impressa*. 3 paratypes with the same label as QCAZI 1373. 2 paratypes with the same label as QCAZI 1373 except for: Injured *Odontomachus bauri*. Ref. Brown 2000.

*Apocephalus comosus* Brown 2000. Paratype QCAZI 1369 £. Ecuador, Sucumbios, Sacha Lodge,  $0.5^{\circ}$ S,  $76.5^{\circ}$ W, 3-13.vi.1994, P. Hibbs. Malaise. 270m. Ref. Brown 2000.

*Apocephalus extraneus* Brown 1997. Paratypes QCAZI 1359. Ecuador, Sucumbios, Sacha Lodge,  $0.5^{\circ}$ S,  $76.5^{\circ}$ W, 23.iv.3.v.1994, P. Hibbs. MT. 270 m. QCAZI 1360. Ecuador, Sucumbios, Sacha Lodge,  $0.5^{\circ}$ S,  $76.5^{\circ}$ W, 14-24.v.1994, P. Hibbs. MT. 270 m. Ref. Brown 1997.

*Apocephalus funditus* Brown 2000. Paratype QCAZI 1370. Ecuador, Sucumbios, Sacha Lodge,  $0.5^{\circ}$ S,  $76.5^{\circ}$ W, 12-22.ii.1994, P. Hibbs, Malaise, 270 m. Ref. Brown 2000.

*Apocephalus melinus* Brown 2000. Paratypes QCAZI 1366 and QCAZI 1367. Ecuador, Napo, Yasuní Bio.Res.Stn.,  $0.67^{\circ}$ S,  $76.36^{\circ}$ W, 20.v.1996, B. V. Brown, inj. *Dolichoderus attelaboides*. Ref. Brown 2000.

*Apocephalus onorei* Brown 1997. Paratype £: QCAZI 1363. Ecuador, Napo, Yasuní Bio. Stn.,  $0.67^{\circ}$ S,  $76.39^{\circ}$ W, 24.v.1996, B. V. Brown. 220 m, over *Acromymex* sp. Ref. Brown 1997.

*Apocephalus quadratus* Brown 1997. Paratype £: QCAZI 1364. Ecuador, Sucumbíos, Sacha Lodge,  $0.5^{\circ}$ s,  $76.5^{\circ}$ W, 23.iv-3.v.1994, P. Hibbs. MT. 270m. Ref. Brown 1997.

*Apocephalus roeschardae* Brown 2000. Paratype QCAZI 1365 £. Ecuador, Napo, Yasuní Bio.Res.Stn.,  $0.67^{\circ}$ S,  $76.36^{\circ}$ W, 22.v.1996, B. V. Brown, 220 m, inj. *Cephalotes atratus*. Ref. Brown 2000.

*Apocephalus securis* Brown 1997. Paratype QCAZI 1361. Ecuador, Pichincha, 17 km E Sto Domingo, Tinalandia, 6-13.v.1987, B.V. Brown, 710 m. Clubhouse windows. Ref. Brown 1997.

*Apocephalus tanyurus* Brown 2000. Paratype QCAZI 1372 ♀. Ecuador, Sucumbios, Sacha Lodge, 0.5°S, 76.5°W, 10-21.x.1994, P. Hibbs, Malaise. 270 m. Ref. Brown 2000.

*Apocephalus torulus* Brown 2000. Paratype QCAZI 1371 ♀. Ecuador, Esmeraldas, Bilsa Biol. Stn., 0.34°N, 79.71° W, 8.v.1996, Brown. Hibbs. Cantley raid *Labidus praedator*. Ref. Brown 2000.

*Apocephalus trifidus* Brown 2000. Paratype QCAZI 1762. Ecuador, Napo, Yasuní Bio. Rest. Stn., 0.67°S, 76.39°W, 24.v.1996, B. V. Brown. Injured *Pachycondyla crassinoda*. Ref. Brown 2000.

#### FAMILY SPHAEROERCIDAE

*Druciatus tricetus* Marshall 1995. Paratypes QCAZI 1346. Ecu., Napo, Tena, 500 m, malaise 2' rainfor. 21-27.v.87, ROM870017 Coote & Brown. QCAZI 1347 \$. Ecu., Pinch. Prov., Rio Palenque Stn., 47 kmS. Sto. Domingo, 29.iv.1987, L. Coote & B. Brown, 180 m, mal. head 1\*lowlandrainfor. Ref. Marshall 1995.

*Opacifrons triloba* Marshall & Langstaff 1998. Paratype QCAZI 1353. Ecu., Pich., 16 km E Santo Domingo, Tinalandia, 4.v.25.vii.85, S & J Peck, 680 m, rainfor.malaise-FIT. Ref. Marshall & Langstaff 1998.

*Opacifrons redundans* Marshall & Langstaff 1998. Paratype QCAZI 1354. Ecu., Napo Prov., Baeza, 18.v.87, L.D. Coote, scr.sweep wet montane, 1500-1700 m, ROM 870013 Forest/Pasture. Ref. Marshall & Langstaff 1998.

*Palaeocoprina equiseta* Marshall 1998. Paratypes QCAZI 1350 and QCAZI 1351. Ecu., Napo, 27 km NW Baeza, 2-6.III.1976, 2700 m., DgTp, S. Peck. Ref. Marshall 1998.

*Phthitia merida* Marshall 1992. Paratypes QCAZI 1348. Ecu., Napo, Prov., Quito- Baeza Rd., above thermal spgs., Papallacta, 3200 m, 22-24.ii.1983, L. Masner. Pan trap. QCAZI 1349. Ecu., Napo, Prov. Quito- Baeza Rd., 4000 m, 18-23.ii.1983, L. Masner. Pan trap in low paramo. Ref. Marshall & Smith 1992

*Rachispoda justini* Wheeler 1995. Paratypes QCAZI 1355 and QCAZI 1356. Ecu., Pich., 16 km E Santo Domingo, Tinalandia, 4.v.85, S&J Peck, 680 m, rainfor. Malaise-FIT. Ref. Wheeler & Marshall 1995.

*Rachispoda praealta* Wheeler 1995. Paratypes QCAZI 1357 and QCAZI 1358. Ecu.; Napo, 4000m, Quito- Baeza, Pass ElfinFor, dungtrap, S. Marshall, 11.iii'79. Ref. Wheeler & Marshall 1995.

#### ORDER HEMIPTERA

#### FAMILY COREIDAE

*Anasa scitula* Brailovsky & Barrera 2000. Holotype \$: QCAZI 1410. Ecuador, Napo, Vía Hollin-Loreto, Km 30, 1100 m, 6/12/87, Lg. A. Rodríguez. 2 paratypes with the same label as the holotype except for: R. Boada. Ref. Brailovsky & Barrera 2000.

*Salapia onorei* Brailovsky 1999. Holotype ♀: QCAZI 1407. Ecuador, Sucumbios, San

Pablo, Río Aguarico, Oct1995, FNischk. Ref. Brailovsky 1999.

*Sephina faceta* Brailovsky 2001. Paratype \$: QCAZI 1408. Ecuador, Napo, Reventador, I-1988, V- Nivel. B. P. Ref. Brailovsky 2001.

#### FAMILIA GERRIDAE

*Potamobates shuar* Buzzetti 2006. Paratypes \$: QCAZI 1606 and QCAZI 1607. Ecuador, Morona Zantiago, Bomboiza, 800 m, 22-III-2004, Carotti & Tirello. Ref. Buzzetti 2006.

#### FAMILIA MIRIDAE

*Anomalocornis peyreti* Couturier & Costa 2002. Paratypes QCAZI 1413 to QCAZI 1434.  
Label 1: Equateur, Pastaza, Chunitayo, 5-XI-2000, T. Peyret col.; Label 2:  
s/inflorescence de *Oenocarpus bataua* Arecaceae. Ref. Couturier & Costa 2002

*Parafulvius henryi* Costa & Couturier 2000. Paratypes QCAZI 1435 \$, QCAZI 1436 \$,  
QCAZ 1437 £, QCAZI 1438 £. Label 1: Equateur, Shushufini, 10-X-1999, L.  
Reynaud & Suarez col.; Label 2: sur *Astrocaryum urostachys* Palmae. Ref. Costa &  
Couturier 2000.

#### FAMILIA PENTATOMIDAE

*Thyanta xerotica* Rider & Chapin 1991. Paratypes QCAZI 1440 to QCAZI 1442. Ecuador,  
Manabí, San Clemente, XII-84, Legit: F. Cuesta. Ref. Rider & Chapin 1991

#### ORDER HOMOPTERA

##### FAMILY MEMBRACIDAE

*Metcalfiella jaramillorum* McKamey 1991. Paratype QCAZI 1404. Label 1: Cuenca, 2400  
m, 2Jan 1986, McKamey. Coll.; Label 2: Ecuador, Azuay, Challuabamba, 11rd km  
NE. Ref. McKamey 1991

*Metcalfiella nigrihumera* McKamey 1991. Paratype QCAZI 1403. Label 1: Ecuador,  
Azuay, Challuabamba, 11rd km NE; Label 2: Cuenca, 2400 m, 3Jan1986,  
McKamey, Coll. Ref. McKamey 1991.

#### ORDER HYMENOPTERA

##### FAMILY APIDAE

*Euglossa lugubris* Roubick 2004. Paratype QCAZI 754. Label 1: Perú, LO, Maynas, Peña  
Negra, km 10 (Purma), 5-7-01, Rasmussen; Label 2: Eugenol. Ref. Roubick 2004.

*Euglossa occidentalis* Roubick 2004. Holotype QCAZI 1268. Ecuador, Napo  
Dept., Yasuní National Park, 13-27 April 1998, D. Roubick; coll. No 33. Paratypes  
12 paratypes with different collection number and the following label: Ecuador,  
Fco. de Orellana Prov., Parque Nacional Yasuní, sept. 2001, E. Báus, D. Roubick  
coll. #91. 3 paratypes with different collection number and with the same label as  
the holotype. 16 paratypes with different collecting number and the following label:

Ecuador, Orellana, PUCE SCYasuní, 250 m, 76°24'19" W, 00°40'32 S, 18-23Feb2001, D. Roubick & E. Báus. QCAZI 1276. Ecuador, Fco. De Orellana Prov., Parque Nacional Yasuní, nov. 1998, E. Báus, D. Roubick. QCAZI 1277. Ecuador, Napo, Tena, Shushufindi, Yasuni, 500 m, 76°30'W, 00°38' S, 3Aug1999, F. Palomeque. TRAP EUCALIPTOL. 2 paratypes with the following label: Ecuador, Fco. De Orellana, Loreto, Cotapino, 640 m, 22May1999, F. Palomeque. QCAZI 1285. Ecuador, Napo, Talag, 600 m, W77°54', S01°03', 12Jun99, H. Zumárraga. 2 paratypes with different coll. Number and the following label: Ecuador, Fco. De Orellana Prov., Parque Nacional Yasuní, dic. 2001, E. Báus, D. Roubick. 17 paratypes with different coll. Number and the following label: Ecuador, Fco. De Orellana Prov. ,Parque Nacional Yasuní, dic. 2002, E. Báus, D. Roubick. QCAZI 1321. Ecuador, Orellana, E.C. Yasuní, 250 m, 00°40'S, 76°23'W 20Nov1999, L. Torres. Ref. Roubick 2004.

*Euglossa orellana* Roubick 2004. Holotype QCAZI 980. Ecuador, Napo Depto, Yasuní National Park, 13-27April1998, D. Roubick; baits; #29. Paratypes 132 paratypes with the same label as the holotype and with different collection number. 7 paratypes with the following label: Ecuador, Napo, Tena, Shushufindi, Yasuni, 500 m, 76°30' W, 00°38'S, 03Aug1999, F. Palomeque. Trap eucaliptol. QCAZI 764. Ecuador, Napo, Tena, Misahualli, Jatun Sacha, 550 m, 77°30'W, 01°03'S, 23Oct1999, P. Carrera. Trap salicilato de metilo. 5 paratypes with the following label: Ecuador, Napo, E.C. Yasuní, 250 m, LW78°58', LS00 56, 22.Apr.1998, F. Palomeque. 2 paratypes with the following label: Ecuador, Napo, Loreto, 9Aug1991, D. Roubick. 189 paratypes with the following label: Ecuador, Orellana, PUCE SCYasuní, 250 m, 76°24'19" W, 00°40'32 S, 18-23Feb2001, D. Roubick & E. Baus. QCAZI 889. Ecuador, Pichin-Napo, Taracoa, S. Abedravo, 18-V-84. 2 paratypes with the following label: Ecuador, Napo, Yuturi Lodge, Río Napo, 0°32'54"S, 76°2'18" W, 270 m, 20Mar1999, R. Brooks, ECU1B99 009 ex: attracted to methyl salicylate. 108 paratypes with the following label: Ecuador, Fco. de Orellana Prov., Parque Nacional Yasuní, dic2002, E. Baus, D. Roubick, coll. #100. 49 paratypes with the following label: Ecuador, Fco. de Orellana Prov., Parque Nacional Yasuní, sep2001, E. Baus, D. Roubick coll. #84. 47 paratypes with the following label: Ecuador, Fco. de Orellana, Yasuní Nat Park, Catholic Univ. Station, Aug 7-17 2004, D. Roubick, coll#113. QCAZI 979. ECUADOR: Napo, Yuturi Lodge, Río Napo, 0°32'54"S, 76°2'18"W, 270 m, 20 MAR1999, R. Brooks, ECU1889 009 ex: attracted to methyl salicylate. Comments: QCAZI 889 \$ and QCAZI 979 \$ labeled as *Euglossa chalybeata* Friese by. R. W. Brooks. Ref. Roubick 2004.

*Euglossa samperi* Ramirez 2006. Holotype QCAZI 1825. SR1906, Apr.8.2005, Bilsa, Naranja trail, 1100, Esmeraldas, Ecuador, 00°21'N, 79° 44'W, 500m, Cineole, Leg S. Ramirez. Ref. Ramirez 2006.

*Euglossa tiputini* Roubick 2004. Paratypes QCAZI 756 \$. Hacienda Ila, Napo, Ecuador, D. Velastegui, Cineole, 12-26-68. QCAZI 757. Ecuador, Napo, Talag, 28Dic1993, 400 m, O. Torres. Ref. Roubick 2004.

*Eulaema napensis* Oliveira 2006. Holotype \$: QCAZI 755. Ecuador, Napo, Jumandi, II/86, Legit: D. Sánchez. Ref. Oliveira 2006. Described under subgenus *Eulaema*.

*Paratrígona onorei* Camargo & Moure 1994. Paratype QCAZI 1325. Ecuador, Napo,

Cosanga, II/ 86, Legit: L. Coloma. Ref. Camargo & Moure 1994.

#### FAMILY DIAPRIIDAE

*Mimopria campbellorum* Masner 1976. Paratype ♀: QCAZI 1599. BRAZIL, Belem, Para, IPEAN, III-23-1970, JM & BA Campbell. Host: *Ecton Hamatum* (Fabr.). Ref. Masner 1976.

#### FAMILY FORMICIDAE

*Leptanilloides nomada* Donoso, Vieira & Wild 2006. Holotype QCAZI 1342. Ecuador, Cotopaxi, Otonga, 1960 m, 79°0.197' W, 0°25.158S, 02Dec2003, Wild & Vieira. Paratype QCAZI 1343. Ecuador, Cotopaxi, Otonga, 1960 m, 79°0.197' W, 0°25.158S, 02Dec2003, Wild & Vieira. Ref. Donoso *et al.* 2006.

*Leptanilloides nubecula* Donoso, Vieira & Wild 2006. Holotype QCAZI 1341. Ecuador, Cotopaxi, Otonga, 1978 m, 17M0722229, 9953647, 24-Jun-2004, D. A. Donoso. Paratypes QCAZI 1339 and QCAZI 1340. Ecuador, Cotopaxi, Otonga, 1978 m, 17M0722229, 9953647, 24-Jun-2004, D.A. Donoso. Ref. Donoso *et al.* 2006.

*Linepithema aztecoides* Wild 2006. Paratype ♀: QCAZI 1338. Label 1: Paraguay, Canindeyú, Res. Mbaracayú, Lagunita, 200 m, 24°08' S, 055°26' W, 13.xi.2002, A. L. Wild #AW1686; Label 2: Humid subtropical medium forest. On low vegetation. Ref. Wild 2006

*Linepithema neotropicum* Wild 2006. Paratype QCAZI 1344. Label 1: Paraguay, Canindeyú, Res. Mbaracayú, Jejuimí, 170 m, 24°08' S, 055°32' W, 25.ix.2002, A. L. Wild, #AW1718; Label 2: humid sub-tropical tall forest edge. Ref. Wild 2006

*Linepithema tsachila* Wild 2006. Holotype ♀: QCAZI 1337. Label 1: Ecuador, Pichincha, ENDESA Forest Res., 700 m, 00°06' N, 79°02' W, 5.xii.2003, A. L. Wild, #AW2212; Label 2: 2<sup>nd</sup> growth forest nest in rotting center of live tree. Ref. Wild 2006

*Pheidole alpestris* Wilson 2003. Paratypes QCAZI 1453 and QCAZI 1454. Label 1: Ecuador, Pichincha, 6 km SE Pifo, 0°15' S, 78°18' W, 2900 m, 16-VIII-1991, P. S. Ward, # 11485 #11486; Label 2: Under stone roadside edge. Ref. Wilson 2003.

*Pseudomyrmex eculeus* Ward 1999. Paratype ♀: QCAZI 1326. Ecu, Prov. Napo, Jatun Sacha, 01°04'S, 77°36'W, 450 m, 13 .ix.1992, B. L. Fisher, # 458 ex: *Tachigali*, rainfor. Ref. Ward 1999.

*Pseudomyrmex insuavis* Ward 1999. Paratype QCAZI 1327. Col Amazonas, Araracuara, 00°38' S, 72°15' W, iv. 1994, G. Gangi #224 ex: *Tachigali hypoleuca*. Ref. Ward 1999.

*Pseudomyrmex ultirix* Ward 1999. Paratype QCAZI 1345. Label 1: Ecuador, Napo, 13 km NNE Archidona, 0°48'S, 77°47' W, 960 m, 7.viii.1991, P. S. Ward. #11393; Label 2: ex: *Triplaris* roadside edge. Ref. Ward 1999.

#### FAMILY POMPILIDAE

*Pepsis multichroma* Vardy 2002. Paratype \$: QCAZI 1974. Ecuador, Azuay, Km 100 Vía Cuenca-Loja, IV-1985, G. Onore. Ref. Vardi 2001.

*Pepsis onorei* Vardy 2002. Paratypes £: 3 paratypes with the following label: Ecuador, Cotopaxi, Las Pampas, 1500, X.1983, G. Onore. 12 paratypes with the following label: Ecuador, Cotopaxi, Las Pampas, 1500, VI.1983, G. Onore. 2 paratypes with the following label: Ecuador, Cotopaxi, Las Pampas, 1500, X. 1985, G. Onore. Ref. Vardi 2002.

#### FAMILY SCELIONIDAE

*Thoron garciai* Johnson & Masner 2004. Paratype \$: QCAZI 1600. Label 1: VENEZUELA, Amazonas, Surumoni, 100m, 3°10'30" N; Label 2: 65°40'30" O, 13-21-vii-1999, J. L. García; Label 3: Trampa amarilla. Ref. Johnson & Masner 2004.

#### FAMILIA VESPIDAE

*Agelaia silvatica* Cooper 2000. Paratypes £: QCAZI 1501. Ecuador, Pichincha, Quito, Río Guajalito, 1800 m, W 78°38'10", S 0°13'33", 15Nov1997, A. Lara. QCAZI 1502. Ecuador, Pichincha, vía Calacalí-Nanegalito, 2000 m, 23JUN1996, L. Torres. QCAZI 1503. Ecuador, Pichincha, Tandapi, 16-I-1988, Legit: S. Gutierrez. QCAZI 1504 and QCAZI 1505. Ecuador, Pichincha, Hda. Palmeras, VI-1986, Lg. F. Bravo. QCAZI 1506 and QCAZI 1507. Ecuador, Pichincha, Palmeras, 23ENE1993, F. Haro. QCAZI 1508. Ecuador, Pichincha, Palmeras, 1800 m, 7NOV1992, J. Molineros SP. QCAZI 1509. Ecuador, Cotopaxi, Las Pampas, VI.85, Legit: G. Onore. QCAZI 1510 to QCAZI 1513 with the same label as QCAZI 1509 except for: XII 85, QCAZI 1514 to QCAZI 1516 with the same label as QCAZI 1509 except for: 2-XI.1985 Legit: F. Bravo. QCAZI 1517. Ecuador, Cotopaxi, Otonga, 2000 m, 6JUL1996, Gonore. QCAZI 1518, with the same label as QCAZI 1517 except for: 19NOV1994 Ssalazar. QCAZI 1519. Ecuador, Cotopaxi, Los Libres, 2000 m, 5NOV1994, Ssalazar. Ref. Cooper 2000.

#### ORDEN LEPIDOPTERA

#### FAMILIA NOCTUIIDAE

*Hemeroblemma laguerrei* Barbut & Lalanne-Cassou 2005. Paratype QCAZI 1577. Equateur, (Tunguraha), Rte de Puyo á Baños, Río Topo, 1400 m, 09-VI-2002, B. Lalanne-Cassou & M. Garnier leg. Ref. Barbut & Lalanne-Cassou 2005

#### FAMILIA NYMPHALIDAE

*Altipedaliodes tena nucea* Pyrcz & Viloria 1999. Paratype QCAZI 1464. Ecuador, Azuay, Jima, 4000 m, V 1997, I. Aldas leg. Ref. Pyrcz & Viloria 1999.

*Manerebia golondrina* Pyrcz & Willmott 2006. Paratype QCAZI 1471. ECUADOR, Prov. Carchi, Res. Forest. Golondrinas, 2150 m, 23.VI. 1999, Leg. Woujtsiak & Pyrcz. Pyrcz *et al.* 2006.

*Manerebia satra pauperata* Pyrcz & Willmott 2006. Paratype QCAZI 1480. ECUADOR, Zamora Chin., Loja-Zamora, 1500 m, 08.11.1996, leg. S. Attal. Ref. Pyrcz *et al.*

2006.

*Manerebia germaniae* Pyrcz & Hall 2006. Paratype QCAZI 1478. ECUADOR, Prov. Pichincha, Aloag Tandapi km 18, Los Alpes, 2700-2750 m, 26. I. 2004, leg. Pyrcz & Garlacz. Ref. Pyrcz *et al.* 2006.

*Manerebia undulata undulata* Pyrcz & Hall 2006. Paratype QCAZI 1475. ECUADOR, Bolívar, Balzapamba, arriba de Sta. Lucía, 2600-2650 m, 03.IX.2003, T. Pyrcz leg. Ref. Pyrcz *et al.* 2006.

*Manerebia inderena similis* Pyrcz & Willmott 2006. Paratype \$: QCAZI 1474. ECUADOR, Bolívar, Balzapamba, arriba de Sta. Lucía, 2600-2650 m, 03.IX.2003, T. Pyrcz leg. Ref. Pyrcz *et al.* 2006.

*Manerebia inderena clara* Pyrcz & Willmott 2006. Paratype \$: QCAZI 1477. ECUADOR, Baeza, Papallacta, 2100 m, 07.IV.1998, leg. A. Neild. Ref. Pyrcz *et al.* 2006.

*Manerebia inderena laeniva* Pyrcz & Willmott 2006. Paratype \$: QCAZI 1476. P. Boyer, Leg. El Tablón, 3000 m, (El Triunfo-Patate), (Tungurahua), 26 km de Baños, EQUATEUR, 21/11/1998. Ref. Pyrcz *et al.* 2006.

*Manerebia inderena mirena* Pyrcz & Willmott 2006. Paratype QCAZI 1472. ECUADOR, Zamora, C. Quebrada de los muertos near Valladolid, m 2550-november 1999, lg. I. Aldas-coll. Bollino. Ref. Pyrcz *et al.* 2006.

*Pedaliodes rumba* Pyrcz & Viloria 1999. Paratype QCAZI 1465. Ecuador, Prov. Cotopaxi, Pilaló, > 2500 < 3000, 1996 07, leg. I. Aldas. Ref. Pyrcz & Viloria 1999. Label data is inconsistent with publication. Ref. Pyrcz & Viloria 1999.

*Pedaliodes morenoi pilaloensis* Pyrcz & Viloria 1999. Paratype QCAZI 1466. Ecuador, Prov. Cotopaxi, Pilaló, > 2500 < 3000, 1996 07, leg. I. Aldas. Ref. Pyrcz & Viloria 1999. Not as deposited in QCAZ

*Pedaliodes arturi* Pyrcz & Viloria 1999. Paratype \$: QCAZI 1467. ECUADOR, Cord.Lag. Negra, 15. V.1998, 3000-3200 m, A. Jasinski leg. One paratype is missing

*Pedaliodes balnearia* Pyrcz & Viloria 1999. Paratype QCAZI 1481. ECUADOR, Tungurahua, Tung-Volcano, 2300-2600 m, 08-05-1996, leg. A. Jasinski. Ref. Pyrcz & Viloria 1999.

*Pedaliodes peucetas restricta* Pyrcz & Viloria 1999. Paratype \$: QCAZI 1470. ECUADOR, Provincia Pichincha, Aloag Tandapi road, approx. 1700, 25.09.1995, Chisiche, leg. Andrew Neild. Ref. Pyrcz & Viloria 1999.

## ORDER MEGALOPTERA

### FAMILY CORYDALIDAE

*Chloronia convergens* Contreras 1995. Paratype \$: QCAZI 1390. Ecuador, Pichincha, Pto. Quito, 12-XII-1982, Lg. P. Navarrete. Ref. Contreras 1995.

*Corydalus clauseni* Contreras 1998. Paratypes QCAZI 1379 f. Ecuador, Pichincha, Puerto

Quito, XII-1982, Lg. Ernesto Martínez. QCAZI 1380 £. Ecuador, Pichincha, Puerto Quito, 20-I-85, Lg. C. Redin. QCAZI 1381 £. Ecuador, Loja, Masanamaca, 16Mar1985, Legit: L. Coloma. QCAZI 1382 £. Ecuador, Pichincha, Puerto Quito, 14-I-84, Leg: R. León. QCAZI 1383 £. Ecuador, Pichincha, Santo Domingo, 6-06-1992, Pedro Jimenez. QCAZI 1384 £. Ecuador, Prov. Pichincha, Puerto Quito, 15-I-1984, Col. M. I. Salazar. QCAZI 1385 £. Ecuador, Puerto Quito, 20-I-85, Legit: C. Redin. QCAZI 1386 £. Ecuador, Pichincha, Puerto Quito, 3-XII-1923, Leg. P. Davila. QCAZI 1387 \$. Ecuador, Napo, Lumbaqui, May1973, Legit: N. Venedectoff. QCAZI 1388 \$. Ecuador, Pichincha, Allurquin, III-1983, Lg. L. Coloma. QCAZI 1389 \$. Ecuador, Pichincha, P.V. Maldonado, 15-III-91, Legit: J. Woolfson. Contreras 1998.

## ORDER ODONATA

### FAMILY LESTIDAE

*Lestes jerrelli* Tennessen 1997. Paratypes QCAZI 1443. Ecuador, Napo Province, pond 12.3 km W, on Loreto Rd, from Coca Rd., elev. 820', 13 June 1995, Coll. By W. Mauffray In copula. Comments: Two specimens in same envelope labeled as *Lestes forficula* Rambur by Bill Mauffray in 1995. Ref. Tennessen 1997.

### FAMILY COENAGRIONIDAE

*Oxyagrion tennesseni* Mauffray 1999. Paratype \$: QCAZI 1444. Ecuador, Napo, Baeza; 10.6 km S, on Hwy 45 near Bermojo, seepage marsh, 16-Jun-1995, Coll Bill Mauffray, Altitude: 5600 ft. Ref. Mauffray 1999.

### FAMILY AESHNIDAE

*Aeshna (Marmaraeschna) brevicercia* Muzón & Von Ellenrieder 2001. Holotype \$: QCAZI 1445. Ecuador, Pichincha, 2300 m, Feb. 1991, C. León. Paratypes QCAZI 1446 \$. Ecuador, Pichincha, Sangolquí, Sep 7 1993, D. Padilla. QCAZI 1447 £. Ecuador, Pichincha, Conocoto, Jun. 28. 1992, P. Fernández. QCAZI 1448 £. Ecuador, Pichincha, Conocoto, 5 Mar 1993, G. Dávalos. QCAZI 1449 £. Ecuador, Imbabura, Ibarra, 2 Nov 1991, F. Martinez. QCAZI 1450 \$. Ecuador, Imbabura, Atuntaqui, 2500 m, Dec. 26 1988, C. León. QCAZI 1451 \$. Ecuador, Pichincha, Sangolquí, Nov 15 1993, D. Padilla. QCAZI 1452 \$. Ecuador, Pichincha, Quito, Apr. 1975, M. L. Pérez. Comments: QCAZI 1445 and QCAZI 1452 labeled as *Aeshna brevifrons* Hagen by Bill Mauffray in 1995. Ref. Muzón & Von Ellenrieder 2001.

## ORDER ORTHOPTERA

### FAMILY GRILLIDAE

*Gryllus abditus* Otte & Peck 1997. Paratypes QCAZI 1391. Ecu., Galap., Floreana, Pta. Cormoran, arid z, mv. Light & night colln sand dunes, 21.IV.92, J. Cook, S. Peck, 92-130. QCAZI 1392. Ecu., Galap., Isabela, NE rim Alcedo, 1100 m, 21 -25. VI.91, shrub forest carrion traps, S. Peck, 91-246. QCAZI 1393. Ecu., Galap., Isabela, SE craterrim, 22-23.VI.91, 1100 m, under rocks in grass, S. Peck, 91-249. QCAZI 1394. Ecu., Galap., Isabela, NE rim Alcedo, 1100 m, 21 -25. VI.91, shrub forest, gen. Colln. S. Peck, 21-247. QCAZI 1395. Ecu., Galap., Isabela, Sierra

Negra, 3-14.III.89, 750 m, pampa, deepsoil traps, S. Peck, 89-98. Ref. Otte & Peck 1997.

*Gryllus isabela* Otte & Peck 1997. Paratypes QCAZI 1396 to QCAZI 1399. Ecu., Galap., Isabela, Alcedo, 20-24.VI.91, Crater rim UV light, 1100 m, S. Peck. 91-286 Luz Ultravioleta. QCAZI 1400. Ecu., Galap., Isabela, NE slope Alcedo, 20-25.VI.91, 850 m, open forest, night colln, S. Peck, 91-244. Ref. Otte & Peck 1997.

#### FAMILY ACRIDIDAE

*Aphanolampis aberrans* Descamps 1978. Neoparatypes: QCAZI 1401 and QCAZI 1402. Prov. Napo, Puerto Napo, Ahuano, 450 m, 16VIII/06 IX 1991. Comments: Neoparatypes designated by Amédégnato & Poulain 1994. Ref. Descamps 1978 [not reviewed].

*Hyalinacris diaphana* Amédégnato & Poulain 1998. Paratypes QCAZI 1486 and QCAZI 1494. Ecuador, Pichincha, Palmeras, Nov 1991, Galo Zapata. QCAZI 1487. Ecuador, (22-10-88), Pichincha, Chillogallo, San Luis Páramo, 3600 m, Legit: A. Quintana. QCAZI 1488. Ecuador, Pichincha, Palmeras, 22-I-84, Leg: I. Yépez. QCAZI 1489. Ecuador, Pichincha, Sangolquí, 15 JAN1993, M. Baldeón. QCAZI 1490. PICHINCHA, ECUADOR, Palmeras, 1820 m, 19-NOV-1994, Santiago Espinosa. QCAZI 1491. Ecuador, Pichincha, Palmeras, 24OCT1992, M.Troya. QCAZI 1492. Ecuador, Pichincha, Vía Los Bancos km13, 20NOV1996, J. Costales. QCAZI 1493. ECUADOR, Pichincha, Río Guajalito, 1200m, 76°48'W, 00°53'S, 6MAR1997, F. GUAMAN. QCAZI 1495. Ecuador, Pichincha, Palmeras, 17Nov 1991, Leg. A. Encalada. Ref. Amédégnato & Poulain 1998.

*Hyalinacris onorei* Amédégnato & Poulain 1998. Paratypes QCAZI 1496 and QCAZI 1497. Ecuador, Cotopaxi, Otonga, 2000 m, 3MAY1997, G. Onore. QCAZI 1498. Ecuador, Cotopaxi, Otonga, 2000 m, 79°5W, 0°27S, 2MAY1997, I. Olmedo. Ref. Amédégnato & Poulain 1998. Male specimens.

#### CLASS ARACHNIDA

#### ORDER ESCORPIONES

#### FAMILY BUTHIDAE

*Tityus jussarae* Lourenço 1988. Allotype ♂: QCAZI 1601. Ecuador, Napo, Archidona, Cueva de Lagarto, 00°56' S, 77°50' W, 2 May. 1988, F. Rodríguez. Ref. Lourenço 1988.

#### FAMILY CHACTIDAE

*Chactas mahnerti* Lourenço 1995. Paratype ♂: QCAZI 1602. Ecuador, Pichincha, La Florida, Cerca de Allurquin, 15 Sep. 1984, L. Coloma. Ref. Lourenço 1995.

#### CLASS ARACHNIDA

#### FAMILIA THERIDIIDAE

*Anelosimus guacamayos* Agnarsson 2006. Paratypes QCAZI 1455 and QCAZI 1456.

Ecuador, Napo, Río Quijos S: 0.17469 W: 77.67926 1329 m 19-Jul-2004.  
Comments: Both paratypes are of opposite sex and are stored in the same envelope.  
Ref. Agnarsson 2006.

*Anelosimus oritoyacu* Agnarsson 2006. Paratypes QCAZI 1457 and QCAZI 1458.  
Ecuador, Napo, Baeza-Lago Rd., 2.4 Km, S: 0.45157, W: 77.88392, 1818 m, 19-Jul-2004. Comments: Both paratypes are of opposite sex and are stored in the same envelope. Ref. Agnarsson 2006.

*Anelosimus baeza* Agnarsson 2006. Paratypes QCAZI 1459 and QCAZI 1460. Ecuador, Napo, Baeza-Lago Rd., 2.6 Km, 1840 m, W. Maddison, 19-Jul-2004. Comments: Both paratypes are of opposite sex and are stored in the same envelope. Ref. Agnarsson 2006.

*Anelosimus elegans* Agnarsson 2006. Paratypes QCAZI 1461 and QCAZI 1462. Ecuador, Napo, Río Salado, 1293 m, L. Aviles, 19-Jul-2004. Ref. Comments: Both paratypes are of opposite sex and are stored in the same envelope. Agnarsson 2006.

CLASS ACARI

FAMILY LOHMANIIDAE

*Heptacarus encantadae* Schatz 1994. Paratypes QCAZI 1463. GAL 87-697 Galapagos, I. Rábida, Littoral, leg: Schatz. Comments: All paratypes (n=5) are under the same QCAZI # in a single vial. Ref. Schatz 1994.

*Torpacarus omittens galapagensis* Schatz 1994. Paratype QCAZI 1608. GAL 87-577 Galapagos, Pinzón, Craterium leg: Schatz. Ref. Schatz 1994.

# Short term response of dung beetle communities to disturbance by road construction in the Ecuadorian Amazon

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**Abstract.** In the tropics, human disturbance continuously challenges initiatives for habitat conservation. In these regions, as economical budgets for conservation shrink, conservation planning requires precise information on when and how different kinds of disturbance may affect natural populations, but also on adequate experimental designs to monitor them. Due to their high diversity, ecological role, stable taxonomy and facilities to sample, dung beetles are used in biodiversity surveys for conservation purposes worldwide. Here we studied the short-term effects of dung beetle communities to an important and widespread ecological disturbance due to road construction in the Amazon basin. We surveyed the dung-beetle community in a spatio-temporal context, i.e. in transects located at 10, 50 and 100-m from a newly constructed, 10-m wide, paved road. The sampling periods took place 1, 3 and 6 months after the construction. During the survey, we collected 4895 specimens that belong to 69 species in 19 dung beetles genera. Six dung beetles species (*Canthon aequinoctialis*, *C. luteicollis*, *Dichotomius forstestriatus*, *Eurysternus caribaeus*, *E. confusus* and *Onthophagus haematopus*) accounted for 55% of all individuals collected. Both species diversity and abundance tended to decrease during the 6 months after the opening of the road, but not with distance from the road. Accordingly, an NMDS analysis revealed clear differences in dung beetle community composition and biomass among the three sampling periods, but not with respect to transect location. However, the number of rare species tended to increase toward the forest interior. A detailed analysis of dung beetle species among transects revealed that 5 species (*Sylvicanthon bridarollii*, *Canthidium* sp. 2, *C. sp. 6*, *C. sp. 7* and *Ontherus diabolicus*) were more abundant when getting further from the road. On the contrary 6 species (*Eurysternus hamaticollis*, *E. velutinus*, *E. confusus*, *E. caribaeus*, *Deltochilum oberbergeri* and *D. orbiculare*) increased in abundance in the transect next to the road. Our study therefore confirmed that while overall community metrics did not respond to road construction, several rare dung beetle species did, within an incredibly rapid time frame. While pattern based descriptions of dung beetle responses to anthropogenic activities are common in the literature, our findings suggest that effect of roads is certainly under emphasized.

**Résumé. Réponse à court terme des communautés de bousiers aux perturbations induites par la constructions de toutes dans l'Amazonie Equatorienne.** Dans les zones tropicales, les activités humaines sont une menace constante pour la conservation des habitats. Les budgets alloués aux efforts de conservation étant réduits dans ces régions, l'établissement de plans de gestion requiert des informations précises sur la manière dont différents types de perturbations affectent les populations naturelles et sur les protocoles expérimentaux adéquats pour suivre l'évolution de ces populations. En raison de leur diversité, de leur rôle écologique clé, de leur facilité d'échantillonnage et de leur taxonomie relativement bien connue, les coléoptères bousiers sont largement utilisés comme indicateurs dans les programmes de conservation dans le monde entier. L'objectif de ce travail est d'étudier les effets à court terme de la construction d'une route sur les communautés de bousiers en forêt amazonienne. Nous avons réalisé une étude spatio-temporelle des communautés de bousiers le long d'un transect composé de site d'échantillonnages localisés à 10, 50 et 100 m de distance d'une route, après 1, 3 et 6 mois de construction. Durant cette étude 4 895 individus appartenant à 69 espèces et 19 genres de bousiers ont été collectés. Six espèces (*Canthon aequinoctialis*, *C. luteicollis*, *Dichotomius forstestriatus*, *Eurysternus caribaeus*, *E. confusus* et *Onthophagus haematopus*) représentaient 55% de tous les individus collectés. Nos résultats ont montré que la diversité spécifique, l'abondance et la composition des communautés de bousiers variaient significativement en fonction du mois de collecte, mais pas en fonction de la distance à la route. Cependant, le nombre d'espèces rares de bousiers tendait à augmenter en s'éloignant de la route. Par ailleurs, une analyse au niveau spécifique a révélé que cinq espèces (*Sylvicanthon bridarollii*, *Canthidium* sp. 2, *C. sp. 6*, *C. sp. 7* et *Ontherus diabolicus*) étaient significativement plus abondantes en s'éloignant de la route. Au contraire, l'abondance de six espèces (*Eurysternus hamaticollis*, *E. velutinus*, *E. confusus*, *E. caribaeus*, *Deltochilum oberbergeri* et *D. orbiculare*) augmentait en se rapprochant de la route. L'utilisation des bousiers comme indicateurs de perturbation à court terme, telle qu'elle est réalisée dans de nombreux pays tropicaux est discutée dans un contexte général de conservation des milieux soumis à des perturbations anthropiques.

**Keywords:** Human disturbance, Ecuador, Scarabaeinae, Tropical rainforest, NMDS.

Like many other South American countries, Ecuador faces important habitat conservation challenges throughout its territory. These place serious pressure on the survival of many species, and the maintenance of biodiversity and ecosystem function (Dangles *et al.* this issue). Although insect biodiversity is crucial for maintaining ecosystem function, our understanding of the overall response of insects to human activity remains limited. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are relevant candidates to assess interactions between anthropogenic disturbances and community composition (Nichols *et al.* 2007). These insects perform key roles in many ecosystems around the world as they provide a suite of vital ecosystem services such as recycling of dead tissue, fecal material, and the dispersal of seeds (Andresen & Feer 2005, Nichols *et al.* 2008). Dung beetles also represent a large proportion of insect biomass, are easily attracted to baits, and have a relatively well-known taxonomy, at least for some groups (Hanski & Cambefort 1991). For these reasons, numerous studies have investigated the impact of habitat disturbance on dung beetle communities in various tropical regions including Eastern Asia (Boonrotpong *et al.* 2004, Shahabuddin *et al.* 2005), Africa (Davis & Philips 2005) and Latin America (Klein 1989, Forsyth *et al.* 1998, Quintero & Roslin 2005, Scheffler 2005, Gardner *et al.* 2008) (see Nichols *et al.* 2007 for a review). Some of these authors have stressed the potential use of dung beetles as bio-indicators for mammal population densities (as many species rely directly on mammal excrement for food and nesting while others are carrion feeders) and environmental changes (e.g., Nichols *et al.* 2009). In Ecuador, environmental monitoring programs have been developed with dung beetles as the focal group (Celi & Dávalos 2001).

Road construction is the main factor leading to forest fragmentation in the Amazon basin (Perz *et al.* 2008). Forest fragmentation has negative ecological consequences such as stream network degradation, spread of exotic invasive species, wildlife mortality and species loss from ecosystems (Trombulak & Frissell 2000; Forman *et al.* 2003), which implies that the Amazon in the near future may become more vulnerable to global change than climate models assume (Perz *et al.* 2008). Roads can affect species by reducing available habitat, affecting patterns of movement, and extending edge microclimatic conditions into forests, further reducing existing habitat (see Dunn & Danoff-Burg 2007 and references therein). In spite of great advances in our understanding of road ecology, much remains to be known about the effects of road construction on ecosystems in the short and long-term (Forman *et al.* 2003).

Recent literature has outlined several long-term effects, both positive and negative, on the structure and function of invertebrate communities along the road-forest continuum (see Dunn & Danoff-Burg 2007). Obviously long-term effects are the most relevant in an ecological perspective. However, most environmental impact studies related to road construction in developing countries are performed at short temporal and spatial scales. In most cases, the objective of these impact studies has been to assess the degree of local perturbations in view of authorizing the further use of the road. Because of limited funding, these impact studies have been limited to several months up to a few years in the best case. Finding biological indicators that can rapidly respond to anthropogenic perturbation is an important issue for environmental assessment. Dung beetle communities are potential candidates as biological indicators, known to show a graded and rapid response to environmental degradation (Larsen & Forsyth 2005).

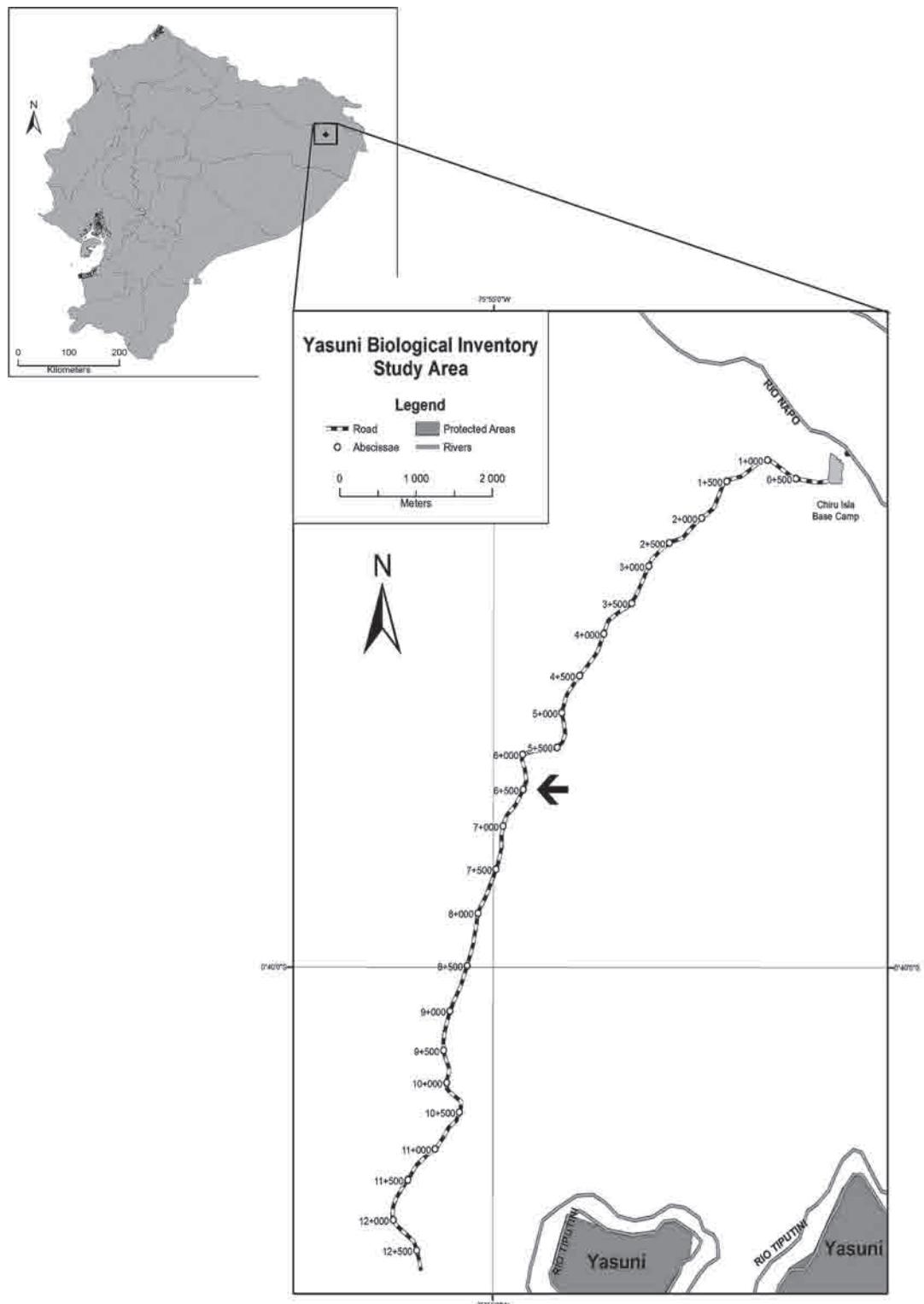
This study examines how insect communities responded to the perturbation of road construction using dung beetles as an indicator group (Halffter & Favilla 1993, Forsyth *et al.* 1998, Davis *et al.* 2001). We studied dung beetle communities in a spatio-temporal context, i.e. at different distances from the road and at different times after road opening. Although overall community composition metrics were not sensitive to these changes, our study found rapid responses of several rare dung beetle species to road construction.

## Material and methods

### Study site

The study site was near the "Chiruisla Station" on the south rim of the Napo River in Sucumbíos Province close to the Chiruisla Village of the Quichua Territory, Ecuador. We selected a 12600 m<sup>2</sup> study area (140 × 90 m) around a central point located at the coordinate 0° 38' 39.2" S, 75° 54' 45.4" W (Fig. 1). This site ranges from 180–250 m in altitude. The climate is tropical and humid. Rainfall and temperature are aseasonal with an annual mean precipitation of 2400 mm. No month receives less than 100 mm (Valencia *et al.* 2004) of rain but December and January are generally slightly drier than the rest of the year. Temperatures range from 22–32 °C and humidity from 56–96%. The whole area is a young landform classified as "western sedimentary uplands," which are fluvial deposits (red clays, brown or gray alluvium) (*sensu* Tuomisto *et al.* 2003). The area has been reported to contain important populations of large mammals with no record of species extirpation (Peres & Dolman 2000).

The Chiruisla Station was controlled by the Petrobras Oil Company. The study plot was located 2 km inside a mature forest south of the Napo River, on a west side of a recently (< 1 month) opened road for oil extraction activities. The road was 12.5 km long and 10 m wide and ended at river. Every 1000 m,

**Figure 1**

Location of the study region in Ecuador (insert) and map of the study area showing the location dung beetle sampling transect (black arrow) along the recently constructed road in Chiruisla.

**Figure 2**

A, photograph of the paved road in Chiruisla (2005). B, schematic drawing of the sampling design used to collect dung beetle communities in Chiruisla.

the road was partly covered by canopy segments thanks to the presence of canopy bridges. These bridges consisted in 40-meter-long sections where the working row of the road was narrowed to seven meters to preserve canopy connections. Before road construction, the forest was considered a primary forest, except for some local disturbances originating from indigenous groups who clear the forest for agriculture. This is an evergreen lowland wet forest that has a canopy mostly 15–30 m high, with some emergent trees reaching 50 m. It was dominated by species of the families Arecaeae (*Iriartea deltoidea*), Euphorbiaceae (*Margaritaria nobilis*), Rubiaceae (*Duroia hirsuta*), Lecythidaceae (*Grias neuberthii*) and Mimosaceae (*Parkia multijuga*).

### Sampling design

From September 2005 to February 2006, we surveyed the study area on three occasions at one, three and six months (September, November and February, respectively) after the opening of the road. Although we tried to control for rain and seasonal differences by limiting our sampling to the early and mid-rainy season we are aware that seasonal effects can still be significant as abundance of dung beetles is sometimes higher at the beginning of the rainy season than in mid-rainy season. For logistic reasons, we were unable to sample the plot before the opening of the road and thus data on the original dung beetle community composition are not available. On each occasion, we surveyed the dung beetle fauna on three transects located at 10, 50 and 100 m inside the forest (L10, L50, L100, respectively, fig. 2). Each transect was composed of 8 traps (T1, T2,..., T8), separated by a distance of 20 m. Trap placement and collection was randomized across transects to control for sampling time effect. Dung beetle communities were sampled using pitfall traps consisting of two stacked 0.5 L plastic cups buried in the ground so that the top rim was aligned with the soil surface (Spector & Forsyth 1998). Two cups were used so that the top cup could be easily removed and replaced again after each collection (Larsen & Forsyth 2005). The top cup was half-filled with water and a small amount of soap to reduce surface tension. Two types of baits, human dung and tuna fish were used in an alternating spatial configuration (fig. 2B). For both bait types, 50 g of bait material was wrapped in nylon mesh (1 mm<sup>2</sup>) and tied with plastic thread to a 30-cm wooden stick. This quantity of bait was sufficient to attract the largest dung beetles at the sites (Peck & Howden 1984). The bait was suspended above the cups which were covered with large leaves positioned at least 20-cm over the trap to protect it from rain and sun. In each sample interval, traps were baited for 6 complete days and beetles were collected daily. Baits were replaced every two days to avoid desiccation (Spector & Ayzama 2003). All insects were preserved in 70% ethanol and returned to the lab for identification.

### Identification of Scarabaeinae

We identified the species of Scarabaeinae using taxonomic keys (Howden & Young 1981, Jessop 1985, Edmonds 1994, Génier 1996, Arnaud, 1997, Cook 1998, Medina & Lopera 2001), unpublished species lists and collections of the QCAZ Museum (PUCE), and assistance of W. D. Edmonds, Marfa, Texas. Where specific identification was not possible, specimens were identified to genus and then assigned to a morphospecies. In total, morphospecies represented 52% of the total collected Scarabaeinae, which is within the range of morphospecies proportions found in other studies in South

America: 42.0% (Ecuador, Celi *et al.* 2004), 43.0% (Peru, Larsen *et al.* 2006), 45.4% (Brazil, Duráes *et al.* 2005), 45.6% (Bolivia, Vidaurre *et al.* 2008), and 61.0% (Brazil, Andresen 2002). In all these studies, *Canthidium* and *Dichotomius* were the most problematic genera to identify to the species level. All specimens were deposited at the museum of Invertebrates at QCAZ Museum of the Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

### Dung beetle biomass estimation

We used linear measurement of elytra length + pronotum length as an estimator of dung beetle biomass. Linear measurements are easier to obtain on dry specimens and there is a highly significant relationship between the log values of these two variables (Radtke & Williamson 2005,  $R = 0.964$ ,  $p < 0.001$ ). When possible, linear measurements were made on at least 5 individuals for each species using a caliper accurate to 0.1 mm. Dung beetle species biomass was estimated from linear measurements according to the equation ( $P < 0.01$ ,  $R = 0.93$ ) used by Radtke & Williamson (2005) in their figure 1. The estimated biomass of each species in each site was calculated by multiplying the mean estimated biomass by the total abundance for that species (see Gardner *et al.* 2008 for further details).

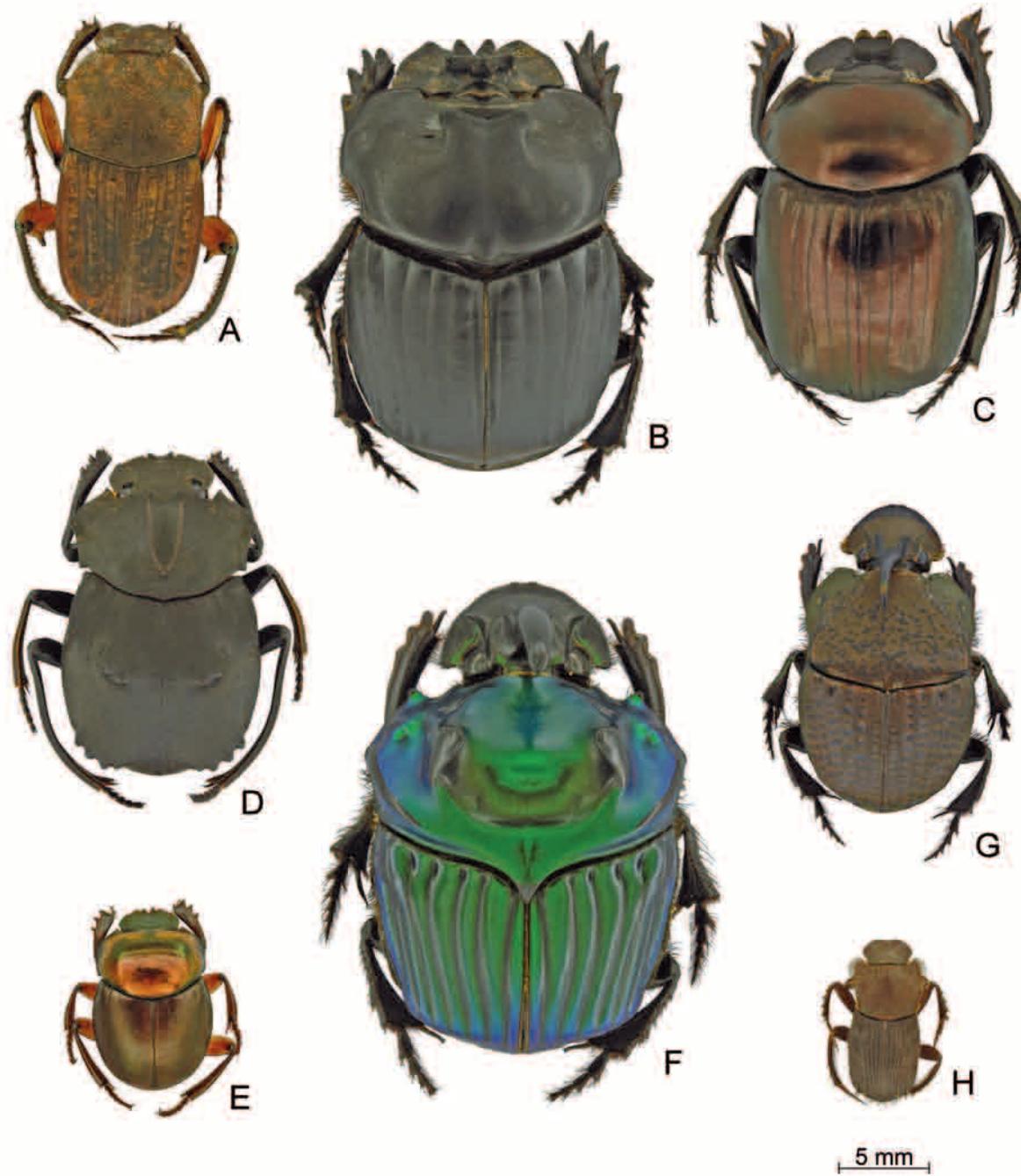
### Data analysis

To determine the degree of completeness of our samples, we calculated species accumulation curves and estimated the true species richness for each sample/day with the Chao 1 estimate using the software EstimateS (Colwell 2006). We then compared quantitatively the differences in community structure of dung beetles between the three distances (10, 50, and 100 m from the road) and three sampling dates (1, 3, and 6 months after the road opening). The number of species, the abundance of individuals and the Shannon Index were calculated for each trap level. We also estimated richness at a transect scale to make comparisons of the total number of species potentially found at each distance from the road. For these analyses, we estimated the Chao1 overall richness using EstimateS (Colwell 2006). Species density, species abundance, and Shannon index per trap were compared among treatments using a two-way ANOVA with distance from road (10, 50, and 100 m), time after road opening (1 month, 3 months, 6 months), and the interaction term as factors. By considering traps as independent units in the ANOVA analysis, we were aware that our analysis may suffer from pseudoreplication (Hurlbert 1984). However, the large differences in dung beetle fauna found between neighboring pitfall traps with similar bait (40-m distance) suggested that the independence hypothesis of adjacent trap was likely true. Because rare taxa (singletons, doubletons, and tripletons) are an important feature of rainforest invertebrate samples (Novotny & Basset 2000), we also compared the presence of rare taxa between the three distances from the road.

We then carried out a non-metric multidimensional scaling (NMDS) analysis to examine patterns of biological similarity in dung beetle assemblages among distance and date. This ordination technique represents samples as points in low-dimensional space, such that the relative distances of all points are in the same rank order as the relative similarities of the samples (Gucht *et al.*, 2005). The Bray-Curtis method was used as a measure of similarity. Samples from the same transect or the same dates were grouped with convex hulls. The NMDS goodness of fit was estimated with a stress function (which ranges

from 0 to 1) with values close to zero indicating a good fit. The difference in composition of the dung beetle community between the three transects and the three dates were tested using an analysis of similarities (ANOSIM). This method has been widely used for testing hypotheses about spatial differ-

ences in plant and animal assemblages, in particular for detecting environmental impacts (Chapman & Underwood 1999). ANOSIM tested the null hypothesis that the within-sites similarity was equal to the between-sites similarity. ANOSIM generates a statistical parameter  $R$  which is indicative of the degree



**Figure 3**

Photographs of several species of dung beetles collected during the study period in Chiruisla (Amazonia, Ecuador). **A**, *Eurysternus caribaeus* (Herbst 1789); **B**, *Coprophanaeus telamon* (Erichson 1847); **C**, *Malagoniella astyanax* (Olivier 1789); **D**, *Deltochilum carinatum* (Westwood 1837); **E**, *Canthon luteicollis* (Erichson 1847); **F**, *Oxysternon conspicillatum* (Weber 1801); **G**, *Phanaeus chalcomelas* (Perty 1830); **H**, *Eurysternus confusus* (Jessop 1985).

of separation between groups; a score of 1 indicates complete separation and a score of 0 indicates no separation (Gucht *et al.* 2005). Monte-Carlo randomization of the group labels was used to generate null distributions in order to test the hypothesis that within-group similarities were higher than would be expected by chance alone. Finally, we determined which dung beetle species contributed most to distinguish transects at different distances from the road by performing a SIMPER analysis on density data for all Scarabeinae taxa. All analyses were performed using PAST (Paleontological statistics, version 1.79) on  $\ln(X + 1)$  transformed data. This procedure is commonly applied to invertebrate assemblage data to reduce the importance of occasional large abundance values (Clarke, 1993).

Finally, we plotted the percentage values for abundance vs. biomass data to detect differences in the analytical weight of individual species in discriminating patterns of dung beetle community structure at the three distances from the road.

## Results

### Patterns in species diversity and abundance

A total of 4895 individuals of 69 species and morphospecies belonging to 5 tribes (Ateuchini,

**Table 1.** Results of the two-way ANOVA analysis on dung beetle community richness.

(A), abundance (B) and Shannon Index (C) at three distance from the road (10, 50 and 100 m) and three sampling dates (at one, three and six months after road opening).

#### A. Richness

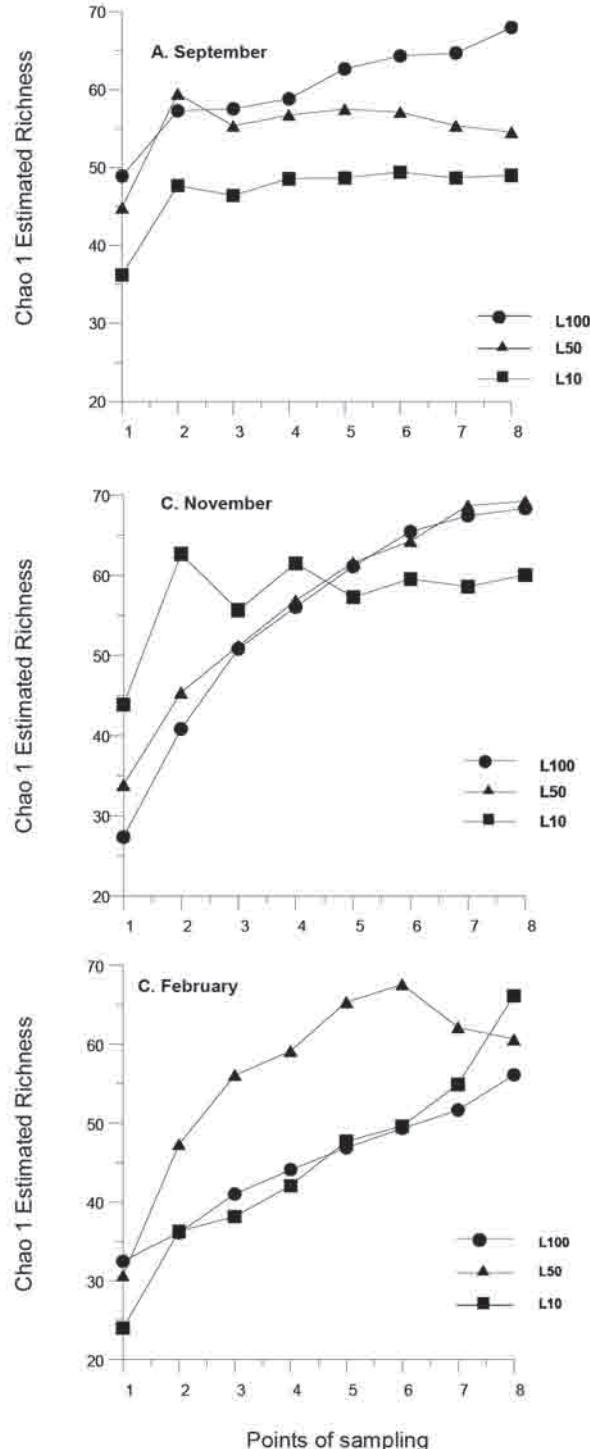
Source	Sum of Squares	Df	Mean Square	F	P
Date	932.583	2	466.292	4.590	0.014
Distance	63.000	2	31.500	0.310	0.734
Date * distance	137.667	4	34.417	0.339	0.851
Error	6399.625	63	101.581		
Total	26643.000	72			

#### B. Abundance

Source	Sum of Squares	Df	Mean Square	F	P
Date	129.104	2	64.552	3.874	0.026
Distance	0.487	2	0.244	0.015	0.985
Date * distance	11.258	4	2.814	0.169	0.953
Error	1049.673	63	16.661		
Total	4806.000	72			

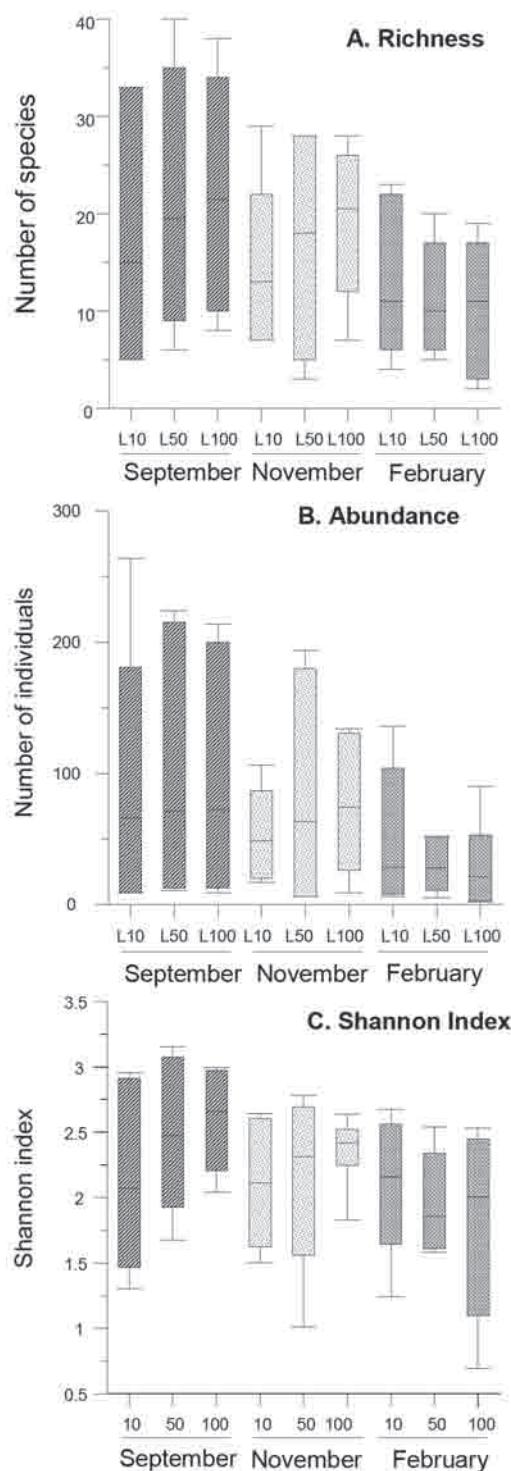
#### C. Shannon Index

Source	Sum of Squares	Df	Mean Square	F	P
Date	2.422	2	1.211	4.428	0.016
Distance	0.274	2	0.137	0.501	0.608
Date * distance	1.083	4	0.271	0.990	0.420
Error	17.232	63	0.274		
Total	367.444	72			



**Figure 4**

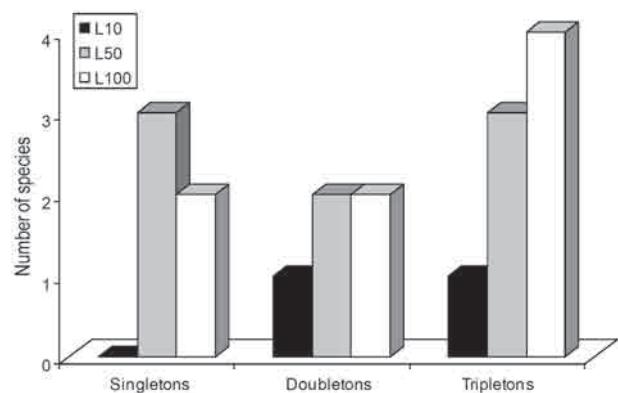
Accumulation curves of Chao1 estimates of dung beetle species richness for each transect (L10, L50, L100) and each sampling date (A: 1 month, B: 3 months and C: 6 months after road opening). Capture units express total sampling effort at one site. Each curve represents 500 randomizations using the program EstimateS (Colwell 2006).

**Figure 5**

Impact of road construction on the dung beetle community richness (A), abundance (B), and Shannon Index (C) at three distances from the road (L10, L50 and L100), during the study period from 1 to 6 months after road opening. For box-whisker plots, the outer edges of the box define the interquartile range, the center line is the median and the bars indicate 1.5 times the interquartile range.

Canthonini, Dichotomiini, Onthophagini, and Phanaeini) of Scarabaeinae, were recorded over the study period, 432 trap-days (see Figure 3 and Appendix 1). Six species (*Canthon aequinoctialis*, *C. luteicollis*, *Dichotomius forstestriatus*, *Eurysternus caribaeus*, *E. confusus* and *Onthophagus haematopus*) accounted for 55% of all individuals collected. The species accumulation curves accounted for 83.4 % of the variance in sampling performance at all sites ( $P < 0.001$ , fig. 4). We estimated that we collected 93.5 % of the true species richness.

Box-whisker plots of species diversity, abundance and Shannon index at the trap level revealed large inter-trap variability for these parameters at the three sampling dates (fig. 5). Median species richness values ranged from 10 (L50, 6 months) to 22 species (L100, 1 month) per trap. Median abundance values ranged from 22 (L100, 6 months) to 75 individuals (L100, 1 month) per trap. Both species richness and abundance tended to decrease during the 6 months after road opening. We found that at the trap level, patterns of species density, abundance, and Shannon index varied significantly from beginning to later in the rainy season (two-way ANOVA,  $F > 3.8$ ,  $p < 0.005$ , Table 1), but not with the distance from the road (two-way ANOVA,  $F < 0.51$ ,  $p > 0.6$ , Table 1) or the interaction term (two-way ANOVA,  $F < 1.0$ ,  $p > 0.4$ , Table 1). One month after road opening, species accumulation curves showed differences in total richness between the three distances with a gradual increase in estimated richness when going further from the road (fig. 4A). However, this pattern was not observed in the two other sampling dates (fig. 4B, C). As a general pattern, the diversity of rare taxa was generally higher in L50 and L100 than in

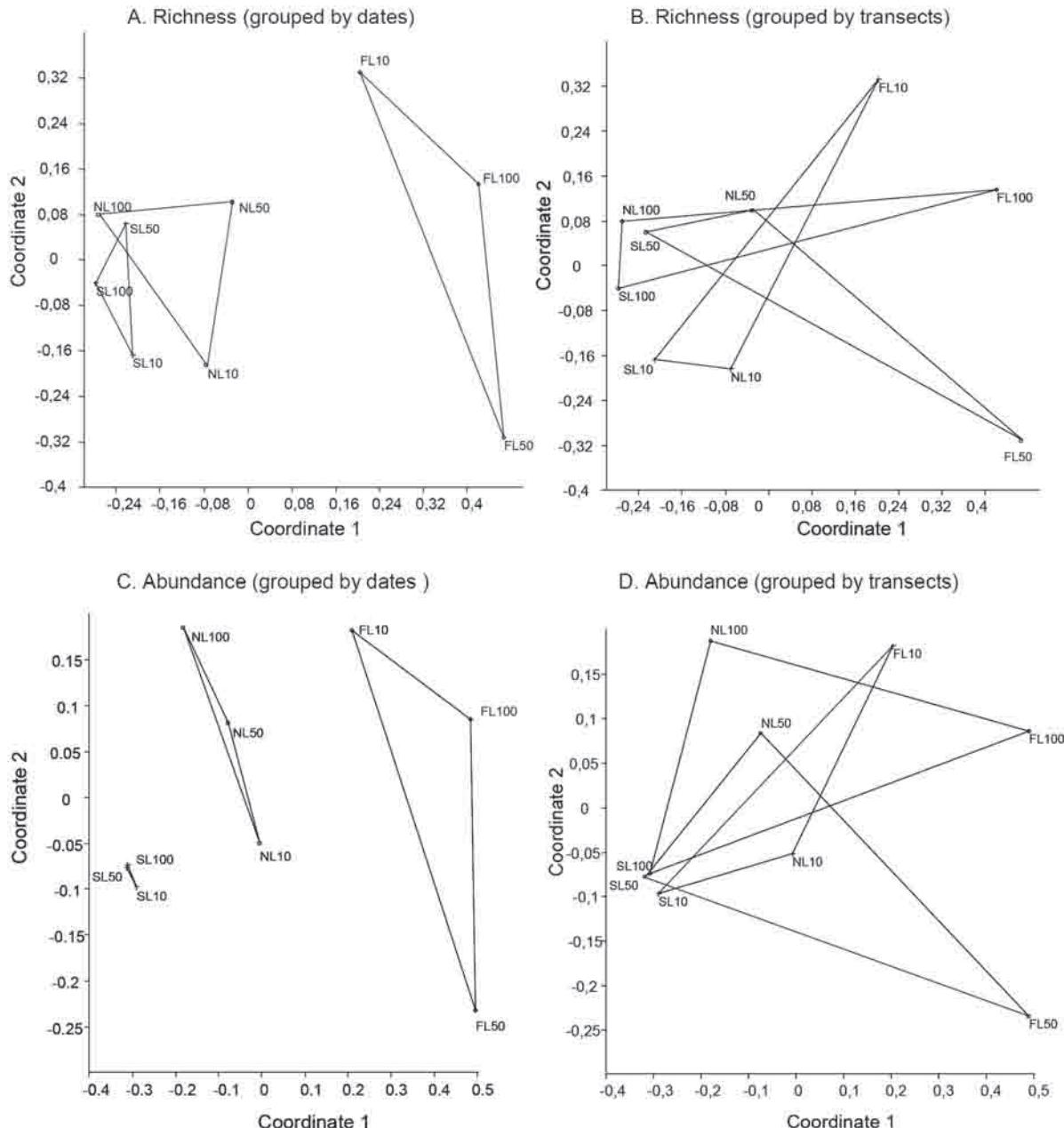
**Figure 6**

Total number of rare dung beetle species (singletons, doubletons, tripletons) found at the three distances from the road (L10, L50, L100) over the study period (from 1 to 6 month after road opening).

L10 (fig. 6). Eleven (*Bdelyrus* sp. 1, *Canthidium* sp. 1, *Canthidium* sp. 8, *Canthon* sp. 2, *Deltocilum orbiculare*, *Deltocilum* sp. 3, *Malagoniella astyanax*, *Onthophagus* sp. 7, *Scatimus strandi*, *Scatimus* sp. 2, *Trichilum* sp. 1) out of the 13 rare species/morphospecies found over the study period, were absent in the transect located 10 m from the road.

### Community composition and biomass

The NMDS analysis revealed clear differences in dung beetle community composition (both richness and abundance) among the three sampling periods (fig. 7A and C). Stress was low (0.01) indicating a high degree of fit. The ANOSIM significantly separated



**Figure 7**

Nonmetric multidimensional scaling (NMDS) analysis of dung beetle communities (A-B richness, C-D abundance) at the three distances from the road (L10, L50, and L100) and the three sampling dates after road opening (1 month, 3 month, 5 months). Triangles show the convex hull (smallest convex polygon containing all points) in each group (A-C sampling date, B-D sampling distance). S: September, N: November, F: February.

the three different sampling periods presented in the NMDS (ANOSIM,  $R = 0.44$ ;  $p = 0.023$  for richness,  $R = 0.66$ ,  $p = 0.004$  for abundance; see convex hulls in Figure 7A and C). Contrastingly, the NMDS showed no significant differences in community composition (both richness and abundance) among transects lines (ANOSIM,  $|R| < 0.2$ ,  $p > 0.900$ , fig. 7B and D). Despite the absence of significant differences for the whole dung beetle communities between transect lines, SIMPER analysis indicated that several changes occurred for some species (Table 2). Of the 22 most discriminatory dung beetle species among transects, 5 species (*Sylvicanthon bridarollii*, *Canthidium* sp. 2, *C.* sp. 6, *C.* sp. 7, *Ontherus diabolicus*) were gradually more abundant when getting further from the road (Table 2). On the contrary 6 species (*Eurysternus hamaticollis*, *E. velutinus*, *E. confusus*, *E. caribaeus*, *Deltocilum obenbergeri*, *D. orbiculare*) increased in abundance in the transect next to the road (Table 2).

Community analyses based upon species abundance and estimated species biomass data produced superficially similar patterns between transects (fig. 8, see also fig. 3 for a visualization of some differences

in size among species). In all cases both large- and intermediate-bodied species contributed the most to patterns based on biomass and abundance data (see the top right corner of each panel). However, these patterns were driven by distinct sets of species. Whereas the top 3 weighted species (*Canthon aequinoctialis*, *Dichotomius fortestriatus*, and *Onthophagus haematopus*) were the same in all transects, they accounted for 47.5% of total estimated biomass at L100 and only for 31.3 % and 29.2% at L50 and L10, respectively. In particular, total estimated biomass of *Dichotomius fortestriatus* decreased by 64% between L100 and L10.

## Discussion

### Dung beetle diversity and composition in the Ecuadorian Amazon

The total number of species found in the study area ( $n = 69$ ) was within the range of dung beetle diversity recorded in other Amazonian regions: 60 species in Leticia, Colombia (Howden & Nealis 1975); 74 species in Tambopata (Spector & Forsyth 1998), Peru and 97 species in Parque Nacional Noel Kempff,

**Table 2.** Results of SIMPER analysis for 22 dung beetle species at three transect lines (L10, L50 and L100).

Log-transformed abundance data provide the percent contribution of each species to average dissimilarity between the three transects. Only species that contributed up to a total of 50% to the separation of transects are listed. Arrows indicate the trend in species abundance with increasing distance from the road.

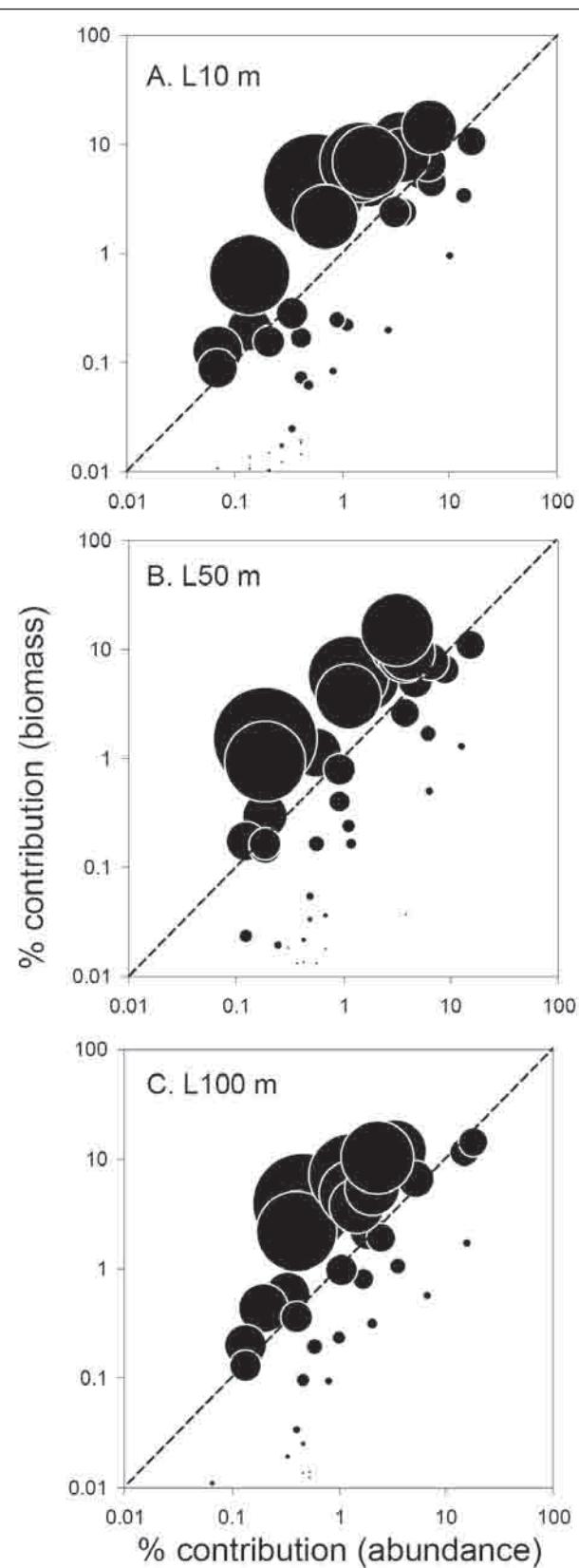
Taxon	Contribution	Cumulative %	L10	L50	L100	Trend
<i>Canthidium</i> sp. 4	1	5	1.55	2.07	1.34	
<i>Sylvicanthon bridarollii</i>	0.82	9	1.19	1.5	1.84	↑
<i>Phanaeus chalcomelas</i>	0.75	12.06	2.71	1.36	1.73	
<i>Canthidium</i> sp. 7	0.72	14.57	1.32	1.44	1.87	↑
<i>Eurysternus hamaticollis</i>	0.72	17.06	2.78	2.51	1.99	↓
<i>Eurysternus velutinus</i>	0.71	19.52	3.4	2.93	2.07	↓
<i>Onthophagus</i> sp. 5	0.70	21.93	1.39	0.462	1.3	
<i>Dichotomius lucasi</i>	0.69	24.32	2.73	2.83	1.99	
<i>Ateuchus murrayi</i>	0.68	26.7	1.43	0.732	1.17	
<i>Eurysternus confusus</i>	0.66	29	4.04	3.37	2.72	↓
<i>Deltocilum obenbergeri</i>	0.61	31.12	3.22	3.12	2.14	↓
<i>Canthidium</i> sp. 6	0.58	33.14	0.693	1.26	1.36	↑
<i>Oxysternon conspicillatum</i>	0.56	35.08	2	2.59	2.49	
<i>Ontherus diabolicus</i>	0.55	37	0.903	1.73	2.16	↑
<i>Onthophagus</i> sp. 6	0.54	38.88	0.366	1.23	0.903	
<i>Deltocilum orbiculare</i>	0.52	40.67	0.924	0.462	0	↓
<i>Onthophagus</i> sp. 1	0.51	42.46	0.903	0.999	0.88	
<i>Canthidium</i> sp. 2	0.48	44.14	0.597	0.999	1.34	↑
<i>Eurysternus caribaeus</i>	0.48	45.8	3.42	3.36	3.04	↓
<i>Canthidium haroldi</i>	0.48	47.46	0.924	0.462	0.999	
<i>Dichotomius ohausi</i>	0.47	49.12	2.82	2.05	2.39	
<i>Uroxys</i> sp. 1	0.47	50.75	0.231	1.06	0.903	

Bolivia (Forsyth *et al.* 1998). Dung beetle species richness and abundance were variable among samples (fig. 5), a feature that was also reported by Radtke *et al.* (2007) in the Ecuadorian Amazon. Both richness and abundance significantly decreased from one to six months after road opening for the three transects, which is probably due to slightly more rainy conditions in the second part of the survey. Rain, temperature, and seasonal conditions in general can greatly influence dung beetle populations, causing surges and declines of particular species from one week to the next (Hanski & Cambefort 1991).

### Impact of road construction on dung beetle communities

Although habitat edges can have profound effects on the spatial distribution of many species (e.g. Lovejoy *et al.* 1986, Murcia 1995, Ries *et al.* 2004, Laurance *et al.* 2007) including beetles (Ewers & Didham 2008), our study provides no clear evidence of short term impact of road opening on dung beetle communities in Chiruisla. In general, diversity, abundance and community composition did not differ significantly among transects located at various distance from the road. Potential explanations for the lack of an impact of the road on dung beetle populations concerns the limited width of the road (10 m) and the absence of further clear-cuts by colonizing people, as access to Chiruisla is controlled by the oil company. Dunn & Danoff-Burg (2007) found that the most important effect of roads on carrion beetle assemblages appeared to be due to road width rather than road type (paved or dirt). A parallel study on the impact of road construction on vegetation revealed that in areas that were not directly disturbed during construction, the road had little effect on the original vegetation composition (J. Jaramillo comm. pers.). This explanation would agree with Halffter & Arellano (2002) who showed that tree cover was the most influential factor determining dung beetle community composition in the neotropics.

Another explanation could be that we did not sample deep enough into the rainforest to get much



**Figure 8**

Percentage contributions, based separately on abundance and biomass data, of individual dung beetle species at the three distances from the road (L10, L50, L100) over the study period (from 1 to 6 months after road opening). Species are represented by black circles, which are scaled by differences in average body mass. Both axes are log-transformed so the species in the top right corner of each panel contribute the most towards the patterns. The diagonal dashed line identifies the position of species that contribute equal weights to analyses based on both data sets. Large-bodied species clearly contributed the most to patterns based on biomass data.

beyond the edge effects, or that our sampling effort was not sufficient (see the spatial extent in the study by Dunn & Danoff-Burg 2007 on carrion beetles). The great olfactory powers of dung beetles in locating feces may also have obscure local population differences over 100 m distances. In a large scale study in the Southern Alps in New Zealand, Ewers & Didham (2008) found that beetle communities differed in species richness and composition from the deep forest interior up to 1 km inside forest. The edge effects recorded in the study were much stronger than in our case, making this explanation improbable.

Theoretically we would have expected opposite responses of dung and carrion beetle community to the road, the former being negatively affected by the road while the latter being attracted by the carrion produced by the road. However, additional analyses revealed no significant differences between these two guilds at the community level, in their response to road construction. Dung beetle richness and abundance were rather constant among transects, ranging from 42–44 species and 480–580 individuals, respectively. Carrion beetles varied from 14–20 taxa and 50–58 individuals depending on date and transects, but with no evident increase when getting closer to the road. For the two guilds, NMDS analyses revealed no differences among transects on both species richness and abundance ( $R < 0.2$ ,  $P > 0.67$ ).

Our analyses revealed two signs of potential effects by road opening. First the number of rare species was greatly reduced in the transect nearest to the road, through time. Rare taxa have proven to be useful indicators of human disturbance (Hecnar & M'clokey 1996, Maurer *et al.*, 1999). Because rare species by definition represent a small number of individuals, sampling for them requires extensive field work to generate well-supported conclusions. Second the estimated biomass of the three dominant dung beetle species decreased with distance to the road. This pattern was mainly due the decrease in abundance of only one species, the two other large-bodied species showed no similar trend. Dung beetle biomass response to perturbation is however debated. On one hand, larger insect species may be more susceptible to local extinction in disturbed areas because they usually have more stochastic population dynamics (Baumgartner 1998). Alternatively, microclimate conditions are likely to be altered at forest edges (e.g. increasing temperature extremes and moisture loss, Williams-Linera *et al.* 1998) and larger body size may confer greater resistance to desiccation (see Grimbacher *et al.* 2008 for a discussion).

### **Insights for planning environmental studies in Ecuador**

The Amazon region exhibits exceptionally high biodiversity (Myers *et al.* 2000), which makes capacity building for environmental governance in the region particularly important. In this context the search for relevant bioindicators of the degree of human disturbance is a priority for all developing nations that contain Amazon forest. Our study gave poor support for the use of dung beetles as indicators of short term-response (from 1 to 6 months) to road construction. However, although road construction might not negatively affect dung beetle diversity and abundance in microlandscapes over short time scales, these conclusions cannot be extrapolated directly to the much larger scales of landscapes and decades (see the MAP initiative concerning the inter-oceanic highway in the Southwestern Amazon (<http://www.map-amazonia.net/>) for further discussion; Perz *et al.* 2008). For example, a study of road impacts on a cloud forest in Puerto Rico 35 years after opening, showed that although there was limited impact on vegetation structure and composition, the recovery of soil resource levels to those of mature forests was extremely slow (Olander *et al.* 1998). After opening, roads foster access to natural resources and facilitate market access for rural producers, which in turn may generate habitat fragmentation and degradation (Perz *et al.* 2008). Developing a sustainable plan for road corridors in the Amazon would require long-term programs proceeded by coordinated data collection and long-term monitoring. This would allow formulation of likely scenarios of long-term road impact, which then could serve as a basis for participatory planning not only with government agencies at national, provincial, and local levels but also with local communities.

Finally, to conclude this last article of the special session of “*Entomology in Ecuador*”, we would like to stress that, in the light of this study, appropriate environmental assessment requires a good taxonomic basis. Limitations in taxonomy expertise represent a great challenge for the use of dung beetles as bioindicators in the mega-diverse rainforest of the Ecuadorian Amazon. Further studies should reveal whether coarser taxonomic data or data on particular dung beetle taxa could be used to detect ecosystem changes with sensitivity. However, in a study on tropical beetles, Grimbacher *et al.* (2008) showed that species data had the greatest sensitivity to environmental change and cautioned against the use of higher taxonomic levels as a standard procedure for the study of environmental change in invertebrate assemblages. Investing resources in insect taxonomy likely represents a critical requirement for measuring the

conservation status of highly endangered Neotropical ecosystems.

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**Appendix 1.**

List of total number of individuals of the dung beetle (Coleoptera: Scarabeinae) species and morpho-species captured in excrement- and tuna fish-baited pitfall traps during the study period (1 month, 3 month and 6 months after road building).

Tribes	Species	Sept 2005	Nov 2005	Feb 2006
Ateuchini	<i>Ateuchus murrayi</i> (Harold 1868)	26	5	1
	<i>Ateuchus scatimoides</i> (Balthasar 1939)	15	4	3
	<i>Ateuchus sp.1</i>	5	10	0
	<i>Ateuchus sp.2</i>	9	3	2
	<i>Ateuchus sp.3</i>	3	3	0
	<i>Canthidium haroldi</i> (Preudhome de Borre 1886)	5	7	3
	<i>Canthidium sp.1</i>	0	1	0
	<i>Canthidium sp.2</i>	12	6	2
	<i>Canthidium sp.3</i>	9	2	0
	<i>Canthidium sp.4</i>	107	12	0
	<i>Canthidium sp.5</i>	10	2	0
	<i>Canthidium sp.6</i>	22	5	2
	<i>Canthidium sp.7</i>	49	8	3
	<i>Canthidium sp.8</i>	3	0	0
	<i>Trichilium sp.1</i>	0	0	2
	<i>Uroxys sp.1</i>	2	6	5
Canthonini	<i>Canthon aequinoctialis</i> (Harold 1868)	248	278	180
	<i>Canthon luteicollis</i> (Erichson 1847)	153	78	12
	<i>Canthon brunneus</i> (Schmidt 1922)	2	1	1
	<i>Canthon sp.1</i>	5	3	1
	<i>Canthon sp.2</i>	0	1	0
	<i>Deltocilium carinatum</i> (Westwood 1837)	9	2	2
	<i>Deltocilium amazonicum</i> (Bates 1887)	3	6	9
	<i>Deltocilium orbiculare</i> (Lansberge 1874)	0	1	10
	<i>Deltocilium obenbergeri</i> (Balthasar 1939)	95	65	25
	<i>Deltocilium sp.1</i>	8	1	2
	<i>Deltocilium sp.2</i>	1	2	2
	<i>Deltocilium sp.3</i>	19	21	12
	<i>Malagoniella astyanax</i> (Olivier 1789)	0	0	1
	<i>Sinapisoma sp.1</i>	0	0	3
	<i>Scybalocanthon sp.1</i>	20	3	9
	<i>Scybalocanthon pygidialis</i> (Schmidt 1922)	3	0	0
	<i>Sylvicanthon bridarollii</i> (Martinez 1949)	21	36	2
	<i>Sylvicanthon sp. 1</i>	0	4	3
Dichotomiini	<i>Bdelyrus sp.1</i>	0	1	0
	<i>Dichotomius fortstriatus</i> (Luederwaldt 1923)	210	201	115
	<i>Dichotomius globulus</i> (Felsche 1901)	5	2	5
	<i>Dichotomius lucasi</i>	112	18	27
	<i>Dichotomius prietoi</i> (Martínez & Martinez 1982)	29	15	14
	<i>Dichotomius mamillatus</i> (Felsche 1901)	80	45	35
	<i>Dichotomius obausi</i> (Luederwaldt 1922)	63	26	25
	<i>Dichotomius sp.1</i>	20	19	9
	<i>Ontherus diabolicus</i> (Genier 1996)	26	15	7
	<i>Scatimus strandi</i> (Balthasar 1939)	0	4	0
	<i>Scatimus sp.1</i>	2	5	0
	<i>Scatimus sp.2</i>	1	0	1
Eurysternini	<i>Eurysternus caribaeus</i> (Herbst 1789)	152	74	51
	<i>Eurysternus confusus</i> (Jessop 1985)	194	105	50
	<i>Eurysternus hamaticollis</i> (Balthasar 1939)	78	42	15
	<i>Eurysternus infexus</i> (Germar 1824)	8	1	0
	<i>Eurysternus vastiorum</i> (Martinez 1988)	10	2	1
	<i>Eurysternus velutinus</i> (Bates 1887)	103	51	38
Onthophagini	<i>Onthophagus haematopus</i> (Harold 1875)	219	282	89
	<i>Onthophagus acuminatus</i> (Harold 1880)	5	12	3
	<i>Onthophagus sp.1</i>	14	6	0
	<i>Onthophagus sp.2</i>	6	9	3
	<i>Onthophagus sp.3</i>	10	8	4
	<i>Onthophagus sp.4</i>	19	11	0
	<i>Onthophagus sp.5</i>	15	2	2
	<i>Onthophagus sp.6</i>	1	1	0
	<i>Onthophagus sp.7</i>	1	0	0
	<i>Onthophagus sp.8</i>	2	1	1
	<i>Onthophagus sp.9</i>	3	2	4
	<i>Onthophagus sp.10</i>	11	7	1
Phanaeini	<i>Coprophanes telamon</i> (Erichson 1847)	23	40	22
	<i>Coprophanes callegarii</i> (Arnaud 2002)	1	7	2
	<i>Oxysternon conspicillatum</i> (Weber 1801)	63	33	15
	<i>Oxysternon silenus</i> (Castelnau 1840)	8	2	0
	<i>Phanaeus chalcomelas</i> (Perty 1830)	26	40	10

# Temporal abundance patterns of butterfly communities (Lepidoptera: Nymphalidae) in the Ecuadorian Amazonia and their relationship with climate

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**Abstract.** Tropical insects show temporal changes in their abundance and climate is one of the most influential factors. For tropical butterflies, few studies have quantified this relationship or analyzed changes in community composition and structure throughout time. Communities of butterflies attracted to rotting-carrion bait in one area of the Yasuni National Park, in Ecuadorian Amazonia were examined for these relationships. Butterfly communities in three different strata of the forest were sampled over 13 months using traps with rotten shrimp bait. In total, 9236 individuals of 208 species were collected between April 2002 and April 2003. The composition and structure of butterfly communities showed significant variation during the survey with a constant replacement of species throughout the year. Additionally, these communities had the highest species richness and abundance during the months with high temperatures and intermediate precipitation. Despite relatively low variation, temperature was the most significant climatic factor explaining differences in butterfly richness and abundance throughout the year. This significant response of butterfly communities to slight temperature variations reinforce the need of temporal studies to better predict how tropical butterfly populations will respond to predicted climate change.

**Résumé.** Phénologie de l'abondance des communautés de papillons (Lepidoptera : Nymphalidae) de l'Amazonie Equatorienne et relations avec le climat. Les insectes tropicaux montrent des variations en abondance qui sont principalement influencées par le climat. En ce qui concerne les papillons tropicaux, relativement peu d'études ont quantifié cette influence ou analysé les changements de structure des communautés le long de l'année. Nous nous sommes intéressés à cette question en analysant les communautés de papillons attirés par des pièges à carcasse en décomposition dans une zone du Parc National de Yasuni, en Amazonie équatorienne. La méthodologie a consisté en un échantillonnage durant 13 mois dans trois strates différentes de la forêt en utilisant des pièges remplis d'appât à base de crevettes en décomposition. Un total de 9236 individus et 208 espèces de papillons ont ainsi été collectés entre avril 2002 et avril 2003. La composition des communautés de papillons a montré une variation significative pendant l'étude, décrivant un patron circulaire avec un remplacement constant des espèces le long de l'année. De plus, ces communautés ont montré une richesse et une abondance maximales pendant les mois présentant des températures élevées et des niveaux de précipitations intermédiaires. En dépit de variations relativement faibles, la température fut le facteur climatique le plus significatif pour expliquer les différences en terme de richesse et d'abondance tout au long de l'année. Cette réponse significative des communautés de papillons à de faibles changements de température en forêt tropicale, renforce la nécessité d'études temporelles afin de mieux prédire comment les populations de papillons tropicaux vont répondre aux changements globaux.

**Keywords:** Rotting-carrion Nymphalid guild, Ecuador, Precipitation, Temporal abundance patterns, Temperature, Tropical rain forest.

Ecuador is one of the most butterfly diverse countries worldwide along with Perú and Colombia, countries that at least have 4 times more land. Ecuador has approximately 4000 species of butterflies (Willmott & Hall *in prep.*) but our knowledge about these insects is still scarce. According to data from 2000–2005,

Ecuador had the highest deforestation rate in Latin America (FAO 2007). As habitat loss is the main cause of butterfly extinction, diversity is being lost before we can quantify or understand it.

Studies on the temporal fluctuations of butterfly species of temperate zones have contributed successfully to regional conservation programs (Sparrow *et al.* 1994). In the same way, this type of research with tropical species could contribute to conservation programs in the Amazonia, especially taking in

consideration that butterflies have been widely used as biological indicators (Brown 1991, Pearson & Cassola 1992, Kremen 1992; 1994, Hill *et al.* 2001, Scoble 1995, Carroll & Pearson 1998, Lawton *et al.* 1998, Brown & Freitas 2000, Fleishmann *et al.* 2005).

In this context, it is important to study factors that influence the diversity and temporal patterns of species richness over time and not only to describe these patterns. Climate has a great influence on several aspects of butterfly communities. In temperate zones, climate is the most important influential factor on Lepidopteran species richness through both direct effects (higher temperature may correlate with higher numbers of species) and indirect effects (weather influences on food availability) (Menéndez *et al.* 2007). Moreover, butterfly populations from those areas are often regionally synchronized (see Pollard 1991) due to the regional correlation in climatic patterns (Sutcliffe *et al.* 1996). Butterfly abundance patterns are generally regulated by food resource availability (phenology of host plants) (Yamamoto *et al.* 2007), which is also regulated by the climate. In the Neotropics, climatic factors (temperature and precipitation) are also important in determining both richness and community structure of butterflies at both the local scale (Atlantic forest butterflies, Brown & Freitas 2000) and at regional scale (48 sites from Mexico to southern Brazil, Brown 2003).

For several decades, it has been known that tropical insects have seasonal changes in their abundance and that climate is one of the most influential factors controlling these patterns (Wolda 1978; 1988 and citations therein). In general, climate acts directly by increasing the mortality of adults and of larvae in all stages of development, and indirectly by affecting food availability (production of new leaves, fruits and flowers). This relationship with plant phenology results because numerous herbivores use specific plant resources during short periods of time, when the quality of these sources is optimal (Hellmann 2002). In comparison with temperate species, tropical insects tend to have less noticeable seasonal peaks and a higher proportion of active species throughout a year, particularly in areas that do not have marked dry seasons (Wolda 1988). In the case of tropical butterflies, changes in temporal abundance patterns have been reported in Asian forests with seasons marked by the monsoon (Spitzer *et al.* 1993) and in aseasonal tropical forests (Hill *et al.* 2003). Additionally, it has been reported that butterfly communities attracted by baits in Ecuadorian Amazonia (area with an aseasonal climatic pattern) fluctuate over the year in abundance and species richness, showing clear peaks and lows (DeVries *et al.* 1997; 1999,

DeVries & Walla 2001). Despite the influence of the climate over tropical butterfly populations, few studies have analyzed quantitatively the relationship between climate and butterfly communities (see Hamer *et al.* 2005) or changes in composition and structure of butterfly communities over the year, and not only the variation in the species richness and abundance. This situation is especially true for the Neotropics, with countries with the highest diversity worldwide: Perú, Ecuador and Colombia.

The primary objectives of this research were: (1) to analyze the variation of temporal patterns (composition and structure) of butterfly communities attracted to carrion baits in an aseasonal forest of Ecuadorian Amazonia; and (2) to quantify the relationship between climatic factors (precipitation and temperature) and variation in abundance and species richness in these Lepidopteran communities over the year.

## Material and methods

### Study area

The study area was located in areas surrounding the Yasuni Scientific Research Station, in the Ecuadorian Amazonia (YSRS, 0°39'03" N, 76° 22'42" W). The station is located in the Yasuni National Park, which with the Huaorani Ethnic Reserve, comprises 1.6 million ha of forest and was declared by UNESCO as a Biosphere Reserve in 1987 (Pitman 2000). The park contains extensive areas of primary forest and is inhabited by indigenous groups. It is divided into different blocks ceded to oil companies which have constructed several roads in the north for prospecting and exploitation (Valencia *et al.* 2004). Trees reach canopy heights of 30-35 m and emergent trees higher than 50 m exist in the area. The most abundant tree species in the park is a palm, *Iriartea deltoidea* Ruiz & Pav. 1798 (Burnham 2002). Elevations range from 200-500 m.a.s.l. Weather is tropical and humid. Rainfall and temperature are aseasonal with a mean annual temperature of 26°C (Burnham *et al.* 2001, Burnham 2002). There is a slightly drier period between December and February (Baslev *et al.* 1987) but the mean temperature remains remarkably stable throughout the year (Pitman 2000). The area receives around 3000 mm<sup>3</sup> of rain per year, based on a 10-year record from a meteorological station located at YSRS.

### Census techniques

Butterflies were successively sampled using Van Someren-Rydon traps (Rydon 1964)

baited with shrimp (*Penaeus vannamei* Boone 1931) that had been fermenting for 11–20 days.

Therefore, the present study focused on the rotting-carrion guild of butterflies, species that feed on decaying organic material. According to Hall & Willmott (2000), this guild has been ignored by most authors, including DeVries *et al.* (1997), who recognized a system of two feeding guilds, one for fruit feeders and one for nectar feeders. We selected rotten shrimp as bait because it attracted at least 20 percent more species and individuals than rotten fruit baits in small experiments carried out by us at YSRS (Checa, unpublished data).

Using a hierarchical sampling design, four sampling sites were located within four 1ha-plots of undisturbed forest (Fig. 1) near YSRS. The distance between two neighboring plots was over 500 m and all sites were similar in terms of altitude (400–450 m) and topography. At each site, three baited traps were set up at three different strata, understory (1.5 m), intermediate (10 m) and canopy (20–27 m). These different strata were sampled due to the different composition and structure reported for tropical butterfly communities vertically in these forests (DeVries 1988; DeVries *et al.* 1997; DeVries *et al.* 1999; Hill *et al.* 2001; Schulze *et al.* 2001; Fermon *et al.* 2003, Dumbrell & Hill 2005, Molleman *et al.* 2006, Barlow *et al.* 2007).

All 48 traps (4 plots × 4 sampling points × 3 strata) were checked daily during the last 11 days of each month from April 2002 to April 2003. The traps were opened and baited on the first trapping day. Over the next 10 days, traps were checked and all trapped butterflies were collected and killed by thoracic compression. Specimens were placed in glassine envelopes. The bait was renewed daily. Traps were checked between 08:00 and 15:00. The sequence of site visitation was randomized to avoid any systematic bias. A total of 130 trapping days were employed during this research.

#### Taxonomical identification

We only analyzed the Nymphalidae species captured, which correspond to the subfamilies Apaturinae, Biblidinae, Charaxinae, Heliconiinae, Limenitidinae, Morphinae, Nymphalinae and Satyrinae. Although, some species of Riodinidae, Hesperiidae and Lycaenidae were also collected, they were not included in the analysis of the present paper.

All collected material was examined in the laboratory and classified to the level of subspecies. Identifications were performed using taxonomic revisions of some Neotropical genera: *Adelpha* (Willmott 2003), *Asterope* (Jenkins 1987), *Catoblepia* (Bristow 1981), *Catonephele* (Jenkins 1985), *Eunica* (Jenkins 1990) and *Opsiphanes* (Bristow 1991). However, as there are not taxonomic treatments for all genera in the study areas, the remaining species were identified by specialists, Gerardo Lamas (University of San Marcos, Perú) and Keith Willmott (University of Florida, USA), who also confirmed the identifications made with the references. The taxonomic classification and nomenclature followed the revision by Lamas (2004). All collected specimens were deposited in the Section of Invertebrates, Museum of Zoology QCAZ of the Pontifical Catholic University of Ecuador.

#### Statistical analyses

Species accumulation curves were used to determine whether the majority of the species from the area were included in the sample. These curves plot the cumulative number of species collected (S) as a function of sampling effort (n). Since the order of the samples included in the process affects the general form of the curve (Colwell & Coddington 1994, Magurran 2004), curves were determined with 100 randomizations. This analysis was conducted for each of the subfamilies included in this study, using the program, Species Diversity & Richness III®.

The variation in the composition and structure of butterfly communities over the year was analyzed using non-metrical multidimensional scaling (NMDS) which uses distance vectors to distinguish groups. In this study, Euclidean distance was selected. The main variable analyzed was time (13 months, from April 2002 to April 2003) and data from different traps and plots during each month were pooled. An Analysis of

Similarities (ANOSIM) was used to test if the differences in structure and composition of butterfly communities throughout the year were significant. A SIMPER analysis was employed to find species that were responsible for the separation of groups (butterfly communities) over time. These analyses were done using the program PAST 1.8© (Hammer *et al.* 2008).

Linear regression models were run to determine if there was a relationship between butterfly population fluctuation and climate variables. These models incorporated autoregressive correlated errors for the repeated observations within each month. The Kenward-Rogers (1997) adjustment to the denominator degrees of freedom in the F-tests was used to account for bias in the estimation of the variance-covariance matrix of the errors. We use the Glimmix procedure to run these models, which fits statistical models to data with correlations due to temporal proximity. The SAS 9.2® program was used to run these analysis.

Despite the correlation between temperature and rain, both variables were used to differentiate the relationship with butterfly population changes over time. If the linear model fits the data well, a residual plot should be a scatter of points that follow a normal distribution and are uncorrelated with the fitted values (Gotelli & Ellison 2004). When the residuals were not normally distributed, the variables were transformed logarithmicly (Gotelli & Ellison 2004). Linear regression models were performed using the total number of species and individuals collected daily with the average temperature and precipitation data for that day. Each subfamily was evaluated individually to determine if each taxonomical group responded differently to the climatic variation.

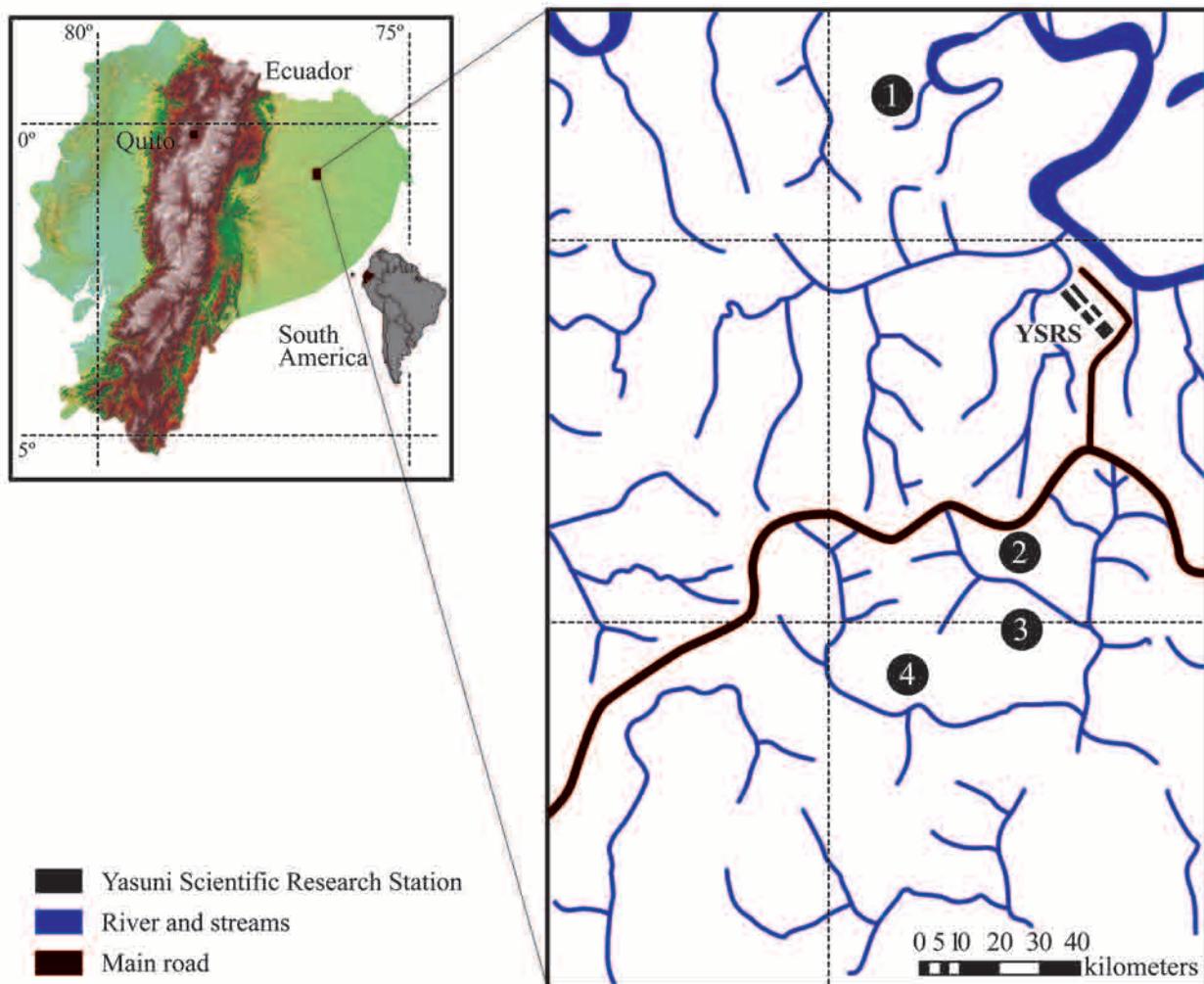
## Results

A total of 10,254 individuals were collected representing 240 butterfly species from the families Nymphalidae, Riodinidae, Lycaenidae and Hesperiidae. In this report, only the data for the Nymphalidae were analyzed. This study group contained 9,236 individuals from 208 species as a subset of the total sample (Appendix 1), more than 90% of the specimens were males. Two new species, *Magneuptychia* sp. and *Chloreuptychia* sp., and two new records for Ecuador, *Eunica violetta* Staudinger [1885] and *Adelpha amazona* Austin & Jasinski 1999, were found (Fig. 2). Twenty singletons and 14 doubletons were registered. *Temenis laothoe laothoe* (Cramer 1777) was the most abundant species with 1,136 individuals (12.3% of the total sample). *Adelpha jordani* Fruhstorfer 1913 was represented by 522 individuals and *Opsiphanes invirae cassina* (Hübner [1808]) was represented by 449 individuals (Fig. 2). The subfamily Biblidinae was the most numerous with 4,408 individuals from 70 species while Apaturinae had the least number of species and individuals (5 and 209 respectively). The accumulation curves for all subfamilies stabilized (Fig. 3) since in the majority of cases only one new species was registered in the last 30 survey days. The subfamily Limenitidinae was an exception, as the species accumulation curve started to stabilize in the ninth month of survey.

## Temporal Patterns of Butterfly Communities

Results from the NMDS analysis showed that the overall composition and structure of the butterfly community changed over the year with a circular pattern of variation. Similarity between butterfly communities collected in different months decreased from April to September 2002 but later increased until the end of the sampling period (April 2003) when the communities were similar in composition and structure to those of April 2002 (Fig. 4). Results of the ANOSIM showed that most of these differences were highly significant ( $p < 0.001$ ), except for consecutive months in the majority of cases, and between April 2002 and April 2003 (Table 1). The SIMPER analysis revealed that the species contributing the most to this

separation of the butterfly communities throughout a year were *Adelpha jordani*, *Panacea procilla divalis* (H. W. Bates 1868), *Dynamine chryseis* (H. W. Bates 1865), *Diaethria clymena peruviana* (Guenée 1872), *Adelpha mesentina* (Cramer 1777) and *A. iphiclus iphiclus* (L. 1758) (Table 2, Fig. 2). These butterflies were among the most numerous in this survey. Together they comprise 1913 individuals, 21% of the total sample. The 34 singleton and doubleton species contributed the least to the observed variation in the NMDS. Together they explained only 6 percent of the variation (Table 2). A constant turnover of species within butterfly communities was observed throughout the year, less than 13 percent of the species were present during all the months of the survey. The subfamilies with the highest number of species during the study,



**Figure 1**

Map of the study area showing the location of the four butterfly sampling sites (1,2,3 and 4) in Yasuni National Park, near the Yasuni Scientific Research Station (YSRS) Ecuadorian Amazon.

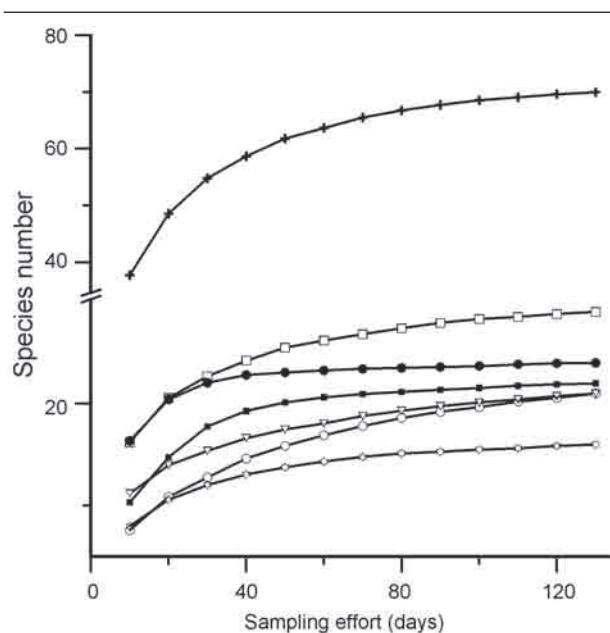
**Figure 2**

Some species collected in YSRS from April 2002 to April 2003. Two new records for Ecuador are included: **A1**, *Adelpha amazona* and **B3**, *Eunica violetta*. The other species are: **C2**, *Narope cyllabarus*; **D4**, *Opsiphanes invirae cassina*; **E5**, *Temenis laothoe laothoe*; **F6**, *Coenophlebia Archidona*; **G7**, *Agrias claudina lugens*; **H8**, *Panacea procilla divalis*; **I9**, *Adelpha jordani*; **J10**, *Anaeomorpha splendida*. All of the photos are presented in the real size of the butterfly. Photos by María F. Checa.

Biblidinae, Charaxinae and Limenitidinae, were also the most abundant overall (Fig. 4).

### Butterfly Communities and Climate

Butterflies attracted to rotting-carrion bait showed a conspicuous fluctuation along the year with clear highs and lows. The highest number of species (145) and the highest abundance (1681 individuals) were collected in September. This peak coincides with the beginning of the period with the least precipitation. Rain level decreased from 424 mm<sup>3</sup> in July to 145 mm<sup>3</sup> in September (Fig. 5). This peak in the species and overall abundance coincides with an increase in average temperature by almost one degree from June to September (from 25.8 °C to 26.7 °C, see Fig. 5). In contrast, the number of individuals and species was the lowest from March to April with an average of 82 species and 310 individuals collected in the period when precipitation started to increase (334 mm<sup>3</sup> in February and 230 mm<sup>3</sup> in March) and the average temperature decreased by almost one degree in comparison to the other months. The warmest period of the year ends in March (Fig. 5). The linear regression models showed a significant relationship between the butterfly population fluctuation and the climate variables (Table 3). The coefficient of temperature was significant in the regression model between the total number species collected each day and the average temperature and precipitation on the same day ( $N = 100$ ,  $\beta_{temp} = 3.11$ ,  $p < 0.01$ ). Similar results were obtained for the regression model between total daily relative abundance of butterflies and temperature and precipitation ( $N = 100$ ,  $\beta_{temp} = 3.93$ ,  $p < 0.01$ ). For these two linear regression models, the average temperature coefficient was higher than the precipitation coefficient (Table 3), indicating that daily temperature explained the highest amount of variation. In both cases, the precipitation coefficient



**Figure 3**

Species accumulation curves calculated for each Nymphalid subfamily, Biblidinae (crosses), Charaxinae (open squares), Heliconiinae (closed squares), Limenitidinae (closed circles), Satyrinae (open circles), Morphinae (triangles), and Nymphalinae (stars).

was negative but not significant, showing that rain increase was linked to a decrease in the butterfly number of individuals and species. In the months when precipitation decreased starting in September, the number of butterflies increased considerably (Fig. 5).

The linear regressions models that were used to analyze daily data (species richness and abundance) of each subfamily independently showed similar results. The coefficients of temperature were significant

**Table 1.** Results of ANOSIM analysis with the  $p$  values of similarity between butterfly communities from each month from April 2002 to April 2003.

	Apr 2002	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 2003	Feb	Mar	Apr
Apr 2002	0.011	0.149	0	0	0		0	0.001	0.132	0.239	0.553	0.303	0.13
May		0.347	0.337	0.173	0.002		0.024	0.439	0.264	0.171	0.013	0	0
Jun			0.06	0.016	0		0	0.075	0.611	0.617	0.153	0.011	0.003
Jul				0.662	0.007		0.065	0.806	0.094	0.053	0.003	0	0
Aug					0.033		0.327	0.622	0.021	0.009	0	0	0
Sep							0.341	0.018	0	0	0	0	0
Oct								0.107	0	0	0	0	0
Nov									0.07	0.042	0.001	0	0
Dec										0.751	0.209	0.017	0.003
Jan 2003											0.24	0.031	0.009
Feb												0.3	0.123
Mar													0.732

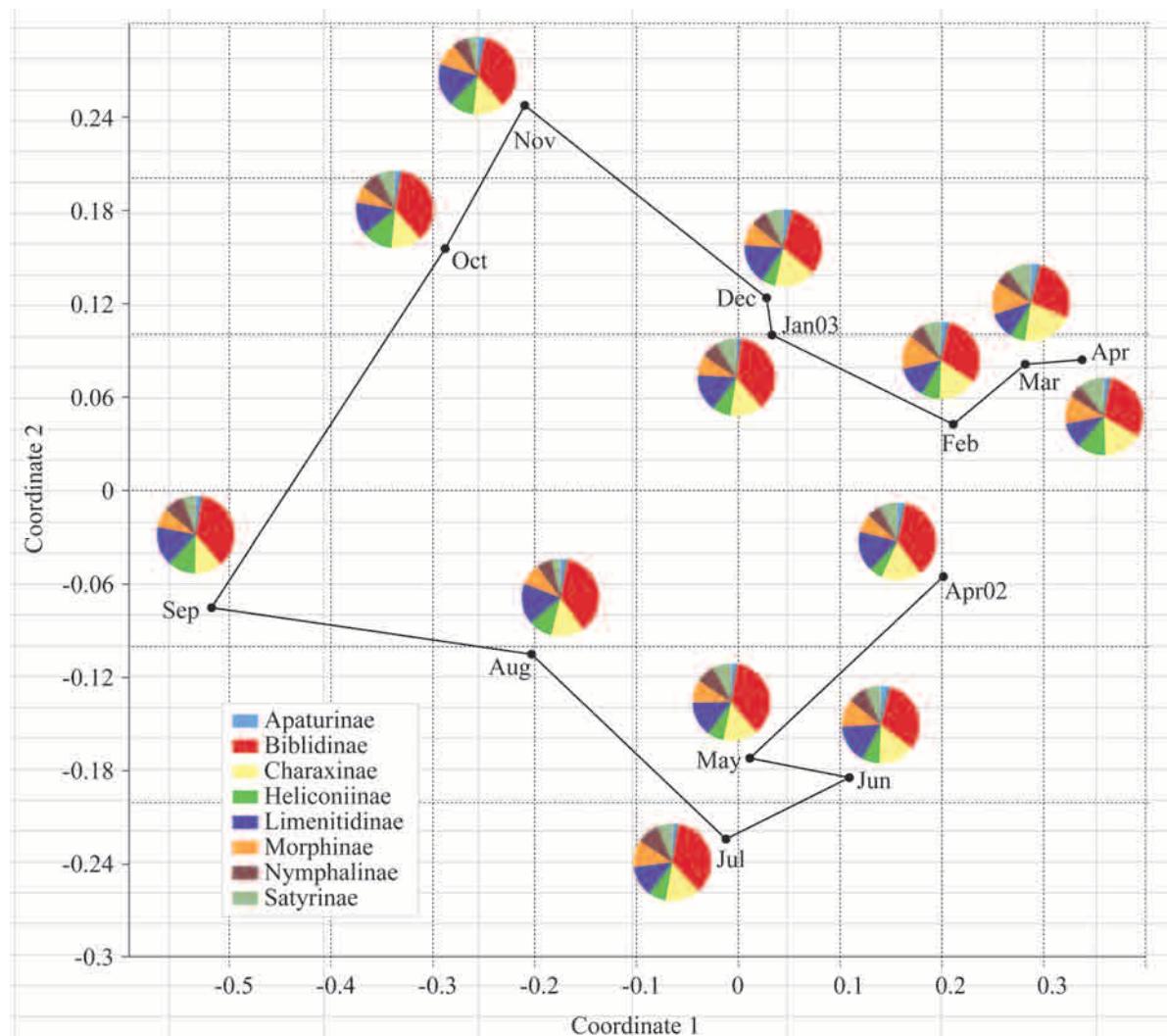
for Biblidinae, Limenitidinae and Charaxinae, but were not significant for Morphinae, Nymphalinae, Heliconiinae, Apaturinae and Satyrinae. However, Satyrinae presented significant coefficients for precipitation (Table 3). The values of the coefficients from the models of each subfamily increased compared to the models of the entire community (pooling all of the subfamilies) indicating a decrease in the variance and a better fit of the variables in linear regression models.

## Discussion

During this survey, 9236 individuals from 208 species of butterflies were collected in

baited traps over 130 days of sampling using 48 traps. This study focused on the rotting carrion guild of butterflies, which is still poorly known; in fact, most of the previous studies focused on rotting-fruit butterflies employing rotten banana as bait (e.g. Pinheiro & Ortiz 1992, Kremen 1994, Shahabuddin & Terborgh 1999, Lewis 2000, Schulze *et al.* 2001, Hill *et al.* 2001, DeVries & Walla 2001, Hamer *et al.* 2003, Fermon *et al.* 2003, Dumbrell & Hill 2005, Hamer *et al.* 2005, Veddeler *et al.* 2005, Molleman *et al.* 2006, Barlow *et al.* 2007, Uehara-Prado *et al.* 2007).

This study found approximately five times as many individuals to be attracted to carrion bait than a similar study by DeVries *et al.* (1999) using fruit bait at a nearby site. These differences could be due



**Figure 4**

Results of the NMDS using Euclidean distance showing differences in the structure and the composition of butterfly communities throughout the year. Circles represent the variation in species richness of the different subfamilies analyzed.

to many factors, most obviously differences between the study location faunas and differences between the total community abundance over the two survey periods. However, different types of bait are also likely to attract both different numbers of species and individuals. Consistent with our results, a study by Hall & Willmott (2000) throughout Ecuador found many more species and individuals of Riodinidae to be attracted to carrión baits than fruit baits. Additional

studies exploring this idea would clearly be valuable.

### Temporal Patterns of Butterfly Communities

The composition of butterfly communities attracted to rotting-carrión bait showed a circular pattern of variation throughout the year (Fig. 4). Among-month differences in butterfly composition were, in general, significant except for consecutive months (Table 1).

**Table 2.** Results of SIMPER method analyzing all of the 13 months of survey together. It is shown the relative contribution (Cont.) of different species to separate butterfly communities along the year and the cumulative percent of explanation (Cu.%) of each species.

Only species that most and less contributed are presented along with their abundance in each sampled month. To determine the contribution of each species, refer to the cumulative percent.

Species	Cont.	Cu.%	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
<i>Adelpha jordani</i>	0,70	1,9	0	0	0	0	29	137	81	119	58	63	13	12	10
<i>Panacea procilla divalis</i>	0,52	3,2	110	32	6	15	3	2	156	35	0	5	10	8	17
<i>Dynamine chryseis</i>	0,45	4,4	0	3	5	5	25	226	4	2	5	11	6	0	2
<i>Telenassa teletusa burchelli</i>	0,44	5,6	0	9	9	25	20	3	1	0	0	2	1	0	0
<i>Diaethria clymena peruviana</i>	0,43	6,7	5	15	17	36	16	17	6	10	1	2	0	1	1
<i>Adelpha mesentina</i>	0,41	7,8	7	19	10	19	18	41	47	48	15	17	4	4	0
<i>A. iphiclus iphiclus</i>	0,40	8,9	4	30	11	22	21	76	61	54	16	18	3	3	3
<i>A. attica attica</i>	0,38	9,9	3	6	5	12	5	18	17	26	7	6	3	0	0
<i>Pyrrhogrya neaerea argina</i>	0,38	10,9	1	1	0	1	16	20	17	6	5	5	1	0	1
<i>Laparus doris doris</i>	0,37	11,9	4	3	1	18	6	7	6	6	0	2	0	0	0
<i>Eunica clytia</i>	0,37	12,8	0	0	1	19	6	23	0	1	2	2	0	0	0
<i>Marpesia chiron marius</i>	0,37	13,8	3	3	4	1	13	8	13	0	0	0	0	0	0
<i>Hermeuptychia hermes</i>	0,37	14,8	10	28	23	36	13	7	5	1	3	1	6	2	4
<i>Pyrrhogrya amphiro amphiro</i>	0,36	15,7	3	3	0	1	5	33	13	7	1	7	1	0	2
<i>Panacea prola amazonica</i>	0,36	16,7	2	4	8	2	0	3	3	10	0	20	1	1	0
<i>Delpha erotia erotia</i>	0,35	17,6	3	13	8	8	7	8	5	19	7	2	5	0	0
<i>Doxocopa pavon pavon</i>	0,34	18,5	0	0	0	0	6	12	4	13	2	0	1	2	0
<i>Callicore cynosura cynosura</i>	0,34	19,4	2	4	4	10	11	7	3	6	1	0	1	0	0
<i>Adelpha thesprotia</i>	0,33	20,3	5	10	5	12	7	14	10	17	6	10	0	1	1
<i>Hermeuptychia fallax</i>	0,04	98,4	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Prepona pheridamas</i>	0,04	98,5	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cissia penelope</i>	0,04	98,6	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hermeuptychia maimoune</i>	0,04	98,7	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Caeruleuptychia scopulata</i>	0,04	98,8	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Dynamine gisella</i>	0,04	98,9	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Dynastor darius stygianus</i>	0,03	99,0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Magneuptychia libye</i>	0,03	99,1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Bia actorion rebeli</i>	0,03	99,1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Adelpha serpa diadochus</i>	0,03	99,2	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Dione juno juno</i>	0,03	99,3	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Tegosa serpia</i>	0,03	99,4	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Catoblepia generosa</i>	0,03	99,5	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Memphis xenocles xenocles</i>	0,03	99,6	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Callicore excelsior elatior</i>	0,03	99,6	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Memphis anna anna</i>	0,03	99,7	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Eunica violetta</i>	0,03	99,8	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Catacore kolyma kolyma</i>	0,03	99,9	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Anartia amathea sticheli</i>	0,03	99,9	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Eunica mygdonia mygdonia</i>	0,03	100	0	0	0	0	0	1	0	0	0	0	0	0	0

A constant turnover of the majority of species over certain periods of time was noted; less than 13% of species were present during the whole year of sampling. The constant presence of some species as *Temenis laothoe laothoe*, *Opsiphanes invirae cassina*, *Adelpha iphiclus iphiclus* and others (Appendix 1) suggests that they have overlapping generations (see Hamer *et al.* 2005). The butterfly species that contributed the most to the differences in the collections throughout the year were, *Adelpha jordani*, *Panacea procilla divalis*, *Dynamine chryseis*, *Telenassa teletusa burchelli* (Moulton 1909), *Diaethria clymena peruviana*, *Adelpha mesentina* and *A. iphiclus iphiclus* (Table 2, Fig. 2). These butterflies were some of the most abundant species in the study, but in contrast with other abundant species like *Temenis laothoe laothoe* or *Opsiphanes invirae cassina*, they were not present throughout the year and they had conspicuous peaks and declines in abundance. These temporal abundance patterns and their relative abundance partially explain why they contributed to the separation of butterfly communities throughout the year of survey. These temporal abundance patterns could also be related to the feeding specialization, indicating these species are probably specialists as polyphagous insects, with a wide range of host plants, show less seasonality than monophagous species that are more intimately associated with the phenology of a single host plant (Novotny & Basset 1998). In general, the temporal patterns of abundance in butterfly communities may be due to a variation in the dynamics of host plants or to a temporal variation in larval mortality (Hamer *et al.* 2005).

### Butterfly Communities and Climate

Plant phenology and climate are key environmental variables that affect butterfly population dynamics (Murphy *et al.* 1990, Spitzer *et al.* 1993; Barlow *et al.* 2007). In the case of abiotic factors, this study confirms the significant relationship between temperature and precipitation and population fluctuation of Neotropical butterflies, despite the overall aseasonality of the study area. There is synchronization between the decrease of precipitation and the increase in the number of captured species and individuals. Trap captures reached the lowest values of the entire year during the period with highest rainfall. It is possible that these data reflect the abundance of adult butterflies, but also the level of activity. However, daily activity, the proportion of butterflies flying, depends on the pool of individuals in a population. Despite overall favorable climatic conditions of high temperature and low precipitation, fewer species and individuals were collected during the days with highest precipitation.

Results from Yasuni concur with other studies about butterflies attracted to fruit baits in aseasonal forests in Ecuadorian Amazonia (DeVries *et al.* 1997; DeVries & Walla 2001) and in other Neotropical areas with marked dry and rainy periods (Barlow *et al.* 2007), where peaks of species richness and abundance were reported after the time of the year with the highest precipitation. There is a negative correlation between this rainfall and butterfly population fluctuation. Similar results were found in a study conducted in Borneo that focused on one species of Satyrinae (Hill *et al.* 2003). Furthermore, temperature is the variable that mostly explained the variation in the trap captures in comparison with precipitation, even though mean temperature only varies over one degree during the whole year. This result may be increasingly important in this century in light of global warming. Butterflies may have an extreme susceptibility to this phenomenon (Lawton *et al.* 1998 and citations therein, Wilson *et al.* 2005). This may have increasing importance in conservation programs.

Temperature's central role in the biology and life history of butterflies can be explained because these insects are ectothermic. Their life cycle, distribution and abundance are directly influenced by temperature (Roy *et al.* 2001). Several key processes for butterfly survival depend on regulation of internal temperature. Defense strategies of butterflies (mimicry, fast flight, etc) are related to their thermal biology (Chai *et al.* 1990). In periods with high precipitation, regularly accompanied by low temperatures, weather prevents flight, and adult mortality is higher due to predation (Bowers *et al.* 1985, Srygley & Chai 1990). In experiments with

**Table 3.** Coefficients ( $\beta$ ) from linear regression models to analyze the relationship between the total butterfly community and each subfamily independently with climatic variables.

Species richness (S) and abundance of butterflies (N) collected daily were used as dependent variables. Significant results are shown with asterisks (\*:  $p<0.05$ ; \*\*:  $p<0.01$ ). Climatic variables used correspond to daily measures recorded at YSRS. One hundred points were included in all of the regressions (N = 100).

Subfamilies	$\beta$ Temperature		$\beta$ Rain	
	N	S	N	S
TOTAL	3.93**	3.11**	-0.01	-0.01
Biblidinae	6.08**	42.97**	-0.04	-0.28
Limenitidinae	4.04*	23.77**	0.11	0.23
Charaxinae	7.45**	5.67**	-0.04	0
Nymphalinae	2.64	2.12	-0.08	-0.07
Morphinae	-2.72	-1.5	-0.03	-0.04
Apaturinae	1.23	0.7	-0.02	-0.02
Satyrinae	-0.21	-1.04	-0.12*	-0.24*
Heliconiinae	1.94	1.34	0.03	0

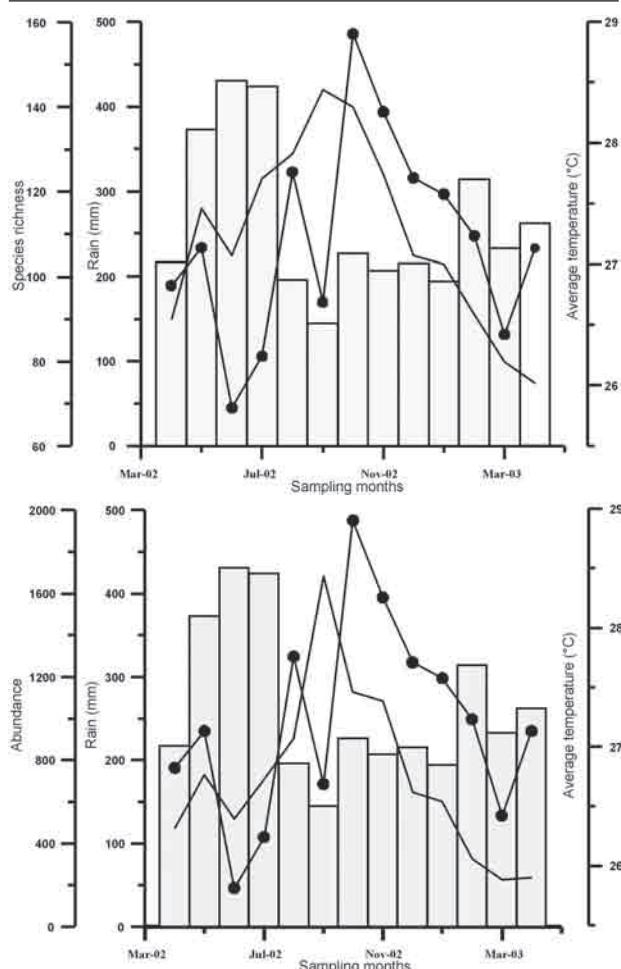
species from temperate areas, fecundity and longevity was higher at higher temperatures ( $>25^{\circ}\text{C}$ ) (Karlsson & Wiklund 2005).

Butterfly population dynamics are also related to plant phenology. Biotic interactions such as herbivory and pollination select for timing of plant phenology patterns (Wright 1996). In a tropical dry forest in Venezuela, butterfly oviposition occurs at the beginning of the rainy period which coincides with the production of new leaves (Shahabuddin & Terborgh 1999). This supports that the time of leaf production and dead plant tissue influence the time of emergence and length of larval stages, egg hatching, diapause and growth (Hellmann 2002). However, in the tropical rain forest of Yasuni, it is possible that a peak of abundance of larvae precedes the increase in adults in months with high rainfall levels (around May). However, this

would not coincide with the period of leaf production, which has been predicted to occur during time of peak irradiance in tropical evergreen forests where moisture deficits are absent (Wright 1996). The peak of species richness and abundance of butterflies could be related to the amount of available resources (flowers and fruits) for adults as well, because many tropical plants show marked flowering and fruiting seasons which may be synchronized between species (Poulin *et al.* 1999). In our sampling area, a parallel study of forest dynamics found a synchronized active period of flower production among most of the trees, shrubs and lianas when rain decreased in June (Aguilar 2004). This study suggests that fruit production, one type of adult food resource, occurs after rain decreases and coincides with butterfly abundance and species richness peaks.

Information about temporal abundance patterns of tropical butterfly communities is still scarce, especially in the Neotropics. Understanding the temporal variation of butterfly communities allows the establishment of environmental trends of these insects but also generates useful information for conservation programs (Murphy *et al.* 1990, Kremen 1994). The analysis of these patterns in relation to weather is crucial due to alarming deforestation rates which are rapidly changing tropical landscapes and modifying tropical climates. This analysis is especially important due to potential negative effects of climate change on butterfly populations (Lawton *et al.* 1998 and citations therein, Wilson *et al.* 2005). As an empirical support of the conclusions by Deutsch *et al.* (2008), our results of the tight relationship between temperature and butterfly population levels suggest that global warming issues will also be of major importance for ectothermic organisms living in tropical regions.

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**Figure 5**  
Variation in species richness (A) and abundance (B) of butterfly communities with climatic variables, rainfall (bars, in mm) and average temperature (dots, in  $^{\circ}\text{C}$ ) from April 2002 to April 2003.

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**Appendix 1. List of the total number of butterfly species attracted to bait (Lepidoptera: Nymphalidae) during the study period: April 2002 to April 2003.**

Classification and nomenclature follow the revision by Lamas (2004), excepting three species marked with asterisk (\*).

Species	2002 Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2003 Jan	Feb	Mar	Apr
<b>Apaturinae</b>													
<i>Doxocopa agathina agathina</i> (Cramer 1777)	3	11	6	15	11	14	15	19	14	10	2	4	2
<i>Doxocopa laure griseldis</i> (C. Felder & R. Felder 1862)	0	3	1	6	1	1	1	0	1	0	0	0	0
<i>Doxocopa linda linda</i> (C. Felder & R. Felder 1862)	1	2	1	3	3	5	1	2	3	2	1	1	1
<i>Doxocopa pavon pavon</i> (Latrelle 1809)	0	0	0	0	6	12	4	13	2	0	1	2	0
<i>Doxocopa zunilda felderii</i> (Godman & Salvin 1884)	1	0	1	0	0	0	0	1	0	0	0	0	0
<b>Biblidinae</b>													
<i>Asterope markii hewitsoni</i> (Staudinger 1886)	4	6	10	7	10	13	6	8	4	4	2	1	1
<i>Batesia hypochlora</i> C. Felder & R. Felder 1862	10	6	5	10	1	2	34	4	14	16	9	6	3
<i>Biblis hyperia laticlavia</i> (Thieme 1904)	3	3	0	1	4	5	5	4	3	6	1	0	0
<i>Callicore cynosura cynosura</i> (Doubleday 1847)	2	4	4	10	11	7	3	6	1	0	1	0	0
<i>Callicore excelsior elatior</i> (Oberthür 1916)	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Callicore hesperis</i> (Guérin-Méneville 1884)	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Callicore hystaspes zelphanta</i> (Hewitson 1858)	0	1	3	2	2	3	2	1	1	1	1	0	0
<i>Callicore pygas cyllene</i> (Doubleday 1847)	4	3	1	4	10	9	10	7	1	2	0	1	0
<i>Callicore texa maimuna</i> (Hewitson 1858)	0	0	0	0	0	1	2	2	0	0	0	0	0
<i>Catacore kolyma kolyma</i> (Hewitson 1852)	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Catonephele acontius acontius</i> (L. 1771)	7	11	5	7	5	3	8	7	13	5	5	2	2
<i>Catonephele numilia numilia</i> (Cramer 1775)	14	13	16	11	4	11	6	15	19	12	6	5	4
<i>Catonephele salacia</i> (Hewitson 1852)	2	2	0	2	0	0	0	0	0	0	0	0	0
<i>Diaethria clymena peruviana</i> (Guenée 1872)	5	15	17	36	16	17	6	10	1	2	0	1	1
<i>Dynamine artemisia glauce</i> (Bates 1856)	0	3	0	0	1	1	2	1	1	0	0	0	0
<i>Dynamine athemon barreiroi</i> Fernández 1928	0	1	0	4	0	2	0	1	1	0	0	0	0
<i>Dynamine chryséis</i> (Bates 1865)	0	3	5	5	25	226	4	2	5	11	6	0	2
<i>Dynamine gisella</i> (Hewitson 1857)	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Dynamine paulina paulina</i> (Bates 1865)	0	5	2	5	5	4	1	0	0	0	1	0	3
<i>Dynamine racidula racidula</i> (Hewitson 1852)	0	0	1	0	0	1	0	1	0	0	0	0	0
<i>Dynamine sara</i> (Bates 1865)	0	1	1	0	1	0	0	1	0	0	0	0	0
<i>Dynamine sosthenes smerdís</i> Tessmann 1928	0	1	0	0	6	34	0	0	0	2	5	0	0
<i>Dynamine vicaria hoppi</i> Hering 1926	0	0	0	0	1	0	3	1	1	1	2	1	1
<i>Dynamine zenobia ampliata</i> Zikán 1937	0	0	0	1	0	3	0	2	0	0	0	0	0
<i>Ectima lirides</i> Staudinger 1885	0	0	0	0	3	2	0	0	0	0	0	0	3
<i>Epiphile orea helios</i> Attal 2003	0	0	0	0	0	3	4	4	7	2	0	0	0
<i>Eunica alpais alpais</i> (Godart 1824)	0	1	1	1	2	16	8	6	1	2	1	0	0
<i>Eunica amelia erroneata</i> (Cramer 1777)	0	1	0	1	1	6	6	1	0	1	0	2	0
<i>Eunica anna</i> (Cramer 1780)	0	0	0	0	1	0	0	1	0	1	0	0	0
<i>Eunica caelina alycia</i> Fruhstorfer 1909	0	0	0	1	0	0	1	0	0	0	0	0	0
<i>Eunica clytia</i> (Hewitson 1852)	0	0	1	19	6	23	0	1	2	2	0	0	0
<i>Eunica concordia</i> (Hewitson 1852)	2	1	4	1	1	8	9	5	6	4	0	0	1
<i>Eunica eurota eurota</i> (Cramer 1775)	0	0	0	2	6	17	3	6	0	2	0	0	0
<i>Eunica malvina malvina</i> (Bates 1864)	0	1	0	2	2	11	3	1	0	1	0	0	0
<i>Eunica marsolia fasula</i> Fruhstorfer 1909	2	0	0	1	0	0	0	0	0	0	0	0	0
<i>Eunica mygdonia mygdonia</i> (Godart 1824)	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Eunica norica occia</i> Fruhstorfer 1909	0	0	0	0	0	0	2	0	1	0	0	0	0
<i>Eunica orphise</i> (Cramer 1775)	1	0	0	2	2	3	0	4	2	1	0	1	2
<i>Eunica pusilla</i> (Bates 1864)	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Eunica sophonisba agele</i> Seitz 1915	6	1	2	4	4	11	5	5	3	4	1	0	3
<i>Eunica sydonia sydonia</i> (Godart 1824)	0	0	0	0	0	2	1	1	0	0	0	0	0

Species	2002 Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2003 Jan	Feb	Mar	Apr
<i>Eunica viola</i> Bates 1864	0	0	1	0	0	0	2	2	0	0	0	0	0
<i>Eunica violetta</i> Staudinger 1885	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Eunica volumna celma</i> (Hewitson 1852)	0	0	0	1	1	0	0	0	0	0	1	0	0
<i>Hamadryas amphinome amphinome</i> (L. 1767)	0	0	0	0	2	10	1	0	0	0	0	0	0
<i>Hamadryas arinome arinome</i> (Lucas 1853)	1	6	0	4	1	6	4	1	6	2	1	2	2
<i>Hamadryas chloe chloe</i> (Stoll 1787)	2	1	0	0	0	2	1	0	1	1	0	0	0
<i>Hamadryas laodamia laodamia</i> (Cramer 1777)	0	0	1	0	1	0	0	1	0	0	0	0	0
<i>Marpesia berania berania</i> (Hewitson 1852)	3	1	0	0	0	0	0	0	0	1	0	0	0
<i>Marpesia chiron marius</i> (Cramer 1779)	3	3	4	1	13	8	13	0	0	0	0	0	0
<i>Marpesia crethon</i> (Fabricius 1776)	0	14	6	1	10	3	4	1	2	0	1	0	2
<i>Marpesia furcula oechalia</i> (Westwood 1850)	0	3	7	3	1	0	1	0	0	0	0	0	0
<i>Myrselia capenae octomaculata</i> (Butler 1873)	10	22	17	14	14	27	18	29	22	14	6	4	3
<i>Nessaea hewitsonii hewitsonii</i> (C. Felder & R. Felder 1859)	2	3	4	2	2	2	1	5	6	3	2	2	0
<i>Nessaea obrinus lesouadieri</i> Le Moult 1933	1	1	0	0	1	2	4	0	1	0	2	2	0
<i>Nica flavilla sylvestris</i> Bates 1864	2	3	7	2	8	9	5	0	0	2	0	1	0
<i>Panacea procilla divalis</i> (Bates 1868)	110	32	6	15	3	2		35	0	5	10	8	17
<i>Panacea prola amazonica</i> Fruhstorfer 1915	2	4	8	2	0	3	3	10	0	20	1	1	0
<i>Panacea regina chalcothea</i> (Bates 1868)	0	0	0	2	1	1	3	0	0	0	0	0	0
<i>Paulogramma pyracmon peristera</i> (Hewitson 1853)	0	1	0	0	1	0	0	0	0	0	0	0	0
<i>Peria lamis</i> (Cramer 1779)	1	0	3	1	0	2	1	0	0	0	0	0	0
<i>Pyrrhogrya amphiro amphiro</i> Bates 1865	3	3	0	1	5	33	13	7	1	7	1	0	2
<i>Pyrrhogrya crameri nautaca</i> Fruhstorfer 1908	6	16	11	18	31	50	13	7	14	11	8	11	12
<i>Pyrrhogrya edocla lysanias</i> C. Felder & R. Felder 1862	3	3	7	7	10	15	4	1	2	4	3	5	1
<i>Pyrrhogrya neaerea argina</i> Fruhstorfer 1908	1	1	0	1	16	20	17	6	5	5	1	0	1
<i>Pyrrhogrya otolais olivencia</i> Fruhstorfer 1908	13	15	20	10	41	70	29	9	15	24	10	7	10
<i>Temenis laothoe laothoe</i> (Cramer 1777)	49	64	63	63						63	29	22	26
<i>Temenis pulchra pallidior</i> (Oberthür 1901)	4	15	12	20	20	31	29	27	13	5	3	3	3
<i>Vila emilia caecilia</i> (C. Felder & R. Felder 1862)	1	1	0	0	1	2	3	1	1	1	0	1	0
<i>Vila eueidiformis</i> Joicey & Talbot 1918	0	0	0	1	0	0	1	0	0	0	0	0	0
<b>Charaxinae</b>													
<i>Agrias claudina lugens</i> Staudinger 1886	2	3	2	1	1	3	2	0	0	0	0	0	3
<i>Anaeomorpha splendida</i> Rothschild 1894	1	0	1	1	0	0	0	0	0	0	0	0	0
<i>Archaeoprepona amphimachus amphimachus</i> (Fabricius 1775)	0	2	0	1	1	1	0	0	1	0	0	1	0
<i>Archaeoprepona demophon demophon</i> (L. 1758)	1	3	6	6	7	14	8	10	14	7	5	4	4
<i>Archaeoprepona demophon andicola</i> (Fruhstorfer 1904)	1	0	5	4	3	5	2	2	4	1	1	1	0
<i>Archaeoprepona licomedes licomedes</i> (Cramer 1777)	4	1	0	2	3	3	4	4	2	1	0	2	1
<i>Archaeoprepona meander meander</i> (Cramer 1775)	1	1	0	0	1	0	0	2	0	0	0	2	0
<i>Coenophlebia archidona</i> (Hewitson 1860)	0	0	0	0	0	0	3	1	0	0	0	0	0
<i>Consul fabius diffusus</i> (Butler 1875)	0	3	4	1	0	0	1	0	3	0	1	1	1
<i>Fountainea euryppyle euryppyle</i> (C. Felder & R. Felder 1862)	3	0	3	1	1	0	1	0	0	0	0	0	1
<i>Memphis acidalia memphis</i> (C. Felder & R. Felder 1867)	16	14	8	7	13	12	7	8	17	10	8	3	5
<i>Memphis anna anna</i> (Staudinger 1897)	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Memphis basilia drucei</i> (Staudinger 1887)	5	13	5	10	5	3	11	25	8	7	12	4	5
<i>Memphis glauce glauce</i> (C. Felder & R. Felder 1862)	0	0	0	0	0	1	0	1	1	0	0	0	0
<i>Memphis moruus morpheus</i> (Staudinger 1886)	1	6	5	4	8	8	3	5	6	6	4	5	0
<i>Memphis offa offa</i> (Druce 1877)	0	0	0	1	1	2	1	2	1	0	1	1	0
<i>Memphis philumena philumena</i> (Doubleday 1849)	1	6	1	0	0	8	2	3	4	2	1	2	1
<i>Memphis polycarmes</i> (Fabricius 1775)	2	7	3	2	4	2	3	8	8	4	4	2	0

Species	2002 Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2003 Jan	Feb	Mar	Apr
<i>Memphis polyxo</i> (Druce 1874)	0	3	2	1	2	2	0	0	1	1	2	1	0
<i>Memphis praxias oblita</i> (A. Hall 1929)	0	1	0	0	1	0	0	0	1	0	0	0	0
<i>Memphis xenocles xenocles</i> (Westwood 1850)	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Prepona dexamenus dexamenus</i> Hopffer 1874	0	1	2	2	2	0	0	0	1	1	0	0	1
<i>Prepona laertes demodice</i> (Godart 1824)	2	9	3	6	8	9	4	11	6	3	3	2	2
<i>Prepona pheridamas</i> (Cramer 1777)	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prepona pseudomphale*</i> LeMoult 1932	0	0	1	0	0	0	1	2	1	0	1	0	0
<i>Prepona pylene eugenae</i> Bates 1865	0	0	0	1	0	1	0	0	0	0	0	1	0
<i>Siderone galanthis thebais</i> C. Felder & R. Felder 1862	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Zaretis isidora</i> (Cramer 1779)	6	9	13	6	9	26	29	19	32	16	16	7	4
<i>Zaretis itys itys</i> (Cramer 1777)	0	2	0	0	0	2	1	1	0	2	1	1	1
<b>Heliconiinae</b>													
<i>Agraulis vanillae lucina</i> C. Felder & R. Felder 1862	0	0	0	1	0	1	1	0	0	1	0	0	0
<i>Dione juno juno</i> (Cramer 1779)	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Dryas iulia alcionea</i> (Cramer 1779)	0	0	1	1	1	1	3	0	0	0	0	0	0
<i>Eueides aliphera aliphera</i> (Godart 1819)	0	0	0	0	0	3	3	2	0	0	0	0	0
<i>Eueides isabella huebneri</i> Ménétriés 1857	0	0	1	1	1	5	6	2	0	0	0	0	0
<i>Eueides lampetra acacates</i> Hewitson 1869	0	1	0	0	0	1	1	0	0	0	0	0	0
<i>Heliconius elevatus willmotti</i> Neukirchen 1997	1	5	1	0	1	4	4	1	0	0	5	2	5
<i>Heliconius erato lativitta</i> Butler 1877	0	1	0	0	1	2	5	0	0	0	0	0	1
<i>Heliconius hecale quitalena</i> Hewitson 1853	2	2	0	1	1	0	1	0	0	1	0	0	3
<i>Heliconius leucadia leucadia</i> Bates 1862	0	0	3	0	0	1	2	1	1	0	0	0	0
<i>Heliconius melpomene malleoti</i> Lamas 1988	2	0	0	0	1	1	0	1	2	0	1	2	2
<i>Heliconius numata bicoloratus</i> Butler 1873	0	1	0	1	1	0	1	1	1	0	0	0	0
<i>Heliconius numata euphrasius*</i> Weymer 1890	2	5	0	2	6	3	5	2	0	2	2	2	0
<i>Heliconius numata laura*</i> Neustetter 1932	0	0	0	0	1	0	1	0	0	1	0	0	1
<i>Heliconius pardalinus julia</i> Neukirchen 2000	0	0	0	0	6	6	0	1	4	3	2	1	2
<i>Heliconius sara sara</i> (Fabricius 1793)	0	1	1	3	0	4	7	1	0	0	0	0	1
<i>Heliconius wallacei flavescens</i> Weymer 1891	0	0	0	0	4	20	3	1	1	0	0	0	0
<i>Heliconius xanthocles napoensis</i> Holzinger & Brown 1982	0	0	1	0	1	2	2	0	1	1	1	1	0
<i>Laparus doris doris</i> (L. 1771)	4	3	1	18	6	7	6	6	0	2	0	0	0
<i>Neruda aoede auca</i> Neukirchen 1997	0	0	0	0	0	5	3	2	0	1	1	0	2
<i>Neruda metharme perseis</i> (Stichel 1923)	0	0	2	0	0	5	0	1	0	0	1	0	1
<i>Philaethria dido dido</i> (L. 1763)	0	0	0	0	0	0	2	0	0	0	0	0	0
<b>Limenitidinae</b>													
<i>Adelpha amazona</i> Austin & Jasinski 1999	0	1	2	0	1	2	1	2	1	0	1	0	0
<i>Adelpha attica attica</i> (C. Felder & R. Felder 1867)	3	6	5	12	5	18	17	26	7	6	3	0	0
<i>Adelpha boeotia boeotia</i> (C. Felder & R. Felder 1867)	2	1	0	1	1	1	10	9	7	2	0	0	1
<i>Adelpha capucinus capucinus</i> (Walch 1775)	7	7	5	19	5	11	12	7	13	7	4	0	1
<i>Adelpha cocala cocala</i> (Cramer 1779)	4	6	3	9	4	5	0	5	3	2	3	1	2
<i>Adelpha cytherea cytherea</i> (L. 1758)	1	8	5	11	14	3	2	0	2	4	5	1	2
<i>Adelpha delinata delinata</i> Fruhstorfer 1913	1	1	1	0	1	2	1	1	1	0	0	0	0
<i>Adelpha epione agilla</i> Fruhstorfer 1907	0	0	0	0	2	11	3	9	1	3	0	2	0
<i>Adelpha erotia erotia</i> (Hewitson 1847)	3	13	8	8	7	8	5	19	7	2	5	0	0
<i>Adelpha fabricia</i> Fruhstorfer 1913	2	2	2	2	2	5	5	5	0	1	0	0	0
<i>Adelpha heraclea heraclea</i> (C. Felder & R. Felder 1867)	0	2	2	1	3	4	1	6	0	1	0	2	0
<i>Adelpha iphiclus iphiclus</i> (L. 1758)	4	30	11	22	21	76	61	54	16	18	3	3	3
<i>Adelpha jordani</i> (Fruhstorfer 1913)	0	0	0	0	29		81		58	63	13	12	10
<i>Adelpha malea aethalia</i> (C. Felder & R. Felder 1867)	1	3	2	1	2	3	2	5	1	0	2	0	0
<i>Adelpha melona leucocoma</i> Fruhstorfer 1915	2	4	2	2	1	2	1	4	1	1	2	1	0

Species	2002 Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2003 Jan	Feb	Mar	Apr
<i>Adelpha mesentina</i> (Cramer 1777)	7	19	10	19	18	41	47	48	15	17	4	4	0
<i>Adelpha messana delphicola</i> Fruhstorfer 1910	5	1	0	3	3	3	6	4	3	3	1	0	0
<i>Adelpha naxia naxia</i> (C. Felder & R. Felder 1867)	0	0	0	0	4	5	0	1	0	0	0	0	0
<i>Adelpha paraena paraena</i> (Bates 1865)	0	0	1	0	0	2	1	2	0	0	0	0	0
<i>Adelpha plesaure phliassa</i> (Godart 1824)	2	2	1	4	1	6	6	8	4	0	0	0	0
<i>Adelpha pollina</i> Fruhstorfer 1915	0	0	1	0	1	1	0	1	0	0	0	0	0
<i>Adelpha serpa diadochus</i> Fruhstorfer 1915	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Adelpha thesprotia</i> (C. Felder & R. Felder 1867)	5	10	5	12	7	14	10	17	6	10	0	1	1
<i>Adelpha thoasa manilia</i> Fruhstorfer 1915	0	0	0	0	1	3	0	1	1	2	0	0	1
<b>Morphinae</b>													
<i>Antirrhea hela</i> C. Felder & R. Felder 1862	0	1	0	1	0	0	0	0	0	0	0	1	0
<i>Bia actorion rebeli</i> Bryk 1953	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Caligo euphorbus euphorbus</i> (C. Felder & R. Felder 1862)	0	0	0	1	0	0	0	0	0	0	0	1	0
<i>Caligo eurilochus livius</i> Staudinger 1886	0	2	2	1	2	2	0	2	3	3	2	0	0
<i>Caligo idomeneus idomenides</i> Fruhstorfer 1903	2	1	1	1	1	2	3	2	1	2	4	2	1
<i>Caligo teucer ecuadorensis</i> Joicey & Kaye 1917	0	0	0	0	0	1	0	0	0	0	2	0	0
<i>Catoblepia berecyntbia midas</i> Stichel 1908	3	4	5	4	6	4	6	3	2	2	4	4	1
<i>Catoblepia generosa</i> Stichel 1902	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Catoblepia soranus</i> (Westwood 1851)	1	1	4	1	1	0	3	1	2	0	2	1	3
<i>Catoblepia xanthicles occidentalis</i> Bristow 1981	0	0	0	1	0	0	0	0	0	1	1	0	0
<i>Catoblepia xanthus rivalis</i> Niepelt 1911	0	0	1	0	0	0	0	2	0	0	0	0	0
<i>Dynastor darius stygianus</i> Butler 1872	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Morpho achilles</i> ssp. (L. 1758)	0	4	5	0	1	1	1	1	0	0	1	0	1
<i>Morpho deidamia neoptolemus</i> Wood 1863	0	0	0	1	0	0	1	0	0	0	0	0	0
<i>Morpho helenor theodorus</i> Fruhstorfer 1907	4	9	5	3	5	2	3	4	1	1	4	2	1
<i>Morpho menelaus occidentalis</i> C. Felder & R. Felder 1862	0	3	3	2	1	2	1	6	1	1	3	1	2
<i>Narope cyllabarus</i> Westwood 1851	0	0	0	0	0	1	0	1	0	1	0	0	0
<i>Opsiphanes cassiae rubigatus</i> Stichel 1904	2	0	2	2	3	3	2	4	1	2	3	3	1
<i>Opsiphanes invirae intermedius</i> Stichel 1902	23	74	5	26	95	16	24	62	7	60	25	7	25
<i>Opsiphanes quiteria quaestor</i> Stichel 1902	6	2	0	0	2	4	0	0	2	0	2	2	4
<i>Selenophanes cassiope cassiopeia</i> (Staudinger 1886)	0	6	10	2	3	11	1	4	1	0	1	4	0
<b>Nymphalinae</b>													
<i>Anartia amathea sticheli</i> Fruhstorfer 1907	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Castilia guaya</i> Hall 1929	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Castilia perilla</i> (Hewitson 1852)	0	2	2	1	0	0	0	1	0	0	0	0	0
<i>Colobura annulata</i> Willmott, Constantino & Hall 2001	6	4	6	8	0	2	1	0	2	7	4	2	2
<i>Colobura dirce</i> (L. 1758)	5	3	4	12	2	10	11	20	9	13	6	4	0
<i>Eresia clio clio</i> (L. 1758)	0	0	0	0	3	4	4	1	0	0	0	0	0
<i>Eresia eunice eunice</i> (Hübner 1807)	0	0	1	1	1	2	2	0	0	0	0	0	0
<i>Eresia nauplius plagiata</i> (Röber 1913)	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Eresia pelonia callonia</i> (Staudinger 1885)	1	5	1	2	1	11	5	9	2	0	1	0	0
<i>Historis acheronta acheronta</i> (Fabricius 1775)	0	0	0	0	0	1	0	5	0	0	0	0	0
<i>Historis odius dious</i> Lamas 1995	0	0	0	1	2	1	2	0	0	1	0	1	1
<i>Metamorpha elissa elissa</i> Hübner 1819	0	2	0	0	0	0	3	2	1	0	0	0	0
<i>Siproeta stelenes meridianalis</i> (Fruhstorfer 1909)	2	5	6	5	2	5	9	2	6	5	1	2	1
<i>Tegosa serpia</i> Higgins 1981	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Telenassa teletusa burchelli</i> (Moulton 1909)	0	9	9	25	20	3	1	0	0	2	1	0	0
<i>Tigridia acesta fulvescens</i> (Butler 1873)	5	8	4	6	7	10	5	7	4	2	1	6	1

Species	2002		May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2003		
	Apr	Jan									Feb	Mar	Apr
<b>Satyrinae</b>													
<i>Caeruleuphychia scopulata</i> (Godman 1905)	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Cissia myncea</i> (Cramer 1780)	0	0	0	1	0	1	0	0	0	0	0	0	2
<i>Cissia penelope</i> (Fabricius 1775)	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cissia proba</i> (Weymer 1911)	1	2	3	2	0	0	1	0	0	0	1	1	1
<i>Erichthodes antonina</i> (C. Felder & R. Felder 1867)	0	0	0	1	0	3	0	2	1	0	1	0	1
<i>Harjesia obscura</i> (Butler 1867)	0	0	1	0	0	0	1	0	0	0	0	0	0
<i>Hermeuptychia fallax</i> (C. Felder & R. Felder 1862)	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Hermeuptychia hermes</i> (Fabricius 1775)	10	28	23	36	13	7	5	1	3	1	6	2	4
<i>Hermeuptychia maimoune</i> Butler 1870	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Magneuptychia libye</i> (L. 1767)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Megeuptychia antonoe</i> (Cramer 1775)	6	9	1	4	6	17	7	17	15	5	1	1	2
<i>Megeuptychia monopunctata</i> Willmott & Hall 1995	0	1	0	0	0	0	0	0	1	0	0	0	0
<i>Pareuptychia hesionides</i> Forster 1964	1	7	1	4	2	8	3	1	2	0	0	1	1
<i>Pareuptychia summandosa</i> (Gosse 1880)	0	0	0	0	0	0	0	0	1	2	0	1	0
<i>Posttaygetis penelea</i> (Cramer 1777)	0	0	0	0	0	2	0	0	0	1	1	1	0
<i>Pseudodebis valentina</i> (Cramer 1779)	0	1	0	1	0	0	1	0	0	0	0	0	0
<i>Taygetis cleopatra</i> C. Felder & R. Felder 1867	2	2	1	2	0	1	2	0	0	2	0	0	0
<i>Taygetis laches</i> (Fabricius 1793)	0	0	0	0	1	0	1	0	0	0	0	0	0
<i>Taygetis leuctra</i> Butler 1870	0	0	0	0	0	0	0	1	0	0	0	1	0
<i>Taygetis thamyla</i> (Cramer 1779)	1	1	3	0	1	3	1	0	2	1	1	1	2
<i>Taygetis virgilia</i> (Cramer 1776)	0	0	0	0	0	0	1	0	1	2	0	0	1

# Composition of a high diversity leaf litter ant community (Hymenoptera: Formicidae) from an Ecuadorian pre-montane rainforest

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**Abstract.** The pre-montane forest of the northern Andes is considered one of the most biodiverse regions in the world. Tools for rapidly assessing biodiversity inventories are currently being developed and may aid conservation efforts. Here, we focus on the use of the Ants of the Leaf Litter (ALL) protocol as such a tool and describe the composition of an Ecuadorian pre-montane leaf litter ant community. Two 200-m transects (i.e. two complete replications of the protocol) with a total of 40 winkler sacs and 39 pitfall traps were analyzed. In total, we collected 4 875 specimens from 103 species, 37 genera and 9 subfamilies. The abundance-based coverage estimator (ACE), an asymptotic estimator of species richness, predicted a total of 109 ant species for the forest floor, making this ant community one of the most diverse recorded in tropical mid-altitude forests. Subsets of the community sampled by winker sacs and pitfall traps differed significantly. Winkler sacs were more efficient than pitfall traps at capturing individual ants (226% more) and species (129% more). Relative to pitfall traps, an analysis of morphology suggested that winker sacs collected a subset of the ant community that was smaller, less mobile and with smaller eyes (e.g. more subterranean). Finally, we present the first published records of the ant species *Acanthognathus teledectus* Brown & Kempf 1969, *Hypoponera distinguenda* (Emery 1890), *Prionopelta amabilis* Borgmeier 1949, *Pachycondyla chyzeri* (Forel 1907) and *Procryptocerus mayri* Forel 1899 for Ecuador.

**Résumé.** Composition d'une communauté de fourmis hautement diversifiée dans la litière d'une forêt pluviale pré-montagnarde Equatorienne. La forêt pluviale pré-montagnarde du nord des Andes est considérée comme l'une des régions qui héberge une des diversités biologiques les plus élevées au monde. Dans un soucis de conservation de ces milieux, on assiste actuellement à un développement croissant d'outils d'inventaire de la biodiversité. Cette étude se focalise sur l'utilisation du protocole « Fourmis de litière » (Ants of the Leaf Litter, ALL) comme outil de description de la composition d'une communauté de fourmis dans une forêt pré-montagnarde de nuages en Equateur. Deux transects de 200 m chacun (c'est-à-dire deux répétitions complètes du protocole ALL) comprenant un total de 40 winker et 39 pièges à interception ont été analysés. Au total, 4 875 individus appartenant à 103 espèces, 37 genres et 9 sous-familles ont été collectés. L'estimateur asymptotique de richesse spécifique ACE (Abundance-based Coverage Estimator) prédit la présence d'un total de 109 espèces de fourmis au niveau du sol forestier, une des diversités les plus grandes jamais documentées pour une forêt tropicale d'altitude intermédiaire. Nous avons trouvé des différences significatives dans la composition des communautés de fourmis entre les deux méthodes d'échantillonnage, pièges à interception et winker. Ces derniers furent plus efficaces pour capturer les fourmis, aussi bien en terme d'abondance (226% en plus) que d'espèces (129% en plus). Une analyse morphologique a de plus montré que les winker échantillonneront des fourmis généralement plus petites, moins mobiles, et avec des yeux plus petits (i.e. plus souterraines) que les pièges à interception. Enfin, cette étude présente le premier registre publié pour l'Equateur des espèces *Acanthognathus teledectus* Brown & Kempf 1969, *Hypoponera distinguenda* (Emery 1890), *Prionopelta amabilis* Borgmeier 1949, *Pachycondyla chyzeri* (Forel 1907) et *Procryptocerus mayri* Forel 1899.

**Keywords:** Formicidae, ALL protocol, Ecuador, Otongachi, Biodiversity.

Biological surveys are the primary source of information for current conservation efforts of systematists and ecologists around the globe. Litter-dwelling ants are central to these efforts (Brühl *et al.* 1998; Fisher 1999; Delabie *et al.* 2000; Longino *et al.*

2002; Leponce *et al.* 2004; Steiner & Steiner 2003; Dunn *et al.* 2007) and standardized survey methods, i.e. the Ants of the Leaf Litter protocol (ALL protocol), have been designed to monitor ant communities in diverse habitats and at different seasons of the year (Agosti *et al.* 2000). Ants are a group of insects that are included in long term biodiversity studies because (1) they are ecologically dominant and diverse in all terrestrial ecosystems, except in the poles (Kaspari,

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Alonso *et al.* 2000); (2) they are easy to sample in short time periods (Agosti *et al.* 2000); and, (3) ant diversity is high and their taxonomy is relatively well-resolved compared to other hyper-diverse insect groups (Lapolla *et al.* 2007). By applying the same methodology, studies worldwide can be easily integrated and used for hypothesis testing at global scale (Ward 2000; Kaspari 2005; Dunn *et al.* 2007).

To collect ants, two sampling techniques, pitfall traps and winkle sacs, predominate in the current literature. Pitfall traps are the most widely used method to study ant diversity and ecology around the world (Luff 1975; Andersen 1991). Cups partially filled with a preserving fluid are buried capturing invertebrates foraging on the forest floor. In open environments, where litter material does not accumulate, ant species tend to show long-legged, epigaeic life-styles and pitfall traps are generally considered the most efficient method for collecting them (Parr & Chown 2001). The use of winkle sacs in the study of ant diversity is common (Ward 1987; Nadkarni & Longino 1990; Fisher 1999; Agosti *et al.* 2000; Lapolla *et al.* 2007). The method consists of a fabric sac, on a metal frame. Leaf litter from the forest floor (usually from 1-m<sup>2</sup> plots) is sifted through coarse mesh and then left for a given amount of time (usually 48-h) inside the sac. The interior of the sac provides a relaxed environment allowing the sifted litter to dry up with time. Invertebrates inside the sac will eventually fall into an ethanol filled cup located at the bottom of the sac. Based on habitat, pitfall traps are recommended for sampling ants in open, less forested, environments, whereas winkle sampling is considered to be more efficient in forested habitats where litter accumulates and serves as shelter for litter-dwelling ants (Olson 1991; Fisher 1999; Agosti *et al.* 2000; Lopes & Vasconcelos 2008). Nevertheless, if a collection method is to be preferred for a particular habitat, a measure of its effectiveness and possible sampling biases in the area should first be addressed (Parr & Chown 2001; Delsinne *et al.* 2008).

Ecuador is one the 17-megadiverse countries of the world (Mittermeier *et al.* 1997), but its ant fauna remains mostly unknown, and taxonomically poorly understood. To our knowledge, only a handful of ant surveys have been undertaken in Ecuador and even fewer have been published (Ward 2000; Kaspari, Alonso *et al.* 2000; Kaspari *et al.* 2003; Ryder *et al.* 2007). Moreover, most ant collections in Ecuador have been carried out in the Ecuadorian Amazon. As a consequence, the ant diversity of coastal and Andean Ecuador, which holds one of the most diverse plant floras of the world (Mutke 2001; Ulloa Ulloa & Jorgensen 1993), remains under-sampled and poorly

represented in taxonomic accounts.

In this study we aimed to redress the lack of information on the ant fauna of the pre-montane forests of northern coastal Ecuador. The objectives of this study were (1) to provide for the first time an standardized ant inventory of a mid-altitude forest from the western slopes of the Ecuadorian Andes; (2) to describe its community composition; and (3), to test for the relative efficiency and sampling bias of pitfall traps and Winkler sacs in this forest.

## Materials and Methods

### Study site and vegetation type

This study was conducted within the Otongachi forest (0°18'49"S; 078°57'15"W, 850-m), in the lowest-most area of the *Reserva Bosque Integral Otonga* (BIO Reserve) managed by the Fundación Otonga. The forest is located on the western slopes of the Ecuadorian Andes, near the town of *La Unión del Toachi* and the Aloag-Santo Domingo road, Pichincha province. Otongachi is near to a state-controlled primary forest called the *Reserva Forestal del Río Lelia*. Together, these forests cover a surface area of 5000 hectares, and are in turn connected to the National Park *Reserva Ecológica Los Ilinizas*. The interaction between these forests has allowed Otongachi to maintain high biodiversity, and subsequently it has become one of the last important refuges for the fauna and flora of the entire region (Nieder & Barthlott 2001a, 2001b; Giachino 2008).

Otongachi covers 20-ha and is a secondary wet pre-montane forest (Cañadas 1983) that was modified until 1990 by selective timber harvesting (G. Onore, *pers. comm.*). It is located in the lowest part of the aseasonal altitudinal range 800-1800-m, with an average annual temperature of 18 to 24 °C, and between 1000 and 2000 mm of annual rainfall. This altitudinal range encompasses approx. 10% of the country area but contains ca. 50% of the country's flora (Mutke 2001, Ulloa Ulloa & Jorgensen 1993). Leaf litter in the forest was composed of plant species from sub-tropical, cloud and Andean forests. Plant species well represented in the area included: *Cedrela odorata* L. "cedro", *Billia Columbiana* Planch. & Linden "pacche", *Elaegia utilis* (Goudot) "lacre", *Guarea kunthiana* A. Juss "colorado", *Pochota squamigera* (Cuatrec.) "frutipan", *Sapium verum* Hemsl. "lechero" and *Nectandra acutifolia* (Ruiz & Pav) "Gigua". In the understory, several species of the genera *Ficus* L., *Tournefortia* L., *Cecropia* Loefl., *Weinmannia* L., *Inga* Mill., *Miconia* Ruiz & Pav. and *Clusia* L. were common (Jaramillo 2001).

### Field methods

We surveyed two transects (hereafter "T-LL1" and "T-LL2") within the Otongachi forest separated by approximately 2-km and located roughly at the same altitude. Fieldwork was done on 10 to 17-IX-2003. In each transect ant assemblages were sampled using a complete replicate of the ALL protocol as described in Agosti *et al.* (2000). The protocol mostly samples ant fauna from the leaf litter (soil surface), but subterranean or arboreal ants may occasionally be captured (Longino & Colwell 1997). Each transect consisted of 20 sampling points separated by 10-m for a total extent of 200-m. At each sampling point, we randomly (1) placed one pitfall trap partially filled with 70% alcohol for 48-h, and (2) collected 1-m<sup>2</sup> leaf litter samples

from which ants were extracted using a winkler sac over 48-h.

### Species identification

Samples were processed in the laboratory. From every sample, at least one individual of each morphospecies was mounted and labeled, and the abundance of the morphospecies was recorded. We used Bolton (1994) and Bolton *et al.* 2006 to identify ant specimens to genus level and check for taxonomical nomenclature, respectively. Specimens were identified to species level with the use of taxonomic keys (Brandão 1990 [*Megalomyrmex*]; Lattke *et al.* 2007 [*Gnamptogenys*]; Fernandez & Palacio 1999 [*Lenomyrmex*]), unpublished species lists and collections of the QCAZ Museum (PUCE), and with the assistance of taxa specialists (F. Serna [*Procryptocerus*], A. Kumar [Ecitoninae], S. Dash [*Hypoponera*]). Where specific identification was not possible, specimens were assigned to a morphospecies. All specimens were deposited in the Invertebrate section of the QCAZ Museum (PUCE), in Quito.

### Species Accumulation Curves

Species accumulation curves provide a standard method to measure the completeness of different biological surveys and to allow comparison among surveys (Longino *et al.* 2002). To construct accumulation curves, we used EstimateS 8.0 (Colwell 2006). We calculated a MaoTau sample-based rarefaction species accumulation curve (Colwell *et al.* 2004) for each sampling transect (T-LL1, T-LL2) and for both transects combined (T-LL1+T-LL2). Specifically, we constructed a data matrix in which we recorded the abundance of each ant species (combining catches from the pitfall traps and winkle sacs) for each sampling point of the two transects.

In order to assess the completeness of our inventory, we estimated the total ant species richness of the Otongachi forest for the same groups previously described. We used the Abundance-based Coverage Estimator (ACE, Chao & Lee 1992) implemented in EstimateS (Colwell 2006). ACE constructs an asymptotic model based on the relative abundance of the rarest species (by default species with less than 10 individuals) in the sample. ACE incorporates an estimate of species that were not collected in the sampling survey (Chao & Lee 1992; Kumar *et al.* 2008), thereby giving an estimate of total species richness.

What is the rate of ant species turnover inside a forest? How much distance should we travel from one collection point to another in order to maximize the number of ant species collected for a given amount of effort? To approximate answers to these questions we employed a Chao's Abundance-based Jaccard similarity measure (Chao *et al.* 2005; Kumar *et al.* 2008) computed in EstimateS 8.0 (Colwell 2006). The Chao-Jaccard index uses abundance data and computes the probability that two random ant species drawn from one of the transects will be found in both transects (Colwell 2006). The analysis is based on the Chao statistics (Chao *et al.* 2005) and therefore it adjusts the results to include an estimate of the species that are not present in our inventory, but are likely to occur in the forest.

### Morphology

To explore whether there was a relationship between the morphology of the collected ant species and the specific collection method, we measured four morphological traits frequently used in ant taxonomy, following Weiser & Kaspari (2006). Up to five specimens from each morphospecies collected in this survey

(Appendix 1) were measured by one of us (GR) using a Leica MZ75 (Bannockburn, IL, USA) stereomicroscope, with a 0.02 precision stage micrometer. Descriptions of morphological measurements are as follows:

HL – Head length. In full-face view, the midline distance from the level of the maximum posterior projection of the occipital margin of the head to the level of the most anterior projection of the clypeal margin.

HW – Head width. In full-face view, the maximum width of the head, exclusive of teeth, spines, tubercles or eyes. Head width was used together with HL as a proxy for head size.

EL – Eye length. We measured maximum eye length at the largest diameter. For ant species with no eyes, such as *Cerapachys* and army ants (Ecitoninae), we arbitrarily assigned the value of 0.02-mm for subsequent analyses (i.e. the minimum micrometer resolution).

FL – Femur length. On side view, we measured femur length, from the trochanter-femur joint to the femur-tibia joint, as a surrogate for leg length. Leg length is commonly linked to foraging capacities in ants (Feener *et al.* 1988).

Principal components analysis (PCA) on morphometric measurements (Jolliffe 2002; Weiser & Kaspari 2006) provides the means to summarize the size and shape of ant specimens and construct a "morphospace" (Pie & Traniello 2007) where morphological associations can be displayed and used for analysis. We performed a PCA to construct an ant community morphospace using these four quantitative morphological traits (see measurements procedure above) (Jolliffe 2002). The analysis was performed using PAST (Paleontological statistics, version 1.79). Measurements were  $\log_{10}$ -transformed to build a covariance matrix (Weiser & Kaspari 2006; Pie & Traniello 2007) from which principal component (PC) scores were extracted. We retained the first two components as they explained 86.8% and 10.8% of total original variance, respectively. PC III and PC IV accounted just 1.7% and 0.4% of the variance, respectively.

### Comparison between collection Methods

We used a one-way ANOVA on log-transformed species abundance and richness data (SPSS v. 10.0) to evaluate the hypothesis that, in the Otongachi forest, winkle sacs collected more ant specimens and species than pitfall traps, respectively. We also used a one-way ANOVA to evaluate the hypothesis that PCI and PCII scores (proxies for morphology) were independent of collection method (e.g. winkle vs. pitfall). To build comparison groups, we included those ant species that were only caught by either winkle sacs or pitfall traps.

The difference in biological diversity between the subsets of the ant community collected by the different methods was assessed with the following set of statistical techniques. First, we carried out a non-metric multidimensional scaling (NMDS) analysis on ant abundance data to examine patterns of biological similarity. This ordination technique represents samples as points in two-dimensional space, such that the relative distances of all points are in the same rank order as the relative similarities of the samples (Gucht *et al.* 2005). The Bray-Curtis index was used to measure the similarity between samples (Field *et al.* 1982) and samples from the same collection method were grouped with convex hulls. The NMDS goodness of fit was estimated with a stress function, which ranges from 0 to 1, with values close to zero indicating a good fit. Second, we performed an analysis

of similarities (ANOSIM) to test the null hypothesis that the within-group similarity was equal to the between-group similarity, as expected by chance alone (Oliver & Beattie 1995; Chapman & Underwood 1999). Significance was computed by permutation of group membership ( $n = 10\,000$ ). ANOSIM generates a statistical parameter  $R$  that is an indicative of the degree of separation between groups; a score of 1 indicates complete separation and a score of 0 indicates no separation (Gucht *et al.* 2005). Finally, we determined which ant species from our survey contributed the most to distinguish collection methods by performing a SIMPER analysis on density data for all Formicidae taxa in the list. To reduce the effects of large abundance catches due to ant's colonial life styles, all analyses were performed on ( $\log X + 1$ ) transformed data (Clarke 1993). We used the statistical software PAST (Paleontological statistics,

version 1.79) to make these analyses.

## Results

### Species diversity

In total, 4 536 specimens from 103 species, 37 genera and 9 subfamilies were collected in the two transects (Table 1) by 39 pitfall traps and 40 winkler sacs (one pitfall trap sample was lost in the field). Winkler sacs were more effective than pitfall traps in terms of the number of individuals (226% more,  $F_{1,1} = 9.45$ ,  $p < 0.01$ ) and species (129% more,  $F_{1,1} = 1.1$ ,

**Table 1.** Summary of taxonomic content of our ant species inventory by subfamily and collection method: pitfall and winkler samples.

Subfamily	Pitfall			Winkler		
	Genera	Species	Workers	Genera	Species	Workers
Amblyoponinae	—	—	—	1	1	44
Cerapachyinae	—	—	—	1	2	16
Dolichoderinae	1	1	549	1	2	26
Ectyoninae	1	2	4	1	3	6
Ectatomminae	2	6	41	2	6	96
Formicinae	5	6	30	3	4	350
Myrmicinae	14	39	721	16	49	2640
Ponerinae	4	12	146	4	14	215
Proceratiinae	—	—	—	1	1	1
Total	27	66	1481	30	82	3394

**Table 2.** Matrix of Principal Components for the morphological analyses of ant communities.

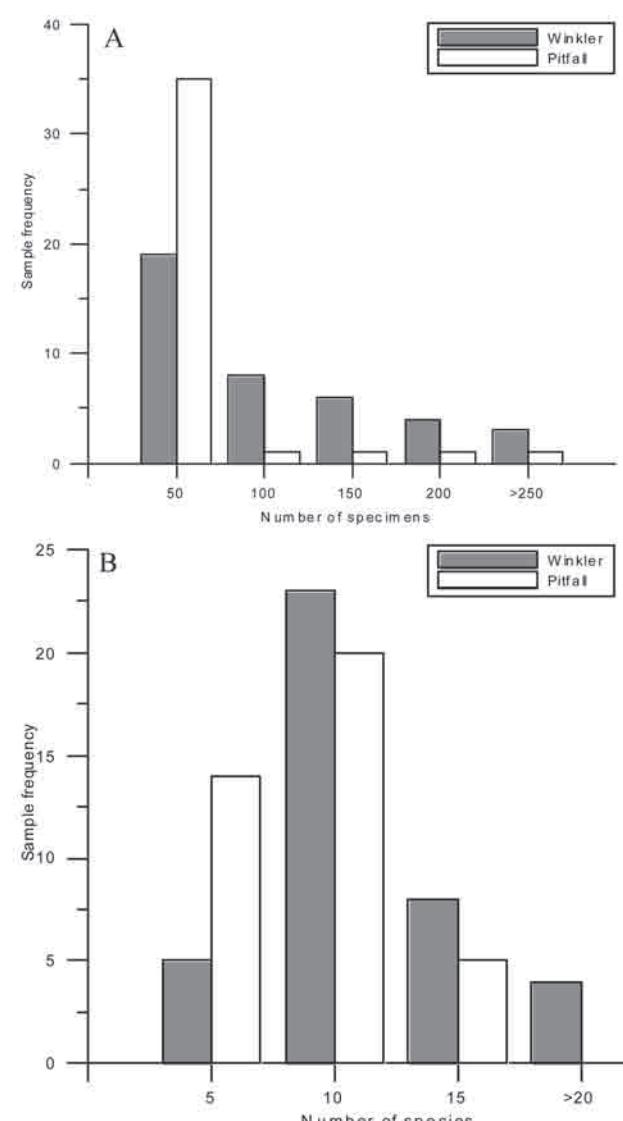
Four morphological measurements, Head Length (HL), Head Width (HW), Eye Length (EL) and Femur Length (FL) were included in this analysis. Eigenvalues and % of Variance explained is given for PCI to PCIV. Only PCI and PCII were retained for further analysis.

Variables	PC I	PC II	PC III	PC IV
HL	-0.3787	0.3764	0.3353	86.88
HW	-0.3812	0.3695	0.5816	10.88
EL	-0.6269	-0.7718	0.1043	1.78
FL	-0.5642	0.3552	-0.7318	0.45
Eigenvalue	3.4221	0.4286	0.0703	0.0176
% Variance	86.88	10.88	1.78	0.45

**Table 3.** One-way ANOVA results from comparison of ant collection methods.

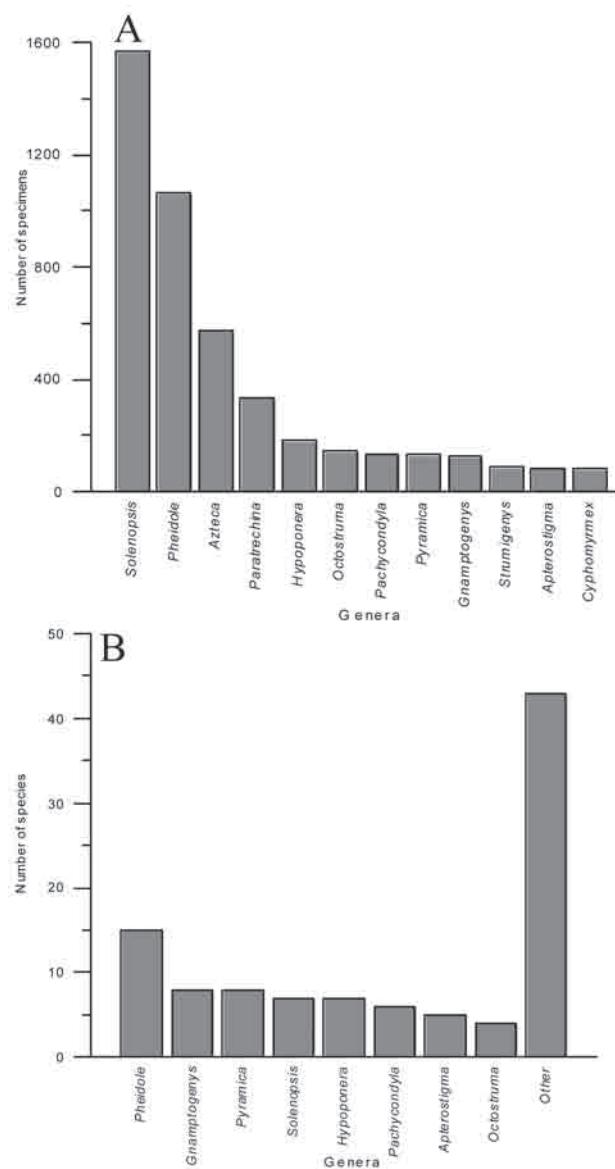
Type III sum of squares, degrees of freedom, mean squares, Fisher F and significance value for comparison between winkler sacs and pitfall traps in PCI, PCII, number of specimens collected and number of species collected.

	Type III SS	d.f.	F	Sig.
PCI	25.83	1	7.66	0.0064
PCII	0.18	1	0.26	0.6119
Specimens	46346.41	1	9.45	0.0029
Species	86.76	1	6.81	0.0108



**Figure 1**  
Taxonomic composition of the Otongachi Forest ant community. **A**, Number of specimens and **B**, species per sample.

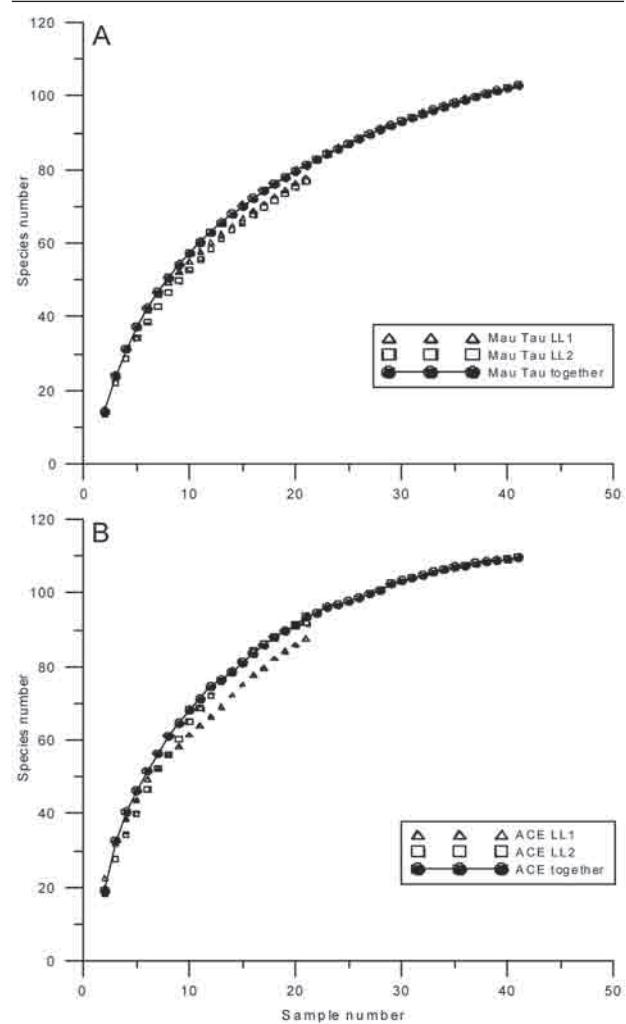
6.81,  $p = 0.01$ ) collected (fig. 1, Table 2 and 3). *Pheidole* ( $S = 15$ ), *Gnamptogenys* and *Pyramica* ( $S = 8$ ), and *Solenopsis* ( $S = 7$ ) and *Hypoponera* ( $S = 7$ ) were the genera with largest number of species (43.7% of total species, fig. 2a). *Solenopsis*, *Pheidole*, *Azteca* and *Paratrechina* were the genera (excluding army ants) with the largest number of individuals captured (72.66% of total abundance, fig. 2b). Ant species common in pitfall traps but not found in winkler sacs included *Ectatomma ruidum* (Roger 1860), *Pachycondyla apicalis* (Latrelle 1802), *P. verenae* (Forel 1922), *Tatuidris tatusia* Brown & Kempf 1968. On the contrary, ants

**Figure 2**

A, Number of specimens and B, species of main ant genera in the survey at the Otongachi Forest.

collected by winkler sacs but absent from pitfall traps were: *Cerapachys* sp. 1, *C. sp.* 2, *Prionopelta amabilis* Borgmeier 1949, *Protalaridris armata* Brown 1980 (fig. 5), *Typhlomyrmex pusillus* Emery, 1894 and several species of *Gnamptogenys*, *Pyramica* and *Strumigenys* (Appendix 1).

Twelve singletons (i.e. species known from one specimen; *Acromyrmex* sp. 2, *Apterostigma* sp. 3, *Camponotus sericeiventris* (Guérin-Méneville 1838), *Discothyrea* sp. 1, *Gnamptogenys minuta* Emery 1896, *Lenomyrmex foveolatus* Fernández 2003, *Megalomyrmex silvestrii* Wheeler 1909, *Myrmelachista* sp. 1, *Pachycondyla* sp. 1, *Pheidole* sp. 12, *Pyramica* sp. 4, *P. sp.* 6, *Trachymyrmex* sp. 1; Appendix 1) were recorded in the inventory. Additionally, 12

**Figure 3**

(A) MaoTau sample-based rarefaction species accumulation curve for transects T-LL1, T-LL2 and T-LL1+T-LL2 of the ant survey (B) Estimate of the total ant species richness at the Otongachi forest using the asymptotic model of the abundance based coverage estimator (ACE).

doubletons (i.e. species in the list known from two specimens; *Acanthognathus teledectus* Brown & Kempf 1969, *Gnamptogenys* sp. 1, *G.* sp. 2, *Hypoponera* sp. 2, *Megalomyrmex bidentatus* Fernandez & Baena 1997, *Octostruma* sp. 4, *Pachycondyla apicalis* (Latreille 1802), *Pheidole* sp. 11, *P.* sp. 15, *Procryptocerus mayri* Forel 1899, *Pyramica* sp. 2, *P.* sp. 5; Appendix 1) were recorded in the inventory. No apparent trend was found with respect to collection methods on collecting singletons or doubletons. Pitfall traps collected 16 species in these categories and winkler sacs collected 12 (Appendix 1).

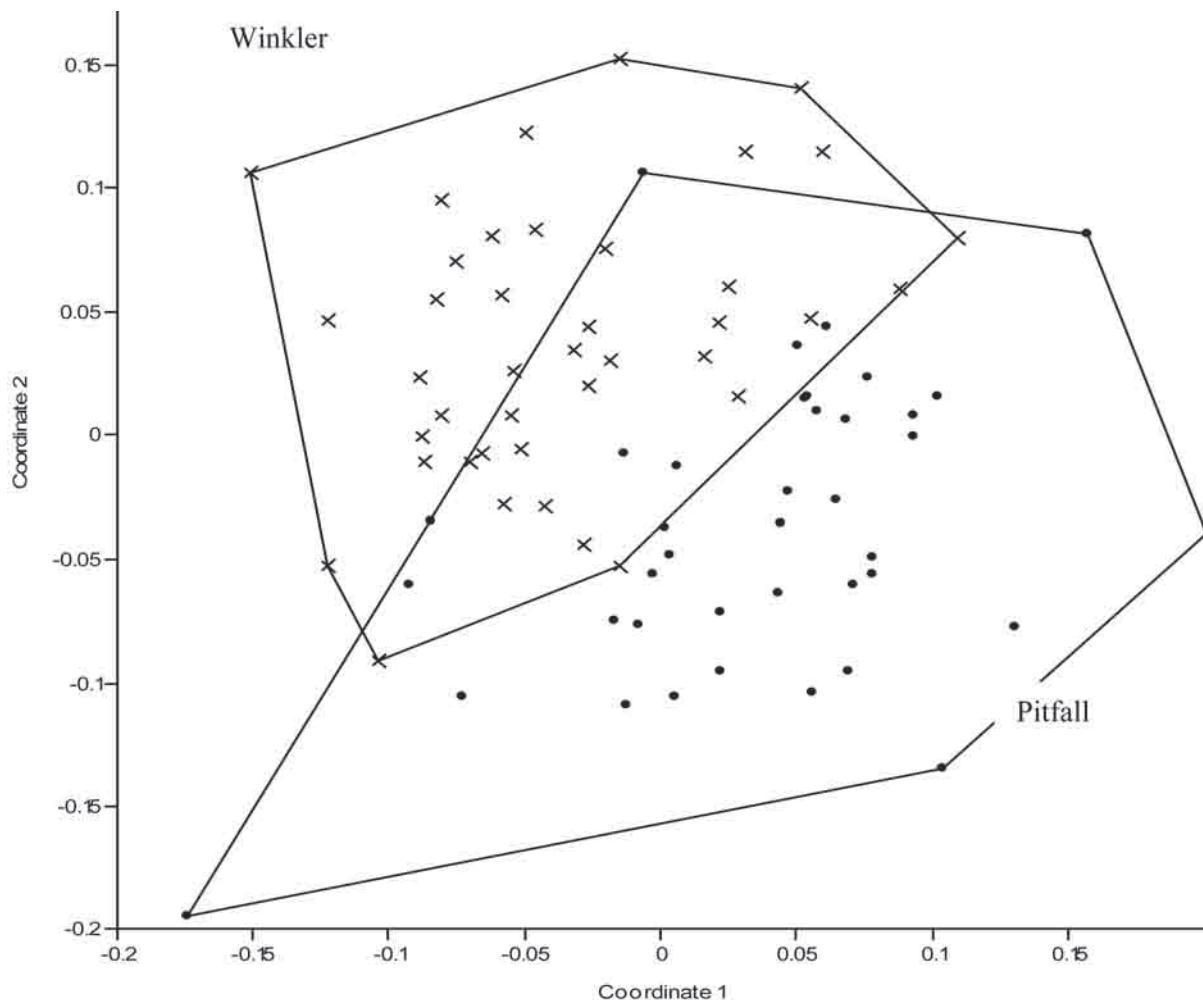
### Species Accumulation Curves

Both MaoTau species accumulation curves and the ACE showed that the ant community was relatively well sampled (fig. 3). MaoTau curves for individual and

coupled transects were similar in shape and showed a negatively accelerating trajectory. The ACE estimated that the species richness of the forest floor was 109 ant species, indicating that our surveys probably missed six ant species from the forest floor. Although the estimated number of shared species by transects T-LL1 and T-LL2 was 71.9, we found 52 species that were shared between transects. Both transects were well sampled and share approximately 83% of their ant faunas (Chao-Jaccard index = 0.83). The total number of species observed in T-LL1 was 78 (ACE estimator = 87.7). The total number of species observed in T-LL2 was 77 (ACE estimator = 88.6).

### Community morphospace

The first two principal components of the ant community morphospace described by the PC analysis



**Figure 4**

Non-metric multidimensional scaling (NMDS) analysis of the different subsets of the ant community under different winkler sacs and pitfall traps. Triangles show the convex hull (smallest convex polygon containing all points) in each group.

accounted for 97.76% of the total variance (Table 2). The first component, PCI, accounted for most of the variation (86.88%) and reflected variation in size, particularly eye length (EL coefficient = -0.63) and femur length (FL coefficient = -0.56). PCII accounted for 10.88% of the variance and was highly correlated with eye size (EL coefficient = -0.77). Overall, species with high loadings on PCI were smaller and presented smaller femurs and smaller eyes (i.e. blind). Species with high loadings on PCII had also relatively small eyes. An analysis of variance of the PC scores of those ants that fell in winkler sacs versus those that fell in pitfall traps showed significant differences for PCI (proxy for overall size, eye length and femur length;  $F = 7.65$ , d.f. = 1,  $p < 0.01$ ), but not PCII (proxy for eye length;  $F = 0.25$ , d.f. = 1,  $p = 0.61$ ) (Table 2).

### Community composition

NMDS analysis revealed significant differences in ant community composition between the two collection methods (fig. 4). Stress was low (0.347) indicating a good degree of fit. ANOSIM significantly separated the two collection methods presented in the NMDS (ANOSIM,  $R = 0.3$ ;  $p < 0.0001$  for richness; see convex hulls in fig. 4). Additionally, SIMPER analysis indicated that several changes occurred for some species (overall dissimilarity = 87.67%). From the 13 most explanatory ant species among collection methods, 9 species (*Solenopsis cf. stricta*, *Solenopsis* sp.1, *Pheidole* sp.2, *Paratrechina* sp.1, *Gnamptogenys bisulca*, *Pheidole* sp.5, *Hypoponera* sp.3, *Cyphomyrmex* sp.3, *Solenopsis* sp.3) were more abundant in winkler

sacs, and 4 species (*Pheidole* sp.6, *Azteca* sp.1, *Pheidole* sp.10 and *Pachycondyla chyzeri*) were more abundant in pitfall traps (Table 4).

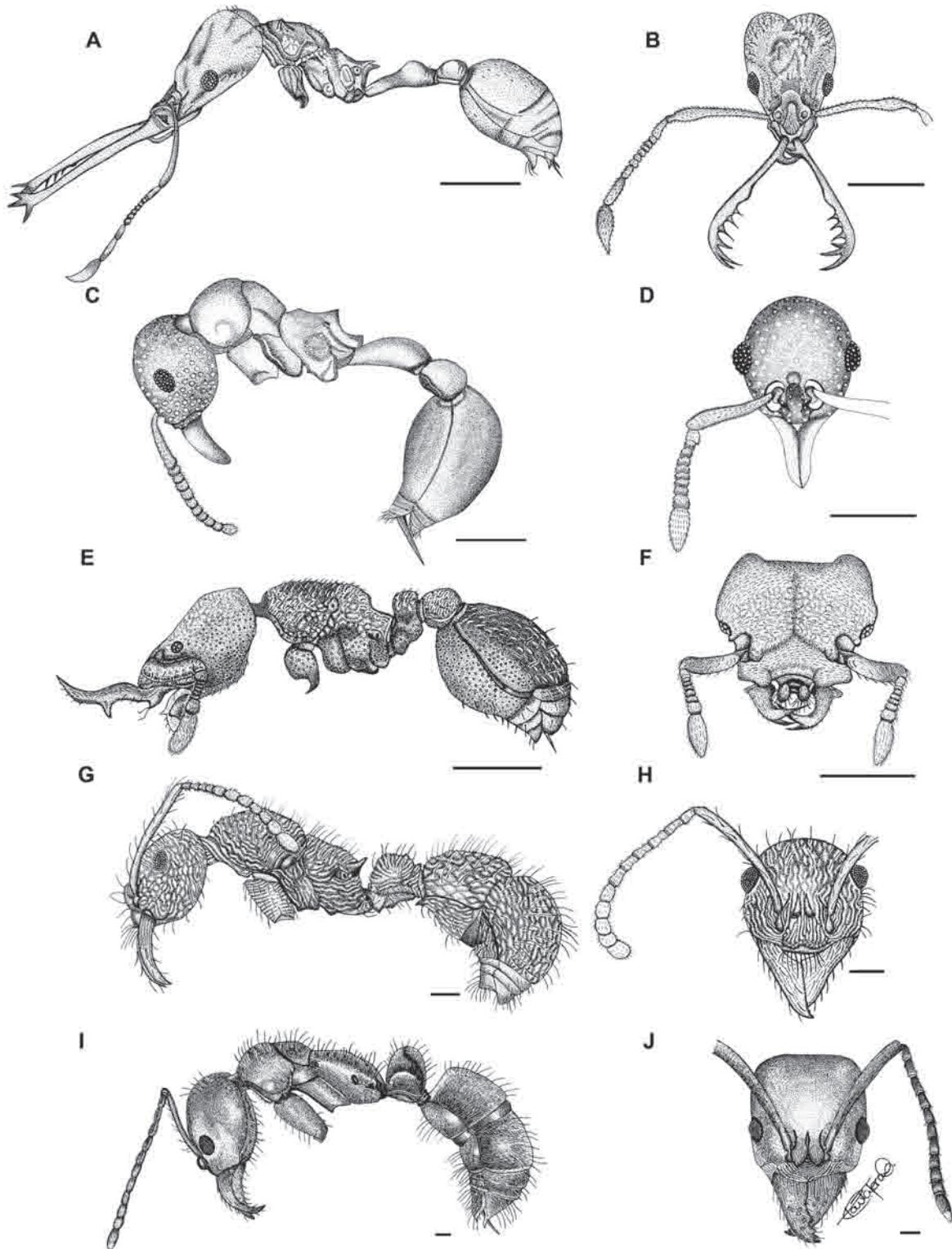
### Discussion

This study documents one of the most diverse ant assemblages currently known for mid-altitude tropical pre-montane forest. We found 9 ant subfamilies and 103 ant species inhabiting the Otongachi forest floor. Similar studies with the same methodology have found from 38–74 species in Guyana (LaPolla *et al.* 2007), to 59–72 in the Brazilian Cerrado (Lopes & Vasconcelos 2008), to 90–91 in the Paraguayan Chaco (Delsinne *et al.* 2008). We recorded for the first time in Ecuador the ant species *Acanthognathus teleiectus* Brown & Kempf 1969 (fig. 5 A–B), *Hypoponera distinguenda* (Emery 1890), *Prionopelta amabilis* Borgmeier 1949, *Pachycondyla chyzeri* (Forel 1907) and *Procryptocerus mayri* Forel 1899. These results lend support for the use of the ALL protocol in biodiversity surveys at taxonomically poorly known localities, especially those with a well-developed litter layer. Our sampling revealed an ant fauna that contained most of the main components of a Chocoan (Neotropical) ant community (Lattke 2003). For example, the ant genera *Pheidole*, *Gnamptogenys* (fig. 5 G–H), *Pyramica*, *Solenopsis*, *Strumigenys*, *Azteca* and *Hypoponera*, that are widespread in the neotropics (Brown 2000; Ward 2000; Kaspari & Majer 2000), accounted for most of the species and specimens in the inventory. However, the assemblage also contained several endemic Andean

**Table 4.** Results of SIMPER analysis for 13 ants species representing 50% (in our case, 51.62%) of the cumulative contribution to the separation between collection methods.

The table provides the percent contribution of each species to average dissimilarity between the two collection methods, based on log-transformed abundance data for pitfall traps and winkler sacs.

Taxon	% Contribution	Cumulative Contribution	Pitfall traps	Winkler sacs
<i>Solenopsis cf. stricta</i>	6.447	7.354	0.353	1.63
<i>Solenopsis</i> sp.1	5.874	14.05	0.534	1.42
<i>Pheidole</i> sp.6	4.785	19.51	1.07	0.279
<i>Pheidole</i> sp.2	4.64	24.81	0.678	0.765
<i>Azteca</i> sp.1	3.746	29.08	0.886	0.182
<i>Paratrechina</i> sp.1	3.459	33.02	0.174	0.807
<i>Gnamptogenys bisulca</i>	2.71	36.12	0.251	0.498
<i>Pheidole</i> sp.5	2.525	39	0.283	0.366
<i>Hypoponera</i> sp.3	2.343	41.67	0.0815	0.591
<i>Cyphomyrmex</i> sp.3	2.291	44.28	0.163	0.437
<i>Pheidole</i> sp.10	2.15	46.73	0.421	0.148
<i>Solenopsis</i> sp.3	2.142	49.18	0.188	0.343
<i>Pachycondyla chyzeri</i>	2.141	51.62	0.46	0.0934

**Figure 5**

Drawings of common ant species in the Otongachi forest. (A, C, E, G, I) Lateral views of the ants. (B, D, F, H, J) Ants in full-face view. **A-B**, *Acantognathus teledectus*; **C-D**, *Lenomyrmex foveolatus*; **E-F**, *Protalaridris armata*; **G-H**, *Gnamptogenys* sp.; **I-J**, *Pachycondyla chyzeri*. Scale bars = 0.5 mm. All drawings by Paula Terán.

mountain species such as *Lenomyrmex foveolatus* Fernandez 2003, *Pachycondyla chyzeri* (Forel 1907) and *Protalaridris armata* Brown 1980 (fig. 5 C–D, E–F, I–J). We argue that the intersection of two fairly distinct ant assemblages, one from the lowland tropical forest and one of the Andean forest may be contributing to the high diversity found in the forest. But more data on current distribution patterns of ant species in Ecuador and their zones of endemism is needed to test these assumptions.

Most of the ant species present in the forest available to be collected by our methods were detected in the list of recorded species (total species number = 103, estimated species number = 109). A high number of ant species was shared by the two transects ( $n = 52$ ; Chao-Jaccard = 0.83; distance between transects = 2-km), suggesting we would need to include additional collection methods and/or new localities from comparatively far distances (e.g. more than 2 km apart) and/or different altitudes to increase the number of species collected.

Recently, the use of morphometric techniques to summarize and analyze biological relationships between ant species and genera has advanced our understanding of ant community composition (Weiser & Kaspari 2006) and caste evolution (Diniz-Filho *et al.* 1994; De Andrade & Baroni Urbani 2000; Pie & Traniello 2007). Our PC analysis based on morphological variables showed significant differences in overall size, EL and FL between ants collected by winkler sacs and the ones collected by pitfall traps. Pitfall traps were prone to collect bigger ants with well-developed eyes and long femurs. These results are in accordance with the hypothesis that pitfall traps collect ants with epigaeic habits (Parr & Chown 2001). Accordingly, ant diversity between the subsets of the ant community sampled under winkler sacs and pitfall traps differed. Ant species that presented more discriminatory power, such as *Solenopsis* cf. *stricta*, *Solenopsis* sp.1, *Pheidole* sp.6, *Pheidole* sp.2, *Azteca* sp.1, *Paratrechina* sp.1 and *Gnamptogenys bisulca*, explained 33% of the total variance and belong to widespread and abundant Neotropical ant genera. Therefore there is an *a priori* reason to prefer a combination of both sampling methods, as opposed to the use of just one method, either winkler sacs or pitfall traps, when collecting ants in a forest with a well-developed litter layer.

Particularly noteworthy is the absence in our species list of several worldwide invasive ants such as *Linepithema humile* (Mayr 1868), *Paratrechina fulva* (Mayr 1862) and *Tapinoma menalocephalum* (Fabricius 1793), already present in the surroundings of the research station at the forest and nearby villages

(vouchers of these species are stored at the ant collection of the QCAZ Museum). The apparent lack of invasive species reinforces the conservation status of the forest and calls for its protection. The low frequency ( $n = 23$ , traps=2) of *Wasmannia auropunctata* in our survey either suggests that (1) *W. auropunctata* is native to this forest, or (2) it is in early stages of the invasion process. The latter would not be surprising considering the proximity of the forest to the town of *La Unión del Toachi* and a primary highway of the country where the two main shipping ports of the country, the main traveling media of invasive species, intersect. Further research is needed to expand and clarify these observations (Le Breton 2003) as well as verify the pest status and origin of these invasive species inside Ecuador.

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## Appendix 1.

### List of ant species collected in Otongachi included in our Inventory.

For each species, the total number of specimens per collection method and transect and the total percentage of occurrence by collection method is included. One asterisk (\*) reflect a singleton and two (\*\*) a doubleton. Data showed for Ecitoninae ant genera reflect occurrence, not abundance

Species	Pitfall		Winkler		Ocurrence(%)	
	T-LL1	T-LL2	T-LL1	T-LL2	Pitfall	Winkler
<b>AMBLYOPONINAE</b>						
<i>Prionopelta amabilis</i> Borgmeier 1949	-	-	4	40	-	7.5
<b>CERAPACHYINAE</b>						
<i>Cerapachys</i> sp. 1	-	-	3	-	-	2.5
<i>Cerapachys</i> sp. 2	-	-	13	-	-	2.5
<b>DOLICHODERINAE</b>						
<i>Azteca</i> sp.1	195	354	15	5	35.9	15
<i>Azteca</i> sp.2	-	-	5	1	-	5
<b>ECITONINAE</b>						
<i>Labidus coecus</i> (Latrelle 1802)	2	-	2	-	5.1	5
<i>Labidus spininodis</i> (Emery 1890)	-	2	1	1	5.1	5
<i>Neivamyrmex</i> sp. 1	-	-	1	1	-	5
<b>ECTATOMMINAE</b>						
<i>Ectatomma ruidum</i> (Roger 1860)	-	6	-	-	2.6	-
<i>Gnamptogenys annulata</i> (Mayr 1887)	-	2	-	-	5.1	-
<i>Gnamptogenys bisulca</i> Kempf & Brown 1968	-	29	19	58	15.4	27.5
<i>Gnamptogenys minuta</i> Emery 1896 *	-	1	-	-	2.6	-
<i>Gnamptogenys</i> sp. 1**	-	2	-	-	5.1	-
<i>Gnamptogenys</i> sp. 2**	-	1	-	1	2.6	2.5
<i>Gnamptogenys</i> sp. 3	-	-	6	-	-	2.5
<i>Gnamptogenys</i> sp. 4	-	-	3	-	-	2.5
<i>Gnamptogenys</i> sp. 6	-	-	4	-	-	2.5
<i>Typhlomyrmex pusillus</i> Emery 1894	-	-	3	2	-	5
<b>FORMICINAE</b>						
<i>Acropyga</i> sp. 1	1	-	24	-	2.6	10

Species	Pitfall		Winkler		Occurrence(%)	
	T-LL1	T-LL2	T-LL1	T-LL2	Pitfall	Winkler
<i>Brachymyrmex</i> sp. 1	—	7	—	3	2.6	2.5
<i>Brachymyrmex</i> sp. 2	—	2	3	2	5.1	10
<i>Camponotus sericeiventris</i> (Guérin-Méneville 1838)*	1	—	—	—	2.6	
<i>Myrmelachista</i> sp. 1*	—	1	—	—	2.6	
<i>Paratrechina</i> sp. 1	7	11	161	157	12.8	38
<b>MYRMICINAE</b>						
<i>Acanthognathus teledectus</i> Brown & Kempf 1969**	—	—	2	—	2.5	
<i>Acromyrmex</i> sp. 1	2	—	3	—	2.6	2.5
<i>Acromyrmex</i> sp. 2*	1	—	—	—	2.6	
<i>Apterostigma</i> sp. 1	—	1	7	6	2.6	5
<i>Apterostigma</i> sp. 2	—	—	7	1	7.5	
<i>Apterostigma</i> sp. 3*	—	—	1	—	2.5	
<i>Apterostigma</i> sp. 4	1	—	21	11	2.6	17.5
<i>Apterostigma</i> sp. 5	—	13	10	5	7.7	7.5
<i>Crematogaster</i> sp. 1	—	—	4	—	2.5	
<i>Crematogaster</i> sp. 2	—	—	14	—	12.5	
<i>Cyphomyrmex</i> sp. 1	1	2	—	—	7.7	
<i>Cyphomyrmex</i> sp. 2	—	3	1	—	2.6	2.5
<i>Cyphomyrmex</i> sp. 3	3	9	23	40	17.9	32.5
<i>Hylomyrma</i> sp. 1	5	5	9	7	15.4	25
<i>Lenomyrmex foveolatus</i> Fernández 2003*	—	1	—	—	2.6	
<i>Megalomyrmex</i> sp. nov.	14	21	1	12	30.8	12.5
<i>Megalomyrmex silvestrii</i> Wheeler 1909*	—	—	—	1	2.5	
<i>Megalomyrmex bidentatus</i> Fernandez & Baena 1997**	—	2	—	—	2.6	
<i>Octostruma</i> sp. 1	1	—	53	—	2.6	10
<i>Octostruma</i> sp. 2	—	3	2	26	2.6	15
<i>Octostruma</i> sp. 3	—	4	33	19	2.6	25
<i>Octostruma</i> sp. 4**	—	—	—	2	2.5	
<i>Pheidole</i> sp. 1	—	7	223	23	2.6	12.5
<i>Pheidole</i> sp. 2	48	43	159	20	41.0	47.5
<i>Pheidole</i> sp. 3	—	—	43	2	22.5	
<i>Pheidole</i> sp. 4	6	2	—	—	10.3	
<i>Pheidole</i> sp. 5	55	—	29	22	15.4	22.5
<i>Pheidole</i> sp. 6	135	73	6	33	53.8	20
<i>Pheidole</i> sp. 7	1	9	—	3	10.3	5
<i>Pheidole</i> sp. 8	—	5	—	—	5.1	
<i>Pheidole</i> sp. 9	—	7	—	—	5.1	
<i>Pheidole</i> sp. 10	29	36	28	—	20.5	7.5
<i>Pheidole</i> sp. 11**	—	—	—	2	2.5	
<i>Pheidole</i> sp. 12*	—	1	—	—	2.6	
<i>Pheidole</i> sp. 13	—	—	3	—	2.5	
<i>Pheidole</i> sp. 14	2	—	6	—	2.6	2.5
<i>Pheidole</i> sp. 15**	—	1	1	—	2.6	2.5
<i>Procryptocerus mayri</i> Forel 1899**	—	2	—	—	2.6	
<i>Protalaridris armata</i> Brown 1980	—	—	39	2	20	
<i>Pyramica</i> sp. 1	—	1	—	10	2.6	10
<i>Pyramica</i> sp. 2**	1	—	—	1	2.6	2.5
<i>Pyramica</i> sp. 3	—	—	36	1	10	
<i>Pyramica</i> sp. 4*	—	—	—	1	2.5	
<i>Pyramica</i> sp. 5**	—	—	2	—	2.5	

<b>Species</b>	<b>Pitfall</b>		<b>Winkler</b>		<b>Ocurrence(%)</b>	
	T-LL1	T-LL2	T-LL1	T-LL2	Pitfall	Winkler
<i>Pyramica</i> sp. 6*	1	—	—	—	2.6	
<i>Pyramica</i> sp. 7	1	—	35	8	2.6	30
<i>Pyramica</i> sp. 8	2	—	15	16	5.1	25
<i>Rogeria</i> sp. 1	—	—	1	2		7.5
<i>Solenopsis</i> cf. <i>stricta</i>	3	27	481	280	28.2	55
<i>Solenopsis</i> sp. 1	10	42	82	217	51.3	70
<i>Solenopsis</i> sp. 2	—	—	126	—		10
<i>Solenopsis</i> sp. 3	2	14	24	40	17.9	15
<i>Solenopsis</i> sp. 4	16	11	1	159	10.3	7.5
<i>Solenopsis</i> sp. 5	—	—	—	10		2.5
<i>Solenopsis</i> sp. 6	—	—	22	—		5
<i>Strumigenys</i> sp. 1	—	—	75	8		7.5
<i>Strumigenys</i> sp. 2	—	—	4	—		7.5
<i>Tatuidris tatusia</i> Brown & Kempf 1968	11	7	—	—	7.7	—
<i>Trachymyrmex</i> sp. 1*	—	1	—	—		2.6
<i>Trachymyrmex</i> sp. 2	—	—	—	3		2.5
<i>Wasemannia auropunctata</i> (Roger 1863)	—	8	—	15	2.6	5
<b>PONERINAE</b>						
<i>Anochetus</i> sp. 1	2	1	—	—	5.1	—
<i>Anochetus</i> sp. 2	—	—	11	—	—	5
<i>Hypoponera</i> cf. <i>reichenspergeri</i>	—	—	8	—		2.5
<i>Hypoponera</i> cf. <i>trigona</i> **	—	1	1	—	2.6	2.5
<i>Hypoponera distinguenda</i> (Emery 1890)	3	8	16	39	10.3	27.5
<i>Hypoponera</i> sp. 1	—	—	—	4		2.5
<i>Hypoponera</i> sp. 2	—	—	6	6		7.5
<i>Hypoponera</i> sp. 3	2	3	59	14	10.3	45
<i>Hypoponera</i> sp. 4	—	2	—	10	2.6	7.5
<i>Odontomachus bauri</i> Emery 1892	6	5	2	15	12.8	7.5
<i>Odontomachus</i> sp. 1	1	2	—	1	5.1	2.5
<i>Pachycondyla harpax</i> (Fabricius 1894)	14	16	5	4	53.8	20
<i>Pachycondyla verenae</i> (Forel 1922)	2	17	—	—	10.3	
<i>Pachycondyla impressa</i> (Roger 1861)	7	14	—	2	30.8	2.5
<i>Pachycondyla chyzeri</i> (Forel 1907)	13	25	—	11	43.6	5
<i>Pachycondyla apicalis</i> (Latreille 1802)**	2	—	—	—	5.1	
<i>Pachycondyla</i> sp. 1*	—	—	1	—		2.5
<b>PROCRERATIINAE</b>						
<i>Discothyrea</i> sp. 1*	—	—	—	1	—	2.5

# Altitudinal distribution, diversity and endemism of Carabidae (Coleoptera) in the páramos of Ecuadorian Andes

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**Abstract.** Species richness and diversity of Carabidae (Coleoptera), as well as rates of endemism, are studied along altitudinal transects in the páramo of Ecuadorian Andes, from 3500 to 5000 m. Whereas a global tendency to reduction of species richness is evident from 4200 m upwards, two zones of high diversity and high proportion of endemic species occur at 3800–4000 m and at 4200–4400 m. Species turnover between grass páramo and superpáramo is significantly higher in drier mountains, especially in the Western Cordillera, than in humid mountains of the Eastern Cordillera. The altitudinal range of Carabid species tends globally to decrease along the vertical gradient, but with important local variations due to microenvironmental factors, especially humidity rate. When compared with recent phytogeographical studies, these results tend to support the idea that the majority of tussock-grass páramo is a secondary anthropogenic ecosystem. On the contrary, it is argued that the xeric landscape of the Chimborazo "arenal" is primordial, based on the presence of a stenotopic and possibly relict species, *Pelmatellus andium* Bates 1891.

**Résumé. Distribution en altitude, diversité et endémisme des Carabidae (Coleoptera) dans les páramos des Andes Equadorienne.** La diversité et le taux d'endémicité des Carabidae (Coleoptera) sont analysés sur plusieurs transects altitudinaux dans les páramos des Andes de l'Equateur, entre 3500 et 5000 m. Alors qu'une tendance générale à la diminution du nombre d'espèces apparaît à partir de 4200 m, deux zones de plus grande diversité et à fort taux d'espèces endémiques ont été mises en évidence à 3800–4000 m et à 4200–4400 m. Le taux de remplacement des espèces entre le páramo herbacé et le superpáramo est nettement plus élevé dans les massifs les plus secs, en particulier dans la Cordillère Occidentale, que dans les massifs humides de la Cordillère Orientale. L'amplitude altitudinale des espèces tend globalement à diminuer avec l'altitude, mais on note d'importantes variations d'une montagne à l'autre ou d'un versant à l'autre, en raison des conditions du milieu (en particulier le degré d'humidité). À partir d'une comparaison avec des études phytogéographiques récentes, on apporte des arguments à l'hypothèse selon laquelle la plus grande partie du páramo herbacé est une formation secondaire d'origine anthropique. À l'inverse, il est suggéré que le paysage semi-désertique de l'"arenal" du Chimborazo est climacique, compte tenu de la présence d'une espèce sténotope et vraisemblablement relict, *Pelmatellus andium* Bates 1891.

**Keywords:** Páramo, Carabidae, Ecology, Biodiversity, Endemism.

Páramo is a tropical alpine ecosystem that ranges in the Andes from northern Peru to the Cordillera de Talamanca in Costa Rica, above continuous forest line (3400–3600 m) and below permanent snowline (4800–5000 m), with particular features such as: low ambient temperatures, higher daily oscillations than seasonal ones, and a high frequency of night frost throughout the year. It is formed by tussock grasses, cushion plants, and sclerophyllous shrubs.

Following its vegetation structure, the páramo has been divided into three altitudinal belts: the subpáramo, which is a transitional zone with the

montane forest, the grass páramo, and the superpáramo (van der Hammen & Cleef 1986; Lutteyn 1999; for Ecuador: Acosta-Solís 1984; Sklenár & Ramsay 2001). Grass páramos occur in Ecuador from about 3400 to over 4000 m. This formation is dominated by bunch- or tussock-forming grasses. In between the grass tussocks grow a diverse assemblage of herbaceous plants, scattered small shrubs and cushion plants. Most grass páramos are burned annually or every few years, presenting therefore morphological and physiological adaptations to survive frequent fires (Lægaard 1992). The superpáramo usually occurs between 4100–4200 m and 4800–4900 m and is subdivided into two belts, the lower and upper superpáramo (Sklenár & Balslev 2005). Lower superpáramo (4100–4200 to 4400–4500 m) is usually richer in species, with sclerophyllous shrubs and cushion plants, but

tussock grasses are usually also important. The upper superpáramo (above 4400–4500 m) is characterised by shortstem grasses, prostrate subshrubs and herbs, acaulescent rosettes and cushion plants. The vegetation is poor and patchy, being confined to a few favourable habitats.

Most of the studies that have been dedicated to the ecology and the biogeography of the páramo deal with plants or vertebrates. Carabid beetles are rarely taken into account in such works, except in local ecological surveys of single mountains (Perrault 1994; Sturm 1994; Moret 2001; Smithers & Atkins 2001; Camero 2003) or in physiological researches (Sømme *et al.* 1996). Nonetheless, Carabidae have proved to be very useful for ecological studies, inasmuch as many of them are stenotopic and linked to specific niches (Thiele 1977; Desender *et al.* 1994; Dajoz 2002). Moreover, in high altitude communities, their high rate of endemism provides valuable data for biogeographic analyses (Noonan *et al.* 1992; Liebherr 1994).

In a recent revision of the Carabidae that live in Ecuadorian páramos above 3400 m (Moret 2005), 204 species were treated and arranged in 16 genera and 8 tribes (table 1). Most of them (94 %) are micropterous, with a very low dispersal power due to the loss of functional metathoracic wings, and are therefore restricted to small montane areas. This paper deals with some of the ecological and biogeographical results of that study, as far as species richness, diversity and endemicity are concerned. It will address the

following questions: How do species richness and beta-diversity vary along altitudinal gradients? How are microendemic species distributed along these gradients? A comparison will also be drawn with the results of recent phytogeographic studies (Lauer *et al.* 2003; Sklenár & Lægaard 2003; Sklenár & Balslev 2005; Sklenár 2006), in order to contribute to a better definition of altitudinal zonation and areas of endemism within Ecuadorian páramos.

### Material and methods

Our taxonomic treatment of the páramo Carabids of Ecuador was based on direct examination of *ca* 8500 specimens found throughout that country above 3400 m. 2481 specimens were collected by the author during several field work periods (1984–1986, July–August 1988, April 1991, January 1995, July–August 1998, July 2001), the rest by 31 collectors or teams of collectors between 1853 and 2002. A detailed checklist of materials can be found in Moret 2005: 21–24 (see also below in the acknowledgment section). A few minor changes were introduced in this data set, following recent revisions of the genera *Bembidion* (Toledano 2008) and *Oxytrechus* (Allegro *et al.* 2008).

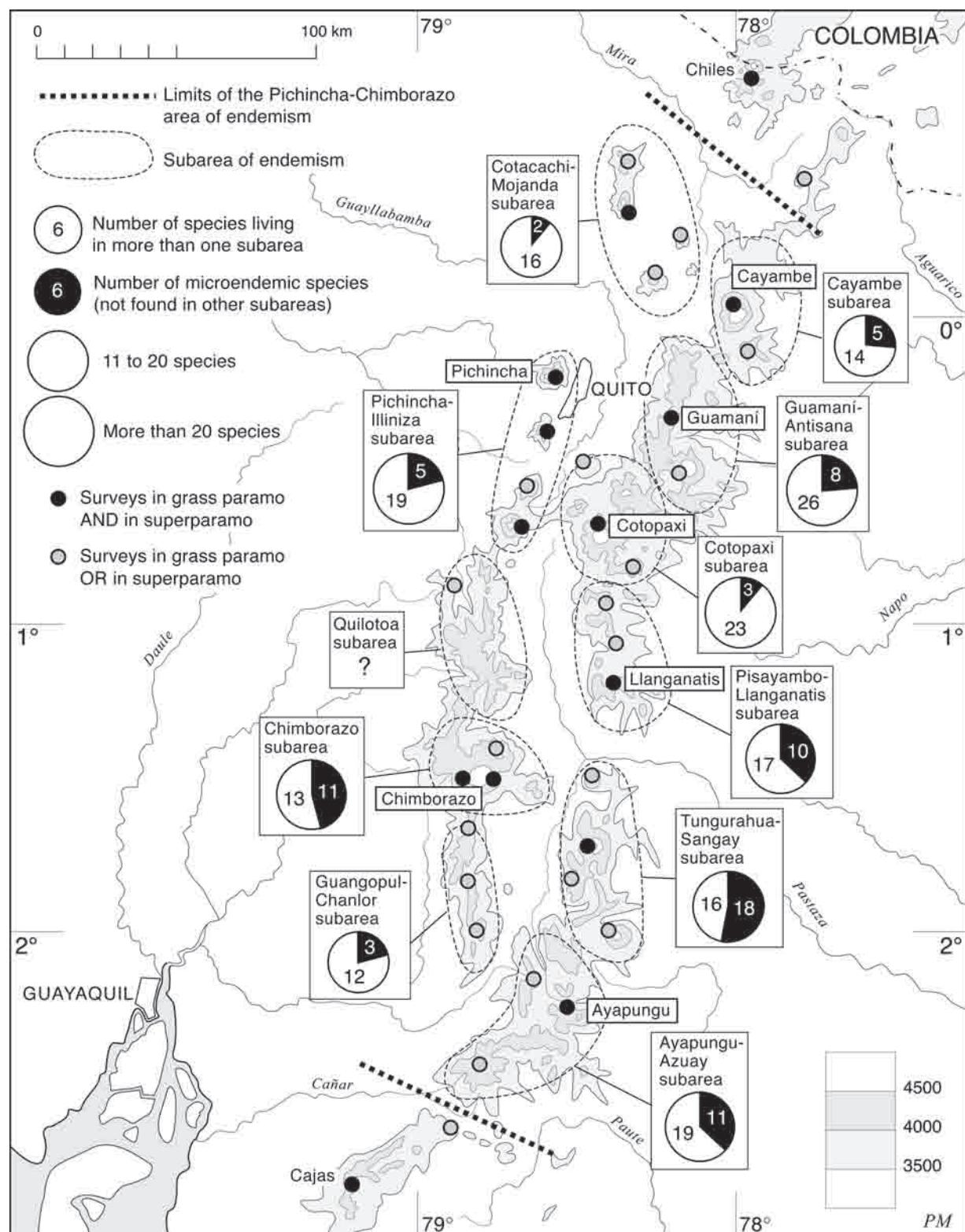
As the first level of analysis, all specimens bearing precise altitudinal data (*ca* 7500) were taken into account as a means to highlight global tendencies at generic level. But this general data set is far too heterogeneous to support accurate ecological and biogeographical analyses, since it sums materials collected by different researchers or travellers, each with distinct purposes and using different techniques.

Thus, at a second stage, in order to allow more precise faunistic assumptions, the focus was restricted to the Pichincha-Chimborazo area of endemism, which has been far better

**Table 1.** Genera of Carabidae found in Ecuadorian páramos above 3400/3500 m.

Am. = American; S.Am. = South American; M./S.Am. = Middle and South American.

Tribe	Genus	Described species in Ecuador	Biogeographic area	Maximum elevation in Ecuador
Migadopini	<i>Aquilex</i> Moret 1989	1	High-andean endemic	4300
Trechini	<i>Trechisibus</i> Motschulsky 1862	3	Austral Am.	4800
	<i>Oxytrechus</i> Jeannel 1927	12	Tropical andine	3800
	<i>Paratrechus</i> Jeannel 1920	16	Montane M./S.Am.	4600
Bembidiini	<i>Ecuadorion</i> Moret & Toledano 2002	30	Montane M./S.Am.	5070
Harpalini	<i>Notiobia</i> Perty 1830	2	Temperate Am.	3850
	<i>Bradycellus</i> Erichson 1837	2	Temperate Am.	3800
	<i>Pelmatellus</i> Bates 1882	12	Montane M./S.Am.	4800
Pterostichini	<i>Blennidus</i> Motschulsky 1865	24	Tropical andine	4900
Platynini	<i>Incagonum</i> Liebherr 1994	2	Temperate S.Am.	3800
	<i>Sericoda</i> Kirby 1837	1	Holarctic	4000
	<i>Glyptolenoides</i> Perrault 1991	2	Tropical andine	3900
	<i>Dyscolus</i> Dejean 1831	89	Neotropical	4970
Dercylini	<i>Dercylus</i> Castelnau 1832	5	Neotropical	4200
Lebiini	<i>Mimodromius</i> Chaudoir 1873	2	Temperate S.Am.	4000
	<i>Lebia</i> Latreille 1802	1	Pantropical	3850

**Figure 1**

Map of the páramos in the central and northern Andes of Ecuador, with the limits of the Pichincha-Chimborazo area of endemism and of its subareas (modified from Moret 2005).

**Table 2.** Characteristics of eight selected altitudinal transects, between 3500 and 5000 m elevation, in seven mountains of the Pichincha-Chimborazo area of endemism.

	Province	Coordinates	Maximum elevation	Climate	Total Nr of species	Micro-endemic species
<b>Pichincha</b> East and South slopes	Pichincha	0°10'S 78°35'W	4794	Medium	18	3
<b>Chimborazo</b> West slope	Chimborazo	1°28'S 78°52'W	6310	Dry	21	6
<b>Chimborazo</b> East slope	Chimborazo	1°28'S 78°46'W	6310	Humid	17	8
<b>Cotopaxi</b> North slope	Cotopaxi	0°40'S 78°26'W	5897	Dry	29	2
<b>Cayambe</b> West and North slopes	Pichincha	0°02'N 77°59'W	5790	Humid	20	4
<b>Guamaní</b> East slope	Napo	0°18'S 78°14'W	4490	Wet	28	8
<b>Llanganatis</b> North slope	Tungurahua	1°10'S 78°20'W	4390	Humid	20	8
<b>Ayapungu</b> West slope	Chimborazo	2°17'S 78°35'W	4730	Humid	27	9

surveyed than the others (fig. 1). In that particular area, the faunistic analysis was limited to 142 species that are true páramo dwellers. Four species that have been registered sporadically at low elevations in the grass páramo were excluded, because they belong predominantly to the upper montane forest fauna: *Bembidion (Ecuadorian) sanctamariae* Darlington 1934 (= *Bembidion (Ecuadorian) gisela* Moret & Toledano 2002), *Glyptolenoides azureus* (Chaudoir 1859), *Incagonum aeneum* (Reiche 1843), and *Dyscolus bordoni* Moret 1993. Three more taxa were dismissed because they are highly specialised azonal species: *Sericoda bembidioides* Kirby 1837 (a widespread pyrophilous insect), *Lebia paramicola* Moret 2005 and *Mimodromius leleupi* Mateu 1970 (two ectoparasitic species).

Finally, special attention has been paid to seven mountains of the Pichincha-Chimborazo area, where complete or almost complete altitudinal transects can be reconstructed along one or several slopes, from the bottom of the grass páramo up to the top of the superpáramo (table 2). Based on these data, altitudinal variation of Carabid diversity was studied between 3500 and 5000 m to test possible occurrences of faunistic zonation, especially between grass páramo and superpáramo (fig. 4).

The altitudinal range of the species was calculated as the

difference between the lowest and highest place where they were collected. Altitudinal data given by the labels of individual specimens were used to work out the number of species collected in any vertical interval of 100 m, as a means to measure species richness per altitude. The following analyses are therefore mostly based on presence-absence data. The lack of long-lasting and systematically planned samples throughout entire vertical transects makes impossible any attempt to measure species abundance with greater precision.

The possibility of quantifying species diversity in vertical transects is hindered too by the heterogeneity of the data set. To compare as a whole the grass páramo Carabid community with that of the superpáramo, as we tried it in a previous work (Moret 2005: tab. 35), is almost impossible, insofar as the definition of these communities is biased by subjective assumptions, due to altitudinal variations of the limit between both floristic belts and to the existence of a transition zone where different faunistic elements overlap. Here we preferred to compare the composition of Carabid communities at four intervals of altitude that were arbitrarily selected: 3600–3700, 3900–4000, 4200–4300 and 4500–4600 m (tab. 3). Species diversity was calculated using the Sørensen similarity index:  $2A / (a_1 + a_2)$ , where  $a_1$  refers to species scores in the sample 1,

**Table 3.** Diversity of Carabid species at different elevations on seven altitudinal transects.  
Columns 2, 4, 6, 8: number of species. Columns 3, 5, 7 (S.I.): Sørensen similarity index.

	3600–3700 m	S.I.	3900–4000 m	S.I.	4200–4300 m	S.I.	4500–4600 m
Pichincha	7	0,71	7	0,27	8	0,75	8
West Chimborazo	11	0,64	11	0,25	5	0,50	3
Cotopaxi	12	0,50	8	0,25	8	0,46	5
Cayambe	8	0,27	7	0,61	6	0,61	7
Guamaní	7	0,44	20	0,44	12		-
Llanganatis	10	0,47	7	0,37	9		-
Ayapungu	11	0,33	7	0,59	10		-

$a_2$  to species scores in the sample 2, and A to scores of species shared between both samples (Koleff 2005).

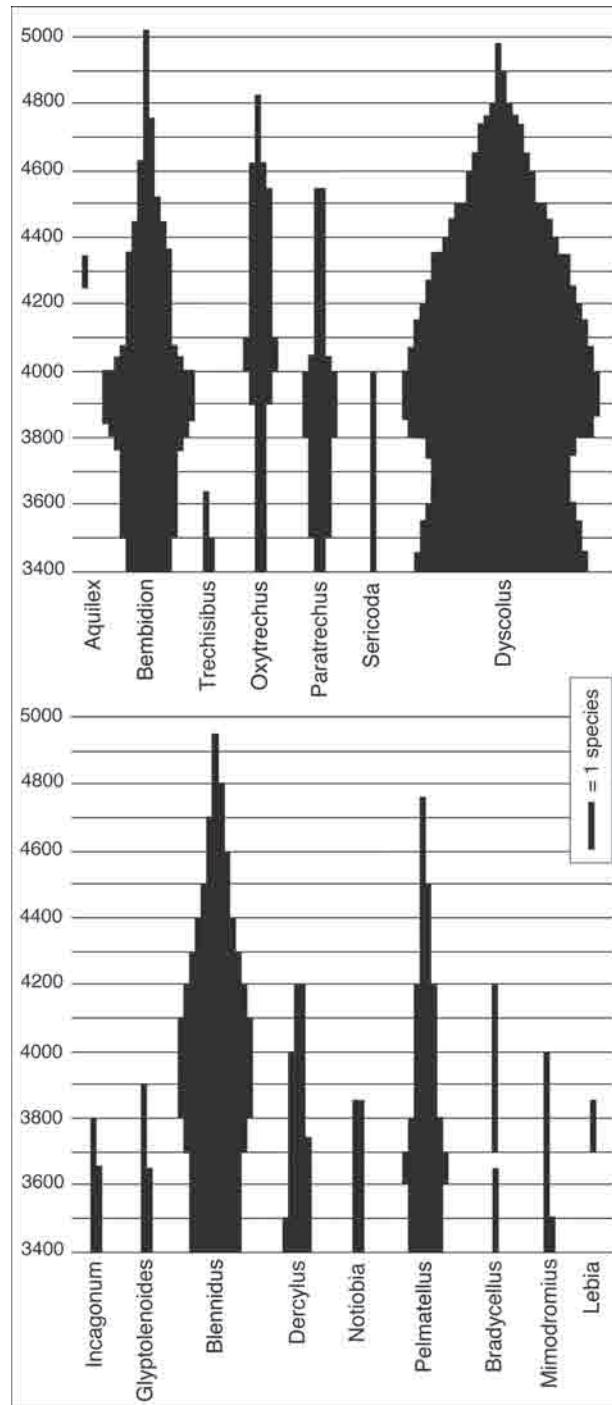
Definition of endemic and microendemic species, as well as areas of endemism, are the result of a previous work (Moret 2005: 262). Based on the distribution patterns of 191 micropterous species (which amount to 94 % of all páramo Carabid species), five areas of endemism were distinguished, from north to south: the Carchi area, the Pichincha-Chimborazo area, the Cajás area, the Saraguro area, and the Loja area. These results are strongly supported by a very high rate of precinctive species (*i.e.*, species that have not been found in any other area): 85.7 % in Carchi, 94.5 % in Pichincha-Chimborazo, 81.4 % in Cajás, 80 % in Saraguro and 100 % in Loja. On a smaller scale within the Pichincha-Chimborazo area (fig. 1), the distributional patterns of microendemic species (*i.e.*, species restricted to areas less than 1000 km<sup>2</sup>) enabled us to define 13 subareas of endemism, where the percentage of precinctive species is 10 % or more.

## Results

### Genus diversity

With only 16 taxa (table 1 and fig. 2), generic richness is low in the Ecuadorian páramo when compared with other neotropical ecosystems. In the nearby Andean montane forest, the number of known genera of Carabidae ranges far above 50 (unpublished data). The number of genera is the highest in the basal zone of the páramo, due to the presence of several genera composed of sylvatic or ruderal species that occasionally enter the grass páramo at low altitudes: *Incagonum*, *Glyptolenoides*, *Notiobia*, *Sericoda*. 14 genera are recorded from altitudes around 3500–3600 m, whilst from 4100 m upwards only 9 genera are found. The fauna of the upper superpáramo, above 4400 m, is restricted to 6 genera (*Bembidion*, *Oxytrechus*, *Paratrechus*, *Dyscolus*, *Blennidus* and *Pelmatellus*), represented there by specialised orobiont forms. In global terms, these six genera are clearly dominant in Ecuadorian páramos (fig. 2). Their curves reveal an optimum of species richness at middle elevations (from 3800 to 4100 m), and only then a progressive diminution. Only one genus, *Aquilex*, is endemic to Ecuadorian high Andes and can be considered as an exclusive páramo specialist. The other genera are all represented in the upper montane forest by species that are adapted to leaf-litter or arboreal habitats.

Species richness varies greatly from one genus to the other, with *Dyscolus* containing 44 % of all species. *Dyscolus* species show a great variety of adaptations to almost every ecological condition that can be found in páramos, from the xeric puna-like “arenal” to the uppermost superpáramo. Other genera are linked with narrower habitat conditions. *Aquilex*, *Paratrechus* and part of *Bembidion* are riparian or highly hygrophile; *Blennidus* and *Pelmatellus* contain a majority of generalist species, along with a few xerophile species.



**Figure 2**

Altitudinal range and species richness of the 16 Carabid genera that live in Ecuadorian páramos (global data). In each 100 m-interval, the number of black vertical bars indicates the number of registered species.

## Species diversity and altitudinal distribution

It is generally assumed that in montane faunas, diversity gradually decreases as altitude increases (Stevens 1992). The case of páramo Carabids is not so straightforward. Whereas a global tendency to reduction of species richness is evident from 4200 m upwards, a completely different situation is observed in the grass páramo between 3400 and 4200 m (fig. 3). In that particular floristic belt, species richness reaches higher scores at medium elevations than at low ones, with a major peak of diversity at 3800–4000 m, as proved by a conspicuous rise of the number of microendemic species. Even in the superpáramo, a minor peak can be detected between 4200 and 4400 m, being characterised by a pause in the decrease of the non-endemic species and a slight recovery of the microendemic ones.

The analysis of individual transects allows a better understanding of these phenomena (fig. 4 and table 3). Two major patterns can be distinguished. A first group of mountains includes Pichincha, West Chimborazo and Cotopaxi, with four characteristics: 1. high or

moderately high similarity within the grass páramo, from 3500 to 4000 m; 2. important turnover of species between grass páramo and superpáramo, as indicated by a very low similarity index (*ca* 0,25) between the 3900–4000 and 4200–4300 m intervals; 3. reduced turnover within the superpáramo; 4. highest species richness around 4000–4200 m in normal conditions (Pichincha). On Cotopaxi and on the West slope of Chimborazo, a sudden collapse of the species richness at the same elevation is due to local factors: arid microclimate and/or recent volcanic activity (see below).

Results of less complete surveys on the Illiniza, Atacazo and Corazón volcanoes suggest that this pattern is widespread all along the Western Cordillera in the Pichincha-Chimborazo area. The case of the Cotopaxi north transect seems to be an exception, as it belongs to the Eastern Cordillera.

A second group is formed by four mountains of the Eastern Cordillera (Cayambe, Guamaní, Llanganatis, Ayapungu), along with the Eastern slope of the Chimborazo in the Western Cordillera. They

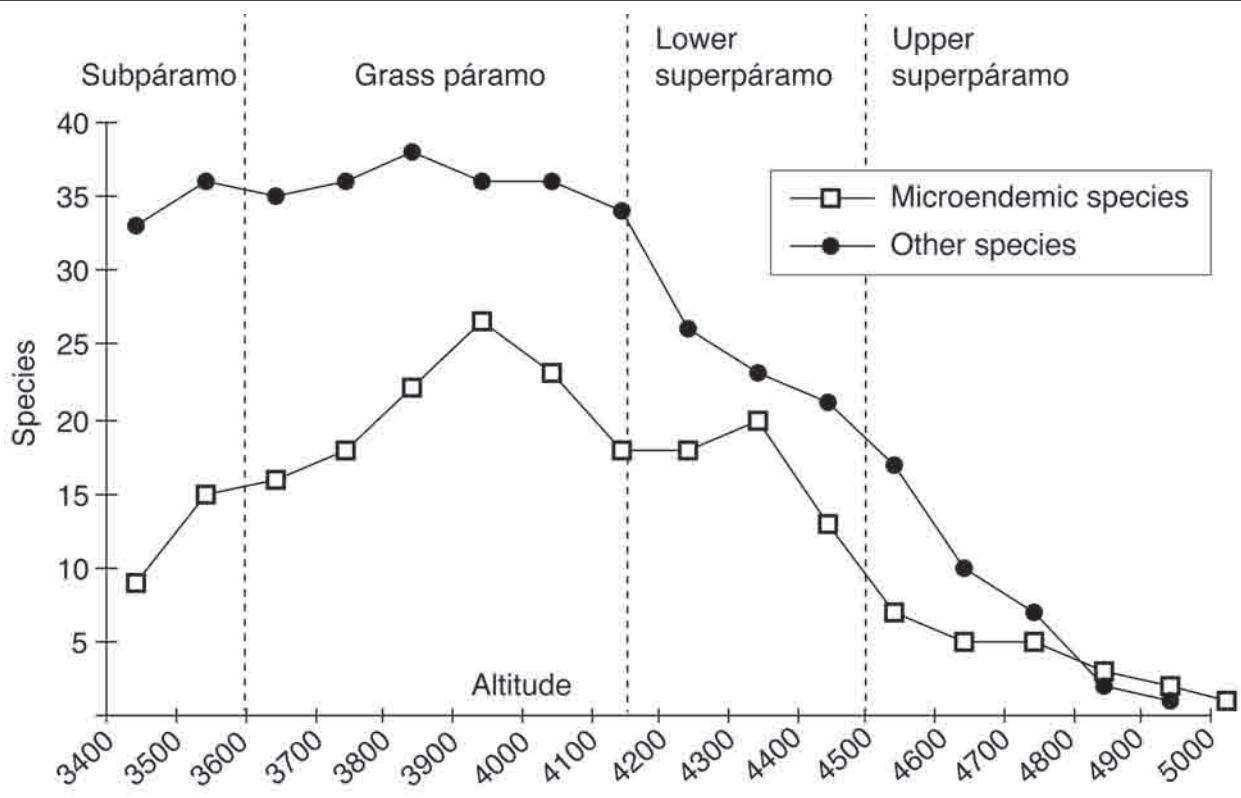
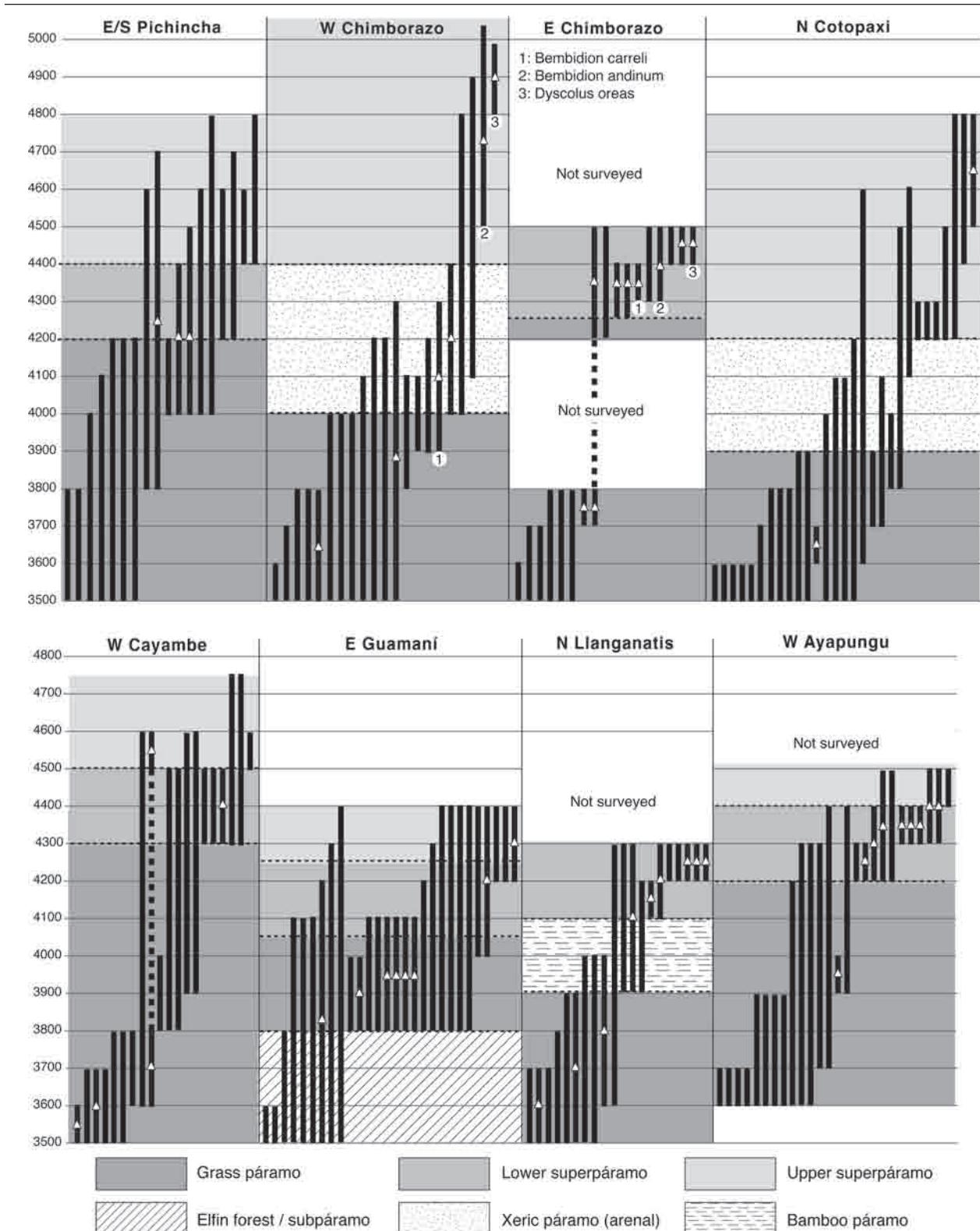


Figure 3

Altitudinal variation of species richness (per 100 metres-intervals of altitude) for 142 Carabidae species of the Pichincha-Chimborazo area of endemism. White squares: microendemic species; black circles: other species.

**Figure 4**

Altitudinal distribution of Carabid species in vertical transects of seven mountains of the Pichincha-Chimborazo area. Details about geographical situations in table 2. White triangles: microendemic species.

present three distinctive traits: 1. similarity is low or moderate between the lower and the upper part of the grass páramo, from 3500 to 4000 m; 2. carabid communities at 3900–4000 m and at 4200–4300 m are moderately similar (Cayambe, Ayapungu) or moderately dissimilar (Guamaní, Llanganatis), but in general terms, similarity index between grass páramo and superpáramo is always higher than in the first group; 3. species richness reaches very high scores in non-disturbed páramos, being extremely high from 3900 to 4100 m in the Guamaní transect (20 different species occurring in that interval), due to exceptional environmental conditions: high humidity, absence of grazing, diverse vegetation.

These global tendencies are locally modified by environmental or historical factors. Disturbances, such as volcanic activity or soil erosion, are important features in some páramos of Ecuador and may significantly alter the general altitudinal patterns (Sklenár & Balslev 2005). For example, species richness has been dramatically reduced by volcanic activity of the last two centuries on the slopes of Cotopaxi, between 3900 and 4200 m (fig. 4), and at all elevations on currently active volcanoes such as the Tungurahua or the Sangay, both in the Eastern Cordillera (Moret 2005). Regarding climatic factors, the case of the arid western side of Chimborazo will be discussed below.

### Altitudinal range

Altitudinal range is quite variable among páramo Carabid species. In the genus *Dyscolus*, the mean altitudinal range is close to 500 m, but some species have been registered at almost all elevations from 3400 m up to 4400 m (Moret 2005: fig. 366). If we discard the species registered at low elevations that are known to live far below 3500 m in the subpáramo, the altitudinal range of Carabid species tends globally to decrease along the vertical gradient, i.e., the species from higher altitudes tend to have a narrower altitudinal range. This result seems to differ from floristic data in similar contexts, since botanical surveys of the Illiniza volcano, situated in the Western Cordillera south of the Pichincha, have shown that the mean altitudinal range of species per altitude increases along the gradient (Sklenár 2006).

The altitudinal range of several widespread species differs greatly from one mountain to another, or even from one slope to the other on the same mountain. These local variations may be important, as shown by a detailed analysis of the distribution of four species of the genus *Dyscolus* (Moret 2005: 246-248). In the case of *Dyscolus diopsis* (Bates 1891) and *D. megacephalus* (Bates 1891), it is quite clear that the range of these

species is broader and starts at lower elevations in humid páramos (Cayambe, Guamaní, Ayapungu), whereas it is much narrower and starts at higher elevations in drier contexts, being usually restricted to the superpáramo (Cotopaxi, Pichincha). On the West slope of Chimborazo, *Dyscolus oreas* (Bates 1891) ranges from 4800 m to 4970 m, in the uppermost portion of the superpáramo, whereas on the East slope, the same microendemic species is present as low as 4400 m (fig. 4, n° 3). A similar pattern is shown by *Bembidion andinum* Bates 1891 (n° 2), but on the contrary *Bembidion carreli* Moret & Toledano 2002 lives higher on the East slope than on the West one (n° 1). These data reveal the role played by local environmental factors on stenotopic flightless insects.

### Distribution of microendemic species

If we take into account all the species of the Pichincha-Chimborazo area, the mean altitudinal range of the best known species –particularly those of the genus *Dyscolus*– appears to be much broader in the widespread species than in the microendemic ones. In other words, there is a positive correlation between restricted geographic area and narrow altitudinal distribution.

Proportion, richness and altitudinal distribution of microendemic species vary greatly from one mountain to another, and do not seem to respond to any clear general patterns. Only in some mountains of the above described second group (Eastern Cordillera + East Chimborazo), we can observe a very high proportion of microendemics in a few particular contexts: Guamaní from 3800 to 4100 m, Llanganatis above 4100 m, Ayapungu above 4200 m, East Chimborazo above 4300. Except in the particular case of Guamaní, these data point to the lower superpáramo as to a hotspot of diversity with a high proportion of microendemics.

### Discussion

The main strategy of páramo insects seems to be behavioural avoidance of cold temperatures and excessive dryness (Smithers & Atkins 2001). It has been demonstrated that resistance to coldness and dessication is surprisingly low among Ecuadorian high-altitude Carabids (Sømme *et al.* 1996). Owing to the lack of physiological adaptation, these insects are in need of shelter under rocks, stones or cushion plants, or among the superficial roots of tussock-grasses, in order to avoid the extreme nycthemeral contrasts of the high Andean climate. Consequently, Carabid communities depend on vegetation structure and soil morphology as well as on the altitudinal factor itself. This is the reason

why many Carabid species have different altitudinal ranges in different mountains, or in different slopes of the same mountain, according to local climatic, pedologic and floristic conditions.

### Diversity in the grass páramo

Carabid assemblages demonstrate that the highest diversity occurs in the upper part of the grass páramo (3900–4100 m) and in the lower part of the superpáramo (4100–4400 m), then falling off steeply into the upper superpáramo. In the grass páramo, species diversity is much higher at high elevations (above 3800 m) than in its lower part (fig. 3). These results contradict the usual assumption of a gradual decrease of diversity and species richness along altitudinal gradients (Stevens 1992). They can be explained at some extent by the fact that the upper limit of the species that are restricted to the grass páramo overlaps with the lower limit of the high altitude orobionts, so that the maximum diversity occurs in a transitional zone where many flightless páramo Carabid species are likely to be found. But the main cause of the relatively depauperate fauna of the grass páramo, between 3500 and 3900 m, is probably anthropogenic.

It has been assumed that the climax vegetation of the Andes was forest up to 4200–4300 m, and that present-day grass páramo is a fire-induced anthropogenic landscape (Lægaard 1992). Carabid distribution and diversity allow us to contribute to this debate with five points. 1/ Species richness is frequently higher in the lower superpáramo, around 4200–4300 m, than in grazed páramos around 3700–3800 m, particularly in the Eastern Cordillera (fig. 4). 2/ There is a high faunistic similarity between forest edge communities and grass páramo communities (Moret 2005). 3/ There is a low or moderately low faunistic similarity between grazed páramo communities and superpáramo communities (table 3). Conversely, there is much less turnover between the upper part of grass páramo and the superpáramo in the few transects, such as Guamaní, where anthropic pressure is low. 4/ In the grass páramo, communities are dominated by a few generalist and eurytopic species, with broad altitudinal ranges: *Bembidion fulvocinctum* Bates 1891 and *B. cotopaxi* Moret & Toledano 2002, *Dyscolus alpinus* (Chaudoir 1878) and *D. denigratus* (Bates 1891), *Blennidus pichinchae* (Bates 1891), *Dercylus cordicollis* (Chaudoir 1883) and *Pelmatellus columbianus* (Reiche 1843). 5/ Percentage of microendemic species is lower in the grass páramo, higher in most of the superpáramos (fig. 4).

These observations indicate clearly that the Carabid communities of the grazed páramo are impoverished,

dominated by typically pioneer or opportunistic species, some of which come from the ecotone habitat of the forest edge. In that way, the results of this study strengthen the hypothesis of the tussock-grass páramo being a secondary anthropogenic ecosystem. In non-disturbed conditions, biotopes similar to the lower superpáramo may have existed locally as low as 3900 m, mixed with patches of *Polylepis* forest, as indicated by the residual presence of superpáramo specialists at elevations between 3900 and 4100 m in almost all the surveyed transects.

Only a few páramos below 4200 m can be considered to represent true climax vegetation, based on a greater species richness and higher percentage of microendemic species. On the one hand, there are the bamboo páramos of the most humid areas of the Eastern Cordillera, whose entomological fauna is still poorly known. A partial survey on the north slope of Llanganatis (table 2 and fig. 4) indicates that the Carabidae that have been found in this type of páramo are both related with the superpáramo community and with the most hygrophilic elements of the lower grass páramo community. In the Guamaní area, the outstanding richness of the Carabid community between 3800 and 4000 m is due to the great diversity of ecological niches in a patchy mosaic of shrub páramo, *Polylepis pauta* mixed woodland and swamps (Lauer *et al.* 2003: 80).

On the other hand, there is the xeromorphic páramo, locally called “arenal”, of the western side of Chimborazo. This desert-like area with very sparse and patchy vegetation, in strong contrast with the dense humid páramo of the eastern side, is the result of a rain-shadow phenomenon on the western leeward side of the mountain. A similar pattern, though less contrasted, is known on the Southwest side of the Antisana, a volcano situated halfway between Guamaní and Cotopaxi. According to Sklenár & Lægaard (2003), there is a higher floristic similarity between the two western and two eastern sides of these mountains, respectively, than between the opposite sides of each mountain. Despite limited faunistic surveys on Antisana, the same conclusion can be drawn from the composition of Carabid communities. On Chimborazo, similarity is very low between the west and east slopes, though a typical xerophilic species of the Chimborazo “arenal”, *Pelmatellus andium* Bates 1891, is present also at the same elevation on the west side of the Antisana.

As to its floristic communities, the dry western Chimborazo has a low species richness and low beta-diversity; it is among the least diverse páramos in Ecuador, with 20 % less plant species than on the opposite humid east side (Sklenár & Lægaard 2003).

According to these authors, the desert-like “arenal” would be an anthropogenic, depauperate landscape “due to the combined effect of (1) rain-shadow of the volcano, (2) human-induced disturbance of the vegetation by cattle-breeding and heavy grazing, and (3) resulting erosion”. This assessment is not supported by faunistic data. Species richness is relatively low in the “arenal”, but its community is quite different from that of standard grass páramo at the same elevation in other mountains of the Western Cordillera. Locally, there is a very low similarity between the “arenal” community at around 4200 m and that of the grass páramo under 4000 m (table 3). Moreover, this xerophile community includes a stenotopic element, *Pelmatellus andium* Bates 1891, which is only known from three arid páramos or superpáramos (Antisana, Cotopaxi, Chimborazo). Owing to its discontinuous distribution in three of the most xeric páramos of the Pichincha-Chimborazo area, this species is likely to be a relict testifying to past cold and dry periods of the last glaciation, from 25 000 to 15 000 BP, when the Ecuadorian Andes were covered by a puna-like landscape down to 3000 m (Colinvaux *et al.* 1997). Taking these data into account, we suggest that the desert-like páramo of the “arenal” has a long history and is not the result of recent anthropogenic disturbances.

### Diversity in the superpáramo

The lower superpáramo (4100–4400 m) is well defined by its faunistic composition. In some of the best sampled transects (Cayambe, Pichincha, East Chimborazo, Ayapungu), this belt proves to be a zone of high biodiversity, especially regarding stenotopic elements. Similar patterns have been highlighted by recent floristic analyses (Sklenár & Balslev 2005; Sklenár 2006). Interestingly, rates of species turnover from grass páramo to lower superpáramo are quite different in humid and dry páramos, i.e. in Group 1 (Western Cordillera + Cotopaxi) and in Group 2 (Eastern Cordillera + East Chimborazo). In Group 1, a sharp threshold in species composition occurs at around 4100 m, which corresponds to the transition between grass páramo and superpáramo. In Group 2, situations are more diverse: in some cases the same species that dominate in the superpáramo are present in the upper belt of the grass páramo (Guamaní), in others there is an important turnover at around 4300 m (Cayambe, Ayapungu). These differences seem to be due to local environmental conditions, especially climatic and hydric factors.

Our data set suggests a positive correlation between humid microclimate and species richness, as illustrated by the most diverse superpáramos of Group 2

(Guamaní, Llanganatis, Ayapungu), which are also the most humid (tables 2 and 3). The number of microendemic species is also very high in these humid superpáramos. These hotspots of diversity correspond to the upper atmospheric condensation level, situated between 4000 and 4300 m in Colombia and Northern Ecuador (Van der Hammen & Cleef 1986: 158; Sklenár 2006). Higher species richness in humid oriental superpáramos is partly due to the presence of specialised riparian hygrophile species that live in streamlets or swampy areas. Such humid biotopes do not exist at the same elevation in drier páramos of the Western Cordillera.

The presence of microendemic species is significantly high in the lower superpáramo of two of the few metamorphic mountains that exist in Ecuador, Llanganatis and Ayapungu (fig. 4). But as it has been stated by Sklenár & Balslev (2005), the significance of this geologic factor for the species distributions remains dubious, whereas humidity probably plays a greater role, insofar as these páramos, along with Guamaní, receive the highest amounts of precipitation among the studied sites.

### Endemism and faunistic similarity

As stated in a previous work (Moret 2005), the distribution of páramo Carabids supports the definition of areas of endemism on different scales (fig. 1). The endemity rates that have been registered among flightless Andean Carabids is far higher than in the flora of the páramo (Sklenár & Jørgensen 1999), opening up prospects for a better understanding of the complex history of that ecosystem during the Pleistocene; but this is a different issue that cannot be treated in this paper.

There is still one point that is worth emphasising. The rates of microendemism and of species richness are clearly higher in the Eastern Cordillera than in the Western Cordillera. Among possible causes, climate must be one of the most important, given the existence of humid areas, appropriate to many Carabid species, in the major part of the Eastern cordillera. But it can also be noticed that the basal volcanic complex of Northern Ecuadorian Andes, Late Miocene to Early Pliocene in age, is much broader and higher in the Eastern Cordillera than in the Western Cordillera; in the latter, the mountains that range above 3500 m result from recent Quaternary volcanism (Barbieri *et al.* 1988). This means that conditions for the development and diversification of a highly specialised montane fauna existed much earlier in the Eastern Cordillera.

Finally, the two groups of mountains we defined above, based on altitudinal distribution of Carabid

species, are congruent with the two major floristic divisions of Sklenár & Balslev (2005). Their first group includes drier páramos (Chimborazo-west, Antisana-west, Iliniza, Cotopaxi, and Pichincha), due to the occurrence of *Plantago nubigena* and *Festuca vaginalis*, whereas their second group, based on the presence of *Pentacalia peruviana*, is composed of humid páramos (Cotacachi, Imbabura, Cajas, Cayambe, and Chimborazo-east).

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# Diversity and distribution models of horse flies (Diptera: Tabanidae) from Ecuador

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**Abstract.** Worldwide information about Tabanidae is biased toward taxonomical research, which has been the main source of diversity data for this group of flies. In Ecuador, studies on horse flies have been irregular since the first descriptions of three Andean specimens in 1848. Catalogues, checklists and collections in national museums demonstrate that despite its size, Ecuador is at present the richest country in number of tabanids species in the Neotropics after Brazil, Colombia and Mexico, and has one of the highest numbers of species per unit area. The tabanofauna is predominantly shared with Colombia (62.6%), Peru (47%), Brazil (35.9%), Panama (35.4%), and Venezuela (30.3%) that have biogeographic areas in common with Ecuador. Endemism rate of this group is around 12.6%, with *Diachlorus*, *Dicladocera*, *Esenbeckia*, *Eristalotabanus* (monotypic), and *Leucotabanus* genera as the most representatives. We add new records of Tabanidae for the country. The genus *Hemichrissops* was recorded for first time. The number of species in Ecuador now totals 198. A catalogue of all Ecuadorian species is compiled with a localities-gazetteer. We also present and discuss for the first time, the distribution of well known horse flies species (*Chrysops varians* var. *tardus*, *Dicladocera macula* and *Fidena rhinophora*) using georeferenced localities and niche modelling analyses.

**Résumé. Diversité et modèles de distribution des taons (Diptera : Tabanidae) de l'Équateur.** L'information existante sur les Tabanidae à l'échelle mondiale concerne principalement la recherche taxonomique qui a été la source principale de données concernant la diversité de ce groupe de mouches. En Équateur, les études sur les taons ont été irrégulières depuis les premières descriptions en 1848 de trois spécimens des Andes. Les catalogues, listes et collections d'espèces dans les musées nationaux démontrent qu'en dépit de sa taille restreinte, l'Équateur représente actuellement l'un des pays néotropicaux les plus riches en espèces de Tabanidae après le Brésil, la Colombie et le Mexique. L'Équateur abrite l'une des plus fortes densités d'espèces par unité de surface. Sa faune de Tabanidae est partagée principalement avec la Colombie (62,6% d'espèces en commun), le Pérou (47,0%), le Brésil (35,9%), Panama (35,4%) et le Vénézuela (30,3%). Le taux d'endémisme de ce groupe en Equateur est d'environ 12,6%. Les genres *Diachlorus*, *Dicladocera*, *Esenbeckia*, *Eristalotabanus* (monotypique) et *Leucotabanus* sont les plus représentatifs. Dans cette étude, nous présentons de nouveaux données de Tabanidae pour le pays (dont le genre *Hemichrissops* observé pour la première fois), menant ainsi à une liste de 198 espèces pour le pays. Un catalogue de toutes les espèces équatoriennes est annexé avec toutes les localités. Pour la première fois pour ces insectes, nous présentons et discutons également la distribution de certaines espèces bien connues (*Chrysops varians* var. *tardus*, *Dicladocera macula* et *Fidena rhinophora*) à l'aide de localités géoréférencées et de modèles de niche.

**Keywords:** Andes, Biogeography, Neotropical Region, Niche modelling, Tabanomorpha.

According to the last catalogue of Neotropical Tabanidae (Fairchild & Burger 1994), 1172 valid species and subspecies have been described from the Neotropical Region of which larvae are known from only 4.1% (Coscarón 2002). In Ecuador, the study

of tabanid flies began with the description of three Andean species from Quito: *Esenbeckia testaceiventris* Macquart 1848, *Tabanus peruvianus* Macquart 1848, and *Dasychela ocellus* (Walker) 1848. Since these first descriptions, sporadic collections and expeditions by international governmental and private institutions have been the main source of diversity information for this group. Most of the Tabanidae records from Ecuador have been reported singly in scattered publications.

Ecological studies on Ecuadorian Tabanidae are scarce as only three reports have been found in the

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literature. Buestán (1980) identified within a one-year survey in the Guayas province, a unimodal peak of abundance for three perennial fly species in the summer. Buestán (2006) reported the transmission of *Dermatobia hominis* bot fly (Diptera: Oestridae) by *Chrysops varians* var. *tardus*. This was the first case of a horse fly-vectorized myiasis reported in Ecuador. Such information makes these flies of particular socio-economic importance. Cárdenes (2007) presented a detailed ecological study of changes in horse fly communities along a 1-km altitudinal gradient in a Chocoan cloud forest. There were significant differences in heterogeneity and evenness of tabanid communities, and an important role of climatic variables in the daily activity of these flies.

The biogeography of Ecuadorian tabanofauna is completely unknown. Only two important works by Fairchild (1969a, 1969b) reviewed the distributional patterns of tabanids in Central and South America. Biogeographic "zones" identified by Fairchild are remarkably similar to biogeographical regions proposed by Morrone (2001, 2006) on which our comments and discussions are based.

Though tabanids have been implicated in transmission of pathogens of relative importance of cattle and humans (Krinsky 1976; Davies 1990; Otte

& Abuabara 1991; Buestán 2006) further research on natural history, vectorial capabilities and control are necessary. A starting point to achieve these goals is the use of numerical technologies such as georeferenced databases, geographical information system (GIS) and niche modelling analyses. These techniques represent the basic elements of modern investigations of species distributions (Elith *et al.* 2006) with widespread applications in biogeography, macroecology, evolution (Graham *et al.* 2004), parasitology and disease transmission (Peterson 2006). It is therefore necessary to rely on complete and updated species georeferenced localities databases of collected specimens. Museum fauna checklists are thus indispensable (refer to Henriques & Gorayeb 1993 and Henriques 1995 for catalogue examples; see Winston 2007 for a discussion on this subject).

We present a revision of the Ecuadorian tabanid fauna. We first compared the taxonomic diversity with other biogeographically-related countries and provide a gazetteer of georeferenced collection localities. Second, we analyze the potential distribution of three well known species (including bot fly vector *Chrysops varians* var. *tardus*) using maximum entropy ecological niche modelling.

**Table 1.** Horse fly diversity in the Neotropical Region.

Top values correspond to the number of shared species between Neotropical countries. Bottom values correspond to the individual percentage of each country shared with another country. Data in parentheses correspond to the number of Tabanidae species per 10,000 km<sup>2</sup> (diversity density). Analyses were based on 1214 Neotropical species.

	Mex.	C. Rica	Pan.	Ven.	Col.	Ecu.	Per.	Bra.	Bol.	Arg.	Chi.
<b>Mexico (1.05)</b>		43 21.3%	38 18.8%	20 9.9%	27 13.4%	18 8.9%	14 6.9%	15 7.4%	10 5%	8 4%	0 0%
<b>Costa Rica (27.6)</b>	43 30.7%		124 88.6%	40 28.6%	83 59.3%	59 42.1%	33 23.6%	35 25%	22 15.7%	12 8.6%	1 0.7%
<b>Panama (20)</b>	38 25%	124 81.6%		46 30.3%	96 63.2%	70 46.1%	38 25%	38 25%	26 17.1%	12 7.9%	1 0.7%
<b>Venezuela (1.2)</b>	20 18.9%	40 37.7%	46 43.4%		80 75.5%	60 56.6%	48 45.3%	61 57.5%	32 30.2%	14 13.2%	1 0.9%
<b>Colombia (2.25)</b>	27 11.5%	83 35.5%	96 41%	80 34.2%		124 53.0%	83 35.5%	81 34.6%	50 21.4%	19 8.1%	1 0.4%
<b>Ecuador (7.72)</b>	18 9.1%	59 29.8%	70 35.4%	60 30.3%	124 62.6%		93 47%	71 35.9%	58 29.3%	22 11.1%	1 0.5%
<b>Peru (1.48)</b>	14 7.4%	33 17.5%	38 20.1%	48 25.4%	83 43.9%	93 49.2%		85 45%	74 39.2%	24 12.7%	11 5.8%
<b>Brazil (0.52)</b>	15 3.4%	35 8.0%	38 8.7%	61 13.9%	81 18.5%	71 16.0%	85 19.4%		76 17.3%	61 13.9%	1 0.2%
<b>Bolivia (1.35)</b>	10 6.8%	22 15.1%	26 17.8%	32 21.9%	50 34.2%	58 39.7%	74 50.7%	76 52.1%		50 34.2%	2 1.4%
<b>Argentina (0.6)</b>	8 4.8%	12 7.3%	12 7.3%	14 8.5%	19 11.5%	22 13.3%	24 14.5%	61 37%	50 30.3%		39 23.6%
<b>Chile (1.42)</b>	0 0%	1 0.9%	1 0.9%	1 0.9%	1 0.9%	1 0.9%	11 10.4%	1 0.9%	2 1.9%	39 36.8%	

## Materials and methods

### Horse fly diversity in Ecuador compared to other Neotropical countries

In order to catalogue all Ecuadorian Tabanidae species, we confirmed the presence of each species in all available publications on Neotropical Tabanidae. We also visited the collections of C-JB, MEPN and QCAZ (see Appendix 3 for the acronyms). A total of 2,893 Ecuadorian horsefly specimens were identified to species level. Such identifications were made using original descriptions, generic revisions and/or specific keys. Identification of MEPN and QCAZ material followed the methodology detailed in Cárdenas (2007). Briefly, it consists of following keys and available original descriptions as well as comparisons with type-specimen illustrations and identified material from museums (e.g. INPA). Morphological measurements were also taken into account when available in literature. Also, comparisons with CAS and MCZ type-materials available online were done in order to confirm the identification of some species. Pictures of type specimens were also sent by curators of foreign museums for evaluation. Frontal and divergence indexes, body and wing lengths of some new records are abbreviated FI (Frontal Index), DI (Divergence Index), BL (Body Length) and WL (Wing Length). C-JB identifications were made by Jaime Buestán.

For comparing Ecuadorian tabanids fauna with other Neotropical countries, we took account new taxonomic descriptions and rearrangements, checklists and reports, published since the last catalogue of Neotropical Tabanidae by Fairchild & Burger (1994) (see Appendix 1 for a complete reference list). In total, two genera, one subgenus and 50 species have been described since 1994. In addition, nine species have been synonymized, one has been revalidated, and two were transferred to related genera. Our analyses are thus based on 1214 valid Neotropical species. The number of species of Tabanidae in each country (see tab. 1 and fig. 3), was therefore based on the Fairchild & Burger's (1994) catalogue and subsequent publications on the Neotropical fauna. In the case of Chile, the scoring of valid species was complemented by the catalogue by Coscarón & González (1991). When the presence of a species in a country was dubious in Fairchild & Burger's catalogue (e.g. "Brazil") the information was discarded unless the presence of the species was confirmed by subsequent publications. For example the presence of *Fidena schildi* in Brazil, questioned in the Fairchild & Burger (1994) catalogue was confirmed by Henriques (1995). Fairchild & Burger (1994) described the distribution of widely-distributed taxa using geographical ranges (e.g. *Dichelacera fasciata* distribution: Nicaragua to Ecuador). In such cases, we included every country intersected by an imaginary parsimonious line between the two cited localities and tried to confirm the presence of species in the hypothetical range. The number of species per country presented in this work is strictly based on species-level identifications and reports available until September 2009. Finally, we calculated every country-specific diversity density of Tabanidae by dividing the total number of species by the corresponding land area of each country in km<sup>2</sup>.

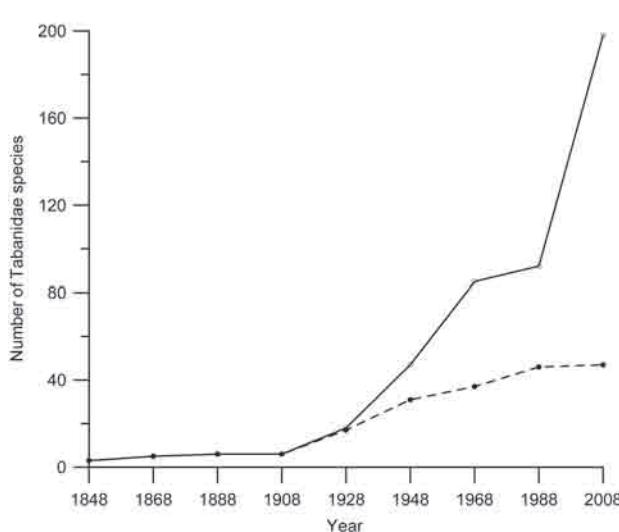
### Horsefly distribution and ecological niche modelling

To characterize the potential distributions (approximation of the fundamental niche) of selected horse fly species in Ecuador, we compiled presence data (realized niche) from voucher

specimens collected in the past two decades and deposited in Ecuadorian collections, and bibliographic records. We selected three species to be modeled based on the number of available records ( $n \geq 20$ , see Hernandez *et al.* 2006), and ease and certainty of identification. These species were *Chrysops varians* var. *tardus* ( $n = 30$ ), *Dicladocera macula* ( $n = 24$ ), and *Fidena rhinophora* ( $n = 22$ ) (see Appendix AS 4 and AS 5 for complete localities records and gazetteer). *Chrysops varians* var. *tardus* is a widely distributed species in Neotropical lowlands and midlands from Panama to southern Brazil including Trinidad, Paraguay, Bolivia, Guyana, Colombia, Ecuador and Peru (Fairchild & Burger 1994). Manrique-Saide *et al.* (2001) also reported this species from Mexico (Campeche and Yucatán States). *Dicladocera macula* is a relatively common species in the Andean countries. Its distributional range covers cool wet highlands of Venezuela, Colombia, Ecuador, Peru and Bolivia (Wilkerson 1979; Fairchild & Burger 1994). *Fidena rhinophora* has been reported from Mexico to eastern Venezuela and Peru (Fairchild & Burger 1994) in areas with high rainfall (between 600–1800 m in Panama, Fairchild 1986).

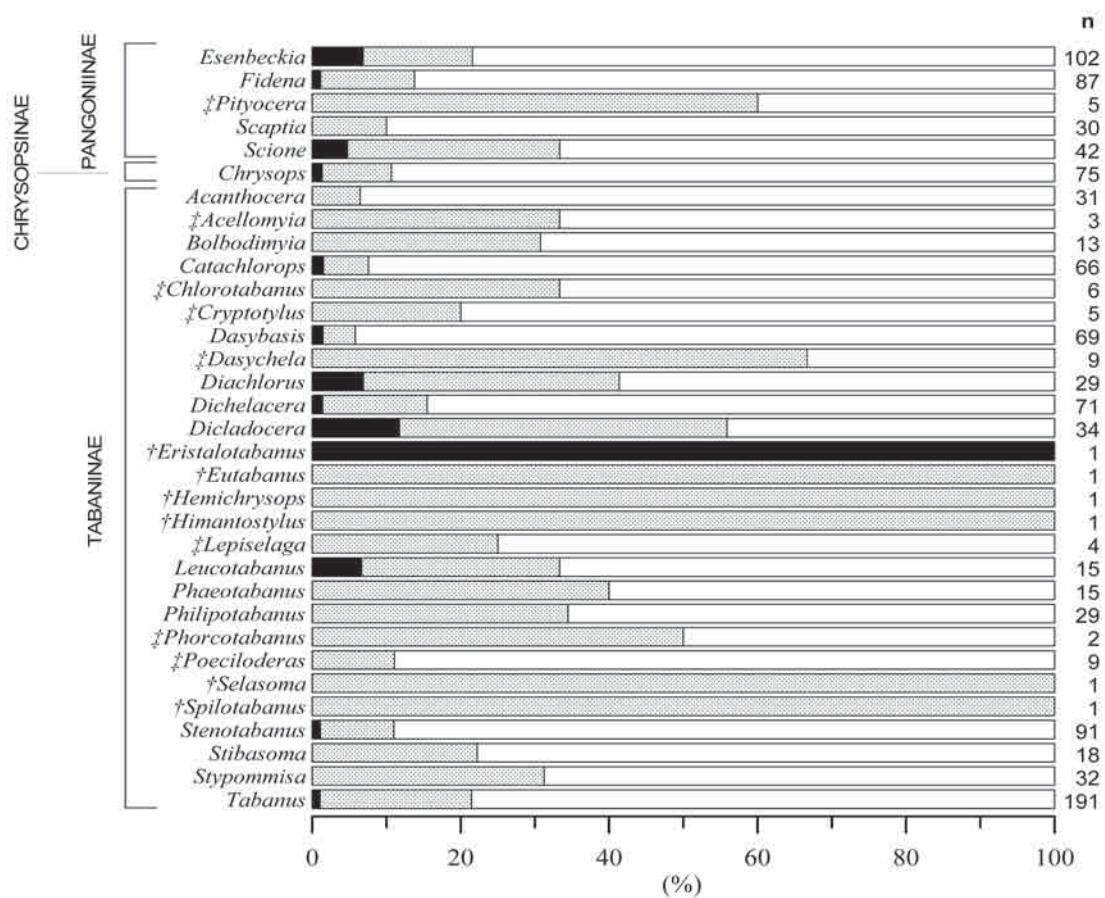
Niche-based modelling was realized using MAXENT (version 3.2.1), a maximum entropy machine learning package freely available online (<http://www.cs.princeton.edu/~schapire/maxent/>) (Phillips *et al.* 2006; Phillips & Dudik 2008). MAXENT has been tested in a wide range of climatic regions and demonstrated to perform well compared to other modelling techniques in predicting potential distribution using small sample presence-only occurrences (Elith *et al.* 2006; Hernandez *et al.* 2006). Likewise, Pearson *et al.* (2007) found positive and significant results with as few as 5 occurrence points under the MAXENT model using a Jackknife validation approach. Georeferencing of all horsefly species first consisted in dividing geographical information into nine categories (Wieczorek *et al.* 2004). Specimens falling into the categories (1) "dubious", (2) "can not be located", and (3) "demonstrably inaccurate" were eliminated. Remaining geographical information (falling into categories 4–9, Wieczorek *et al.* 2004) were checked using various available gazetteers (IGM 1978–1982, 1982–1996; QCAZ Herpetological section gazetteer; Falling Rain Genomics 2006) or by consulting original collectors whenever possible. The georeferencing process used digital maps and GIS software with WGS84 datum. Following the "point radius method" proposed by Wieczorek *et al.* (2004) we calculated the uncertainty (error) associated to every georeferenced locality. "Point radius method" consisted in taking each locality as a circular space of probabilities and a radius to describe the maximum distance from a fixed point (georeferenced locality) within which the actual locality is expected to occur (Wieczorek *et al.* 2004). We assumed an error of 0 Km. for all the localities georeferenced using a GPS in the field (not for collections older than 2004).

Nineteen continuous climate and elevation variables (available online at <http://www.worldclim.org/current.htm>, Hijmans *et al.* 2005; spatial resolution ~1 km × 1 km) were used to examine the potential distribution of the three selected species in Ecuador (X: -81.009156, -75.193084; Y: -5.012689, 1.456729). Original climate and topographic grid files were converted to ASCII raster files using DIVA-GIS v. 5.4. Georeferenced localities per species were transformed to the UTM coordinate system to minimize imprecision. Every map was the result of the analysis of all of the data. For evaluation purposes, we randomly selected 75% of localities as training data and the



**Figure 1**  
Descriptions (dashed line) and addition of new records (solid line) of horse flies species from Ecuador since 1848.

remaining 25% were used for testing model results. Models were validated using receiver operating characteristic (ROC) analysis, which evaluates model performance independently of arbitrary thresholds at which presence of the species might be accepted (Pearce & Boyce 2006). The ROC analysis assesses model performance by plotting the proportion of presence points correctly predicted vs. the proportion of absences correctly predicted across all possible thresholds. Good model performance is characterized by large areas under this curve (AUC) (Elith *et al.* 2006). AUC values ranges from 0 to 1 where 1 indicates perfect discrimination, and 0.5 random discrimination. Values below 0.5 indicate that models are worse than a random prediction therefore, results under 0.5 may not be taken into account (Elith *et al.* 2006). To avoid sample auto-correlation, we used the “remove duplicate presence records” option. Regularization multiplier, maximum number of iterations, convergence threshold, and maximum number of background points (pseudo-absences), were set by default. For threshold selection we chose the “equal training sensitivity and specificity” threshold (Liu *et al.* 2005). A jackknife test was then performed with all data to estimate the weight of each environmental variable in the model. Finally, based on test



**Figure 2**  
Richness of endemic (solid boxes) and native species (dotted boxes) within Ecuadorian genera (empty boxes) in the Neotropics. *n* corresponds to the number of described Neotropical species per genera. Names denoted by † are monotypic. An ‡ symbol is assigned to taxa with specific richness (*r*)  $2 \leq r < 10$ . Total number of analyzed species *N* = 1089.

results, we compared raster maps of variable contributors with the obtained distribution models of each species in order to infer intraspecific climatic and habitat preferences.

## Results

### A historical review of the Ecuadorian tabanid fauna

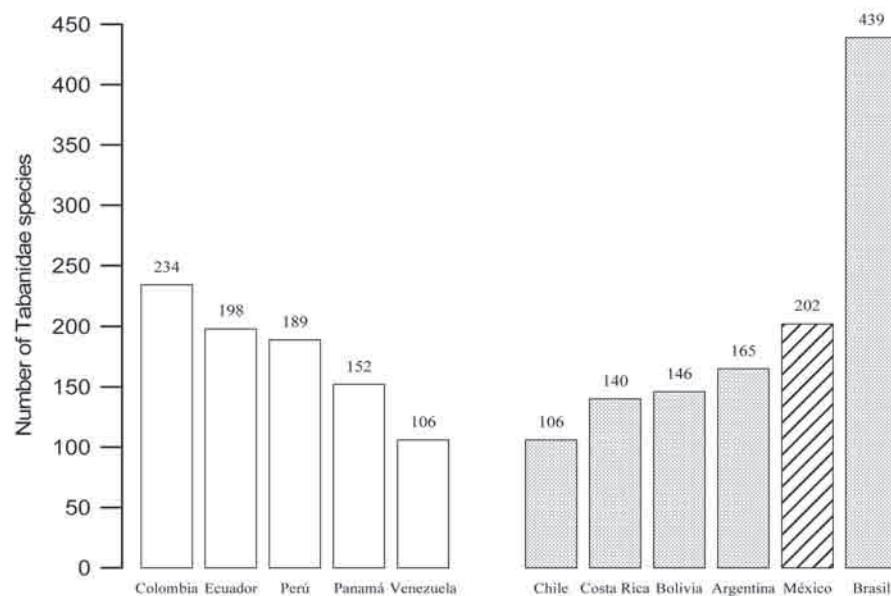
The evolution of tabanid descriptions in Ecuador showed in Figure 1, represents the accumulation of valid species described and/or recorded from Ecuador since 1848. Our work lists a total of 198 Tabanidae species from Ecuador. Since late 1920's, the number of documented Tabanid species has been based mostly on collection surveys rather than on descriptions of Ecuadorian fauna, which clearly reflects the poor systematic research from Ecuadorian entomologists within this group. Since 1920, two periods characterize the temporal trend of horsefly species description in Ecuador (fig. 1, solid line). The first period (1928–1988) mainly nourished by the works of Kröber (1934), Campos (1952), Fairchild & León (1957), Patrick & Hays (1968), Fairchild (1971) and Buestán (1980) show a 4-fold increase in Tabanid species descriptions since 1920's. During the second period (1988–2008) the 1980's knowledge on Tabanid fauna was duplicated in only two decades. Species lists presented in Fairchild & Burger (1994), Cárdenas & Vieira (2005), Buestán

*et al.* (2007) and the present work, all contributed to the exponential description of Ecuadorian horse flies species during the last two decades.

### Diversity of Ecuadorian horse flies

We registered a total of 198 tabanid species with 2 subspecies and 5 varieties for Ecuador. Species belonged to 33 genera, 5 tribes and 3 subfamilies (Appendix 2) and represented 16.3% of the current Neotropical tabanofauna. Around 2.1% of Neotropical species are endemic to Ecuador (12.6% of its tabanofauna) with *Diachlorus*, *Dicladocera*, *Eristalotabanus* (monotypic), *Esenbeckia*, and *Leucotabanus* as the most representative genera (fig. 2). Despite its limited size, Ecuador is the richest country in number of tabanid species in the Neotropics after Brazil, Colombia, and Mexico (fig. 3) and has the highest density of species diversity *per unit area* after Panama and Costa Rica (tab. 1).

We report for the first time in Ecuador the presence of six species: (1) *Hemichrissops fascipennis* collected from north-western Ecuador (western foothill forest); the specimen fits very well with the Wilkerson (1979) and Fairchild (1986) descriptions, and INBio plates (Burger *et al.* 2002). (2) Two females of *Chrysops bulbicornis*, sampled from eastern lowlands (Amazonia, amazonian tropical rain forest), in agreement with Lutz's (1911) original description, figured structures, and with Coscarón (1979)'s key, descrip-

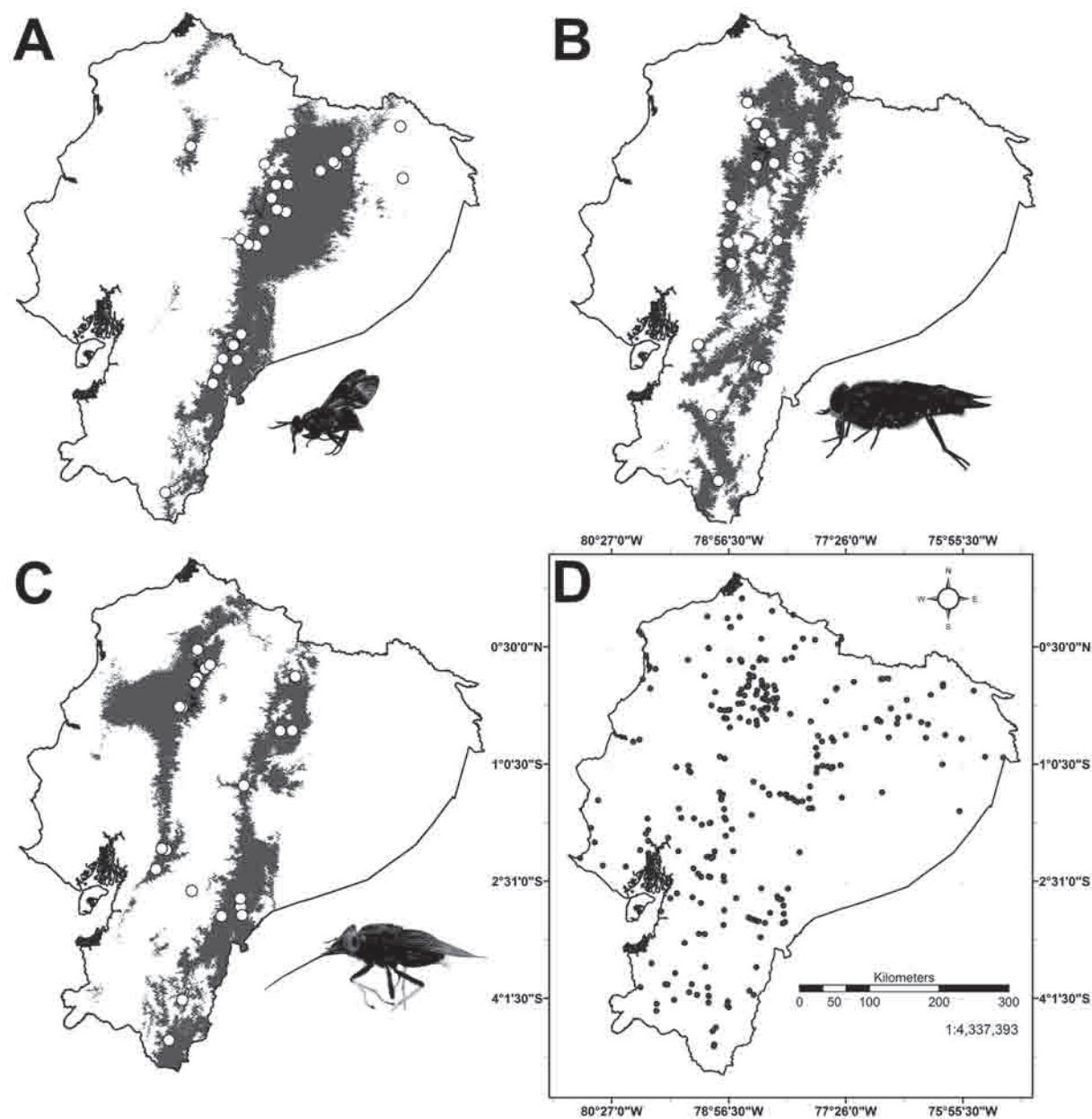


**Figure 3**

Number of catalogued species *per country* in the Neotropics. Empty boxes are assigned to countries that share biogeographical provinces with Ecuador; dotted boxes are assigned to countries that share biogeographical sub-regions with Ecuador; slashed boxes correspond to countries that share regional biota with Ecuador. Biogeographical categories follow Morrone (2001, 2006).

tion and figures. (3) *Stenotabanus penai* specimens collected from north-western lowlands (Costa, deciduous forest) in agreement with the key in Chainey *et al.* (1999) (structure and coloration), figures, and morphological dimensions ( $\bar{x}$  FI = 3;  $\bar{x}$  WL = 7.47 mm;  $\bar{x}$  BL = 8.09 mm; N = 12). (4) One specimen of *Diachlorus scutellatus*, eastern Ecuador (Amazonia,

amazonian tropical rain forest) was identified following Macquart's original description provided by Lutz (1913), and Wilkerson & Fairchild's (1982) key. (5) *Philipotabanus porteri*, from 6 specimens collected in north-western Ecuador (Costa, chocoan tropical forest), identified using Fairchild's (1975) key, original description, figures, and online images of the holotype



**Figure 4**

Distribution models of three species of Ecuadorian horse flies. Black areas correspond to potential distribution modeled with >85% probability of occurrence (>75% for *Dicladocera macula*). Grey areas correspond to “equal training sensitivity and specificity” threshold which is different for each species. White dots correspond to collecting localities. A, *Chrysops varians* var. *tardus* (AUC = 0.947; threshold: 22.5%); B, *Dicladocera macula* (AUC = 0.971; threshold: 30.8%); C, *Fidena rhinophora* (AUC = 0.958; threshold: 26.31%); D, General Ecuadorian Tabanidae collections.

deposited in MCZ ( $\bar{x}$  FI = 4.06;  $\bar{x}$  DI = 1.2;  $\bar{x}$  WL = 9.03 mm;  $\bar{x}$  BL = 9.88 mm; N = 6). (6) One female of *Phaeotabanus prasiniventris* (collected in alcohol, lighter colours), from north-eastern Ecuador (Amazonia, amazonian tropical rain forest), identified by K. M. Bayless, agrees with structures and wing patterns of two INPA females specimens of the same species (det. by A. L. Henriques) from P.N. Jau, Rio Jau, Igarapé Miratucu, Brazil.

### Ecuadorian tabanid fauna compared to other Neotropical countries

The Ecuadorian tabanofauna is predominantly shared with Colombia (62.6%), Peru (47%), Panama (35.4%) and Venezuela (30.3%), with which Ecuador shares biogeographic provinces (tab. 1). 35.9% of Ecuadorian Tabanofauna is in common with Brazil which shares the Amazonian biogeographic sub-region with Ecuador (Morrone 2006). Chile has a singular tabanid fauna, sharing no species with Mexico, 10.9% with Peru and 36.7% with Argentina reflecting the high endemism (around 53.8%) of this country. Similarly, Mexico shares 21.3% and 18.8% with Costa Rica and Panama, respectively (tab. 1). This confirms a gradient of specific richness and singularity, with lower diversity and higher singularity of tabanid fauna in southern and northern temperate and subtropical countries. The tabanid fauna of Andean countries showed higher degree of resemblance (see the percent of species shared between Venezuela, Colombia, Ecuador, Perú and Bolivia, tab. 1).

Comparisons of diversity densities in Neotropical countries (tab. 1) rank Ecuador as one of the most diverse territories *per unit area* (7.7 species *per* 10,000 km<sup>2</sup>). Costa Rica and Panama are by far, the most diverse countries in proportion to their size (27.6 and 20 species *per* 10,000 km<sup>2</sup> respectively). Regardless of the great number of species and the relatively high number of ecosystems, Brazil has the lowest specific density in Latin America (0.52 species *per* 10,000 km<sup>2</sup>), followed by Argentina and Mexico (0.6 and 1.1 species *per* 10,000 km<sup>2</sup>, respectively).

### Ecological niche modelling distribution of three Tabanid species

#### *Chrysops varians* var. *tardus* Wiedemann 1828

Most specimens of *C. varians* from Ecuadorian collections and in the literature were reported from amazonian tropical rainforests and eastern foothill and montane forests in a relatively large altitudinal range (200–1900 m) with only one record in a western montane forest (Río Guajalito Scientific Station, Santo Domingo Prov.). Modelled potential distribution for > 85% probability values of suitable habitat (maximum rate prediction = 91.67%) corresponds to central and southern eastern Andean slopes in amazonian and foothills-montane forests at elevations between 600 and 1300 m (fig. 4A, black regions). The MAXENT “equal training sensitivity and specificity” cumulative threshold calculation assume presences of *C. varians* to areas over 22.5 % of presence probability (fig. 4A, grey

**Table 2.** Contribution of environmental variables to horse fly species distribution models.  
Analyses are based on MAXENT parameters. The highest values are in bold.

Horse fly species	Environmental variables (only the most representative)	contribution (%)	Jackknife analysis of regularized model gain (%)	
			if isolated	if omitted (gain decrease)
<i>Chrysops varians</i> (Total model gain: 1.61)	- precipitation driest month	28.4	~ 27.9	~ 0
	- mean temperature wettest quarter	22.5	~ 48.8	~ 0
	- annual mean temperature	12.5	~ 34.2	~ 0
	- precipitation seasonality	12.4	~ 38.5	~ 18.8
	- altitude	4	~ 40.6	~ 3.1
	- mean temperature warmest quarter	0	~ 40.6	~ 0.6
<i>Dicladocera macula</i> (Total model gain: 1.82)	- altitude	69.4	~ 83.3	~ 0
	- mean temperature warmest quarter	7.3	~ 85	~ 0
	- max. temperature warmest month	3.3	~ 86.1	~ 0
	- annual mean temperature	1.5	~ 85	~ 0
	- min. temperature coldest month	1.2	~ 80.6	~ 0.4
	- mean temperature driest quarter	0.9	~ 80.6	~ 0
	- mean temperature coldest quarter	0	~ 85	~ 0
	- mean temperature wettest quarter	0	~ 80.6	~ 0
<i>Fidenia rhinophora</i> (Total model gain: 1.59)	- altitude	31.2	~ 55.3	~ 5.7
	- precipitation wettest quarter	14.9	~ 9.4	~ 0
	- precipitation seasonality	11.8	~ 22	~ 7.6
	- temperature annual range	8.6	~ 9.3	~ 8.8

zones,  $p < 0.001$ ). Precipitation of the driest month, mean temperature of the wettest quarter, annual mean temperature and precipitation seasonality predicted 28.4%, 22.5%, 12.5%, and 12.4% of the distribution model, respectively (tab. 2). Jackknife analysis revealed that mean temperature of the wettest quarter, followed by altitude and mean temperature of the warmest quarter, explained most of model variation when isolated (48.8%, 40.6%, and 40.6% respectively). AUC values ranged from 0.947 to 0.922 (using 75% and 25% of data, respectively), indicating a good discrimination of species presence/absence.

#### *Dicladocera macula* (Macquart 1846)

In Ecuador *D. macula* has been recorded between 1600–3400 m on both sides of the Andean cordillera within eastern and western montane forests, paramo and Andean shrubs, which was confirmed by our niche model analysis (fig. 4B). The MAXENT “equal training sensitivity and specificity” cumulative threshold calculation assumed presences in areas over 30.8% of presence probability (fig. 4B, grey zones,  $p < 0.001$ ). Maximum rate of prediction was of 78.35%. However, based on the MAXENT default output graphic and > 75% predictions, we identified two areas of higher suitable habitat corresponding to western montane forest bioregions (fig. 4B, black regions). The analysis of environmental variable contributions estimated that 69.4% of the model prediction was related to altitude and temperature variables (tab. 2). Further Jackknife analyses (tab. 2) revealed an important contribution of the maximum temperature of the warmest month by itself ( $\sim 86.1\%$ ). The omission of any of these variables had a negative repercussion on the gain of the model. AUC values ranged from 0.971, to 0.923 (using 75% and 25% of data respectively), indicating a good discrimination of species presence/absence.

#### *Fidena rhinophora* (Bellardi 1859)

In Ecuador *F. rhinophora* has been recorded between 500–2500 m in chocoan tropical rainforests, Andean shrubs and western/eastern montane and foothills forests. Niche modelling analyses showed a moderately specific potential distribution of the species in montane forests of Andean slopes on both sides of the cordillera, which however had the highest distribution probability (fig. 4C). Potential distribution analysis of >85% probability values of suitable habitat (maximum rate prediction of 93.61%) corresponded to north-western Ecuador, through tropical rainforests to montane forests (fig. 4C, black regions). The MAXENT “equal training sensitivity and specificity” cumulative threshold calculation assumed presences of *F. rhinophora*

in areas over 26.31% of presence probabilities (fig. 4C, grey zones,  $p < 0.001$ ). The relative estimates of environmental variable contributions pointed to altitude, wettest quarter, and seasonality precipitation as the most important variables, explaining 31.2%, 14.9%, and 11.8% of the model variance, respectively. Consistently, Jackknife analysis showed that altitude presented the most important information, and that annual temperature range, precipitation seasonality, and altitude, significantly reduced model gain when omitted ( $\sim 8.8\%$ ,  $\sim 7.6\%$  and  $\sim 5.7\%$ , respectively). AUC values ranged from 0.958 to 0.96 (using 75% and 25% of data, respectively), indicating a good discrimination of species presence/absence.

## Discussion

### Ecuadorian horsefly diversity

Despite the low number of studies on the Ecuadorian tabanid fauna, compared to Panama (Fairchild 1986) and Costa Rica (Burger *et al.* 2002), our review revealed a high density of species diversity per unit area for the country (tab. 1). This result agrees with species densities reported for other families of Ecuadorian insects (Dangles *et al.*, this issue for a thorough review) as well as other groups such as amphibians (Ron *et al.* in press) and vascular plants (Jørgensen & León-Yáñez 1999).

*Diachlorus*, *Esenbeckia* (*Esenbeckia*) and *Leucotabanus*, which are Andean and sub-Andean genera, are relatively specialized within their tribes (Fairchild 1969b), and are represented by high rates of endemism (fig. 2). These genera are possibly representing an altitudinal “niche evolution” outcome related to the Andes uplift (based in a Wiens & Donoghue (2004) species diversification altitudinal view). Their endemism might also be a consequence of adaptive radiation pushed by recent vicariance processes (Hughes & Eastwood 2006; Ribas *et al.* 2007; Garzíone *et al.* 2008) as it has been proved for other groups of insects (Brühl 1997) although this has to be confirmed by historical biogeographic studies based on strong phylogenies. This should partly explain the high rate of endemism of the Andean genus, *Dicladocera*, as well as the probable recent diversification of monotypic genus *Eristalotabanus* (Fairchild 1969b) (fig. 2).

The overall relatively low rate of Ecuadorian species endemism (2.06% of Neotropical species, fig. 2) can be explained by the low sampling effort and the scarcity of taxonomical studies on Diptera in the country (Donoso *et al.* this issue). This assumption is supported by the disproportion between recorded

species and the relatively low number of Ecuadorian new species descriptions (fig. 1): new descriptions are mostly published by foreign entomologists with sampling areas clustered around Quito (fig. 4D). There is an evident lack of surveys in many biogeographical zones such as in the dry shrubs of southern Amazonian and the north-central Chocoan tropical rainforests. Buestán *et al.* (2007) presented a list of about ten “new” species neither confirmed nor described, illustrating the poor knowledge of the extant fauna in Ecuador and its potential higher endemism. It should also be noted that nearly all Ecuadorian collections represent understorey fauna, for what canopy surveys might provide many surprises.

### **Tabanid diversity in the Neotropics and its relation with Ecuadorian fauna**

Morrone’s (2006) biogeographic areas for Latin America and the Caribbean Islands presented a good classification of the biogeographical distribution of tabanid species (tab. 1). The Ecuadorian provinces of Chocó, Cauca, Western Ecuador, Napo and North Andean Paramo shared with Colombia, and Tumbes-Piura, Napo, and North Andean Paramo shared with Peru could explain the high number of Ecuadorian tabanid species in common with the two countries. Furthermore 35.5% of the Ecuadorian tabanofauna was in common with Brazil (Amazonian subregion) whose biogeographical provinces of Varzea, Ucayali and Yungas are probably the most influential for the distribution of equatorial Amazonian tropical rainforest biota.

Consistent with Morrone (2006), Chile has served as a refuge for “ancestral” biota such as the genera *Veprius* and *Protodasyphya*. It also shared genera such as *Dasybasis*, *Pseudotabanus* and *Scaptia* with the Austral Kingdom and presented an overlap of Neotropical and Andean taxa like *Esenbeckia* subgenus *Astomyia* and *Palassomyia* (Fairchild 1969b; Burger 1999). Mackerras (1961) suggested that the “modern” west-Pacific tabanid fauna might have evolved from temperate Antarctica, southern Africa and Holarctic regions with dispersal to subtropical and tropical regions, where an extraordinary radiation took place. The “primitive” genus *Dasybasis* might be an example of such radiation after migrations from Patagonia northward through the Andean chain (Fairchild 1969b; González 1999, Morrone 2006). The absence of species in common between the Mexican and Chilean tabanid fauna reflects the geographic and climatic isolation of Chile, as asserted by Fairchild (1969b) and Morrone (2006). The apparent low diversity of tabanid fauna of Venezuela, known as a megadiverse country with an

area 3.5 times Ecuadorian territory, is likely to be due to the absence of studies on this family.

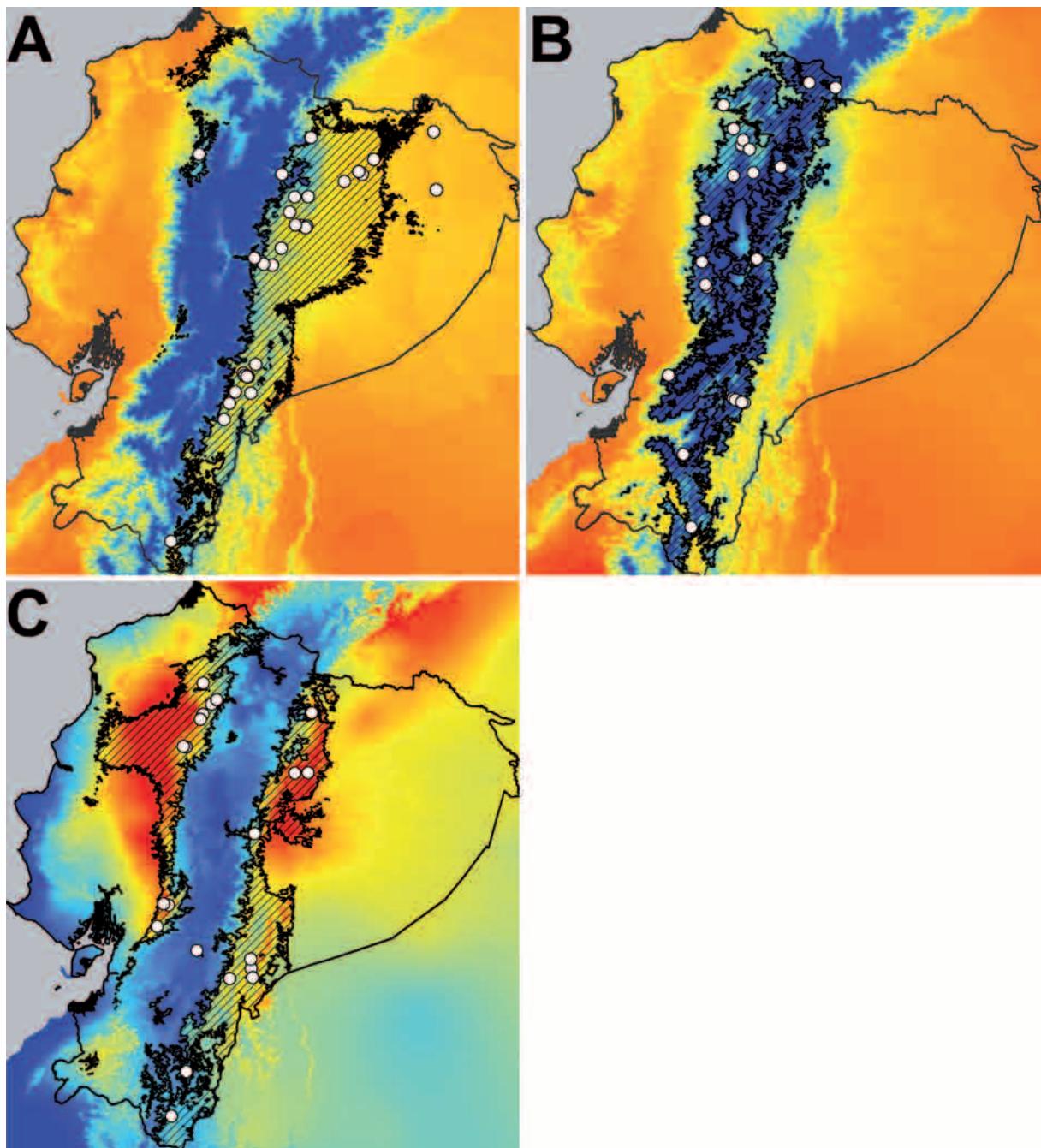
### **Niche modelling**

To our knowledge, this study is the first to use niche modelling analyses to study horse fly distribution. Our aim was to illustrate possible distributions of selected species restricted to the Ecuadorian territory, rather than trying to find their “exact” suitable habitat (fundamental niche). We are aware that for better results, even at the country level, it is necessary to work with more distribution data (collecting localities), especially from other countries. Another limitation of our modelling approach is that most specimens were collected during the periods of greater horse fly abundance (e.g. Cárdenas 2007), generally during the optimal months of population abundance during the dry season (Buestán 1980; Desquesnes *et al.* 2005; Oliveira *et al.* 2007). Museum collections are likely to best represent horse fly optimal habitats. Tabanid presence in less optimal habitats may therefore be underestimated; in few cases horse fly peak abundances have for example been reported at the beginning or within the rainy season (Barros 2001; Velásquez de Ríos *et al.* 2004). Our results illustrated more essentially the regions that have similar environmental conditions to where the species are known to occur rather than predicting actual limits to their distributional range (Pearson *et al.* 2007). Furthermore, nothing is known about the responses of tabanids to other environmental variables such as deforestation, presence of cattle or climate change. Additional physiological and phenological studies are therefore necessary to describe present (and future) horse fly distribution ranges in a more accurate way. For example, mechanistic niche modelling would allow incorporating the functional traits of organisms and model its distribution, beginning from its physiological responses and constraints to spatial data, into a more natural fundamental niche (as described by Kearney & Porter 2009). Our study should therefore be considered as a first step towards more detailed studies on the biogeography and the macroecology of this group of flies.

Altitude was one of the most discriminant variables to explain species distribution, contributing to 69.4% and 31.2% of model predictions for *D. macula* and *F. rhinophora*, respectively. According to Körner’s (2007) explanations on how altitude relates to many other environmental variables it was no surprising to find such results. For example, the author enumerates some general and relevant altitude-related characteristics that affect species distribution, among them, the reduced atmospheric temperature at higher altitudes,

which has strong implications for ambient humidity. As an illustration of this importance, the variables that best explained *D. macula* distribution were all altitudinal-thermal related (tab. 2). Further Jackknife

analysis showed that maximum temperature of the warmest month explained most of model gain. Körner (2007) also explained that precipitation, wind velocity and seasonality may greatly differ from one region to



**Figure 5**

Distribution models of three species of Ecuadorian horse flies (hatched area) superposed to key environmental factors (colour gradient scale,  $\sim 1 \text{ km} \times 1 \text{ km}$  WorldClim layers, Hijmans *et al.* 2005, where red colour corresponds to higher values and blue colour to lower values). **A**, *Chrysops varians* var. *tardus* and mean temperature of the wettest quarter; **B**, *Dicladocera macula* and maximum temperature of the warmest month; **C**, *Fidena rhinophora* and precipitation of the wettest quarter.

another. However, the author shows a global tendency where precipitation in temperate latitudes for example, tends to increase with the increasing of altitude, while in Equatorial latitudes precipitation tends to diminish. This phenomenon is particularly true for Ecuador (fig. 5C, precipitation of the wettest quarter). According to Körner (2007), precipitation, wind velocity and seasonality are not altitudinal-related because gradients can go in any direction depending on local topography and climatic conditions, but they may affect species distribution due to intraspecific adaptations to such conditions at precise sites and periods of the year. This probable intraspecific adaptation seems to be well illustrated by *F. rhinophora* potential distribution (fig. 4C and 5C), for which precipitation is probably one of the most important driving variables (tab. 2).

To further investigate the role of environmental variables on the distribution of the three horse fly species we compared the modeled distribution of the species and the raster map of the most important variables explaining its distribution (fig. 5). We found that *D. macula* preferred habitat with medium to low values of maximum annual temperatures (fig. 5B). A similar pattern was found when comparing its distribution with the mean temperature of the warmest and coldest quarter variables (results not shown), which probably represent the developing and dormancy seasons for this species, respectively. This would suggest that the contribution of the altitudinal variable is mainly explained by low temperature values. A comparison of *F. rhinophora* distribution with precipitation of the wettest quarter showed that the probabilities of finding *F. rhinophora* were greater within medium to high precipitation values during the three wettest months of the year (Fig. 5C). This coincides with Fairchild (1986) who states that Panamanian specimens were distributed in areas of heavy rainfall. Finally, the distribution of *C. varians*, which was mainly explained by variables dependent on both precipitation and temperature, was preferentially limited to areas of medium to high temperature and precipitation values, with low annual variations (fig. 5A). The altitude contribution estimated by the Jackknife analysis should therefore be considered as an effect of the thermal characteristic of lowlands rainforests. All this suggest that the three modeled species are highly adapted to the altitude they inhabit and therefore to all of the characteristics described by Körner (2007), explaining why altitude contributed to all models in such a high proportion.

The possible presence of the modeled species abroad the actual collecting sites are not astonishing. The three species are wide distributed in Neotropics (Fairchild & Burger 1994) and seemed to be restricted to specific

climatic variables. Horse flies hold a strong thoracic flight muscular system (Bonhag 1949) and are among the speediest flying insects of the world (up to 40 m/s for large species such as *macula* or *rhinophora*). This would allow them to fly long distances in relatively short time (2.4 km in one-two days, see Cooksey & Wright 1987) what could explain its apparently strong dispersal capacities.

## Conclusions

A taxonomic school of Ecuadorian Tabanidae researchers is indispensable in order to document the family's complex diversity. Collaboration with foreigners programs and institutions (e. g. INPA and Partnerships for Enhancing Expertise in Taxonomy, Tabanidae PEET program, Bayless *et al.* 2008) must improve Neotropical and Ecuadorian taxonomical knowledge of the Tabanidae. Likewise, further ecological research on the tabanid fauna is necessary to understand the role and functionality within ecosystems. Macro-ecological modelling analyses for example, may help to answer both biogeographic and evolutionary questions, basic information for conservation analyses and governmental policy decision-making.

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## Appendix 1.

### Bibliographic references of taxonomic and geographic publications since the last catalogue of Neotropical Tabanidae published by Fairchild & Burger (1994).

Lists are chronologically ordered.

**Genus or Subgenus descriptions.** Chainey & Hall (1996); Burger (1999); González (1999).

**Species descriptions.** Henriques (1993); Barros & Gorayeb (1995); Henriques & Rafael (1995); Chainey & Hall (1996); González & Henry (1996); Henriques & Gorayeb (1997); Burger (1999); Chainey *et al.* (1999); González (1999); Goodwin (1999); Henriques & Rafael (1999); González (2000); Coscarón (2001); Burger (2002); González (2004a); González (2004b); Rafael & Ferreira (2004); Limeira-de-Oliveira & Rafael (2005); González (2006a); Gorayeb & Barros (2006); Henriques (2006); Limeira-de-Oliveira (2008); Limeira-de-Oliveira *et al.* (2009).

**Other taxonomical descriptions such as immature stages, unknown adults, type and rare specimens redescriptions and/or ultrastructure body parts descriptions.** Henriques & Rafael (1995); Burger (1996); Coscarón *et al.* (1996); Coscarón *et al.* (1998); González (1998); Bermúdez & Bermúdez (1999); Burger (1999); Coscarón (1999); Coscarón *et al.* (1999); Coscarón (2000); Coscarón (2001); Coscarón & González (2001); González (2001); Burger (2002); Coscarón (2002); Coscarón & Iide (2003); González & Sanhueza (2003); González (2004c); González & Flores (2004); González *et al.* (2004); Rafael & Ferreira (2004); González (2006b); Godoi & Rafael (2007); González (2007); Krolow & Henriques (2008).

**Taxonomical rearrangements.** Henriques & Rafael (1995); Chainey *et al.* (1999); González (1999).

**Checklists and occurrence reports.** Henriques & Gorayeb (1993); Chainey *et al.* (1994); Henriques (1995); Chainey & Hall (1996); Henriques & Rafael (1999); Coscarón (2000); Coscarón (2001); Manrique-Saide *et al.* (2001); Burger *et al.* (2002); Tiape Gómez *et al.* (2004); Cárdenas & Vieira (2005); Buestán *et al.* (2007); Krolow *et al.* (2007); Turcatel *et al.* (2007).

## Appendix 2.

### Catalogue of Ecuadorian species of Tabanidae.

This catalogue is based on Fairchild & Burger (1994) classification and new taxonomical rearrangements listed in Table 1. Specimens reported for the first time for Ecuador are marked with \*.

We do not include the next list of species apparently wrongly labeled as present in Ecuador due to possible nomenclatural-taxonomical confusions, misidentifications, uncertainties, and lack of voucher specimens as stated by Fairchild & León (1986) and other publications: (1) *Esenbeckia vulpes* cited by Campos (1952) from San Eduardo, Azogues (Cañar? - Guayas? prov.), (2) *Tabanus lineola* cited by Campos (1952) from Guayaquil, El Salado, Durán, Bucay, (Guayas prov.), San Rafael (Guayas prov.?), Azogues (Cañar prov.), (3) *Tabanus trilineatus* cited by Campos (1952) from Guayaquil, El Salado, Durán, (Guayas prov.), San Eduardo (Cañar? - Guayas? prov.). (4) *Catachlorops castanea* cited by Bigot (1892) in Fairchild & León (1986) from Santa Inés (Pichincha prov.). (5) *Dasychela limbaticornis* cited by Kröber (1940) in Fairchild & León (1986) from Ecuador, Cordillera. (6) *Tabanus subruber* cited by Surcouf (1919) from Santo Domingo de los Colorados (Santo Domingo prov.). (7) *Catachlorops nigripalpis* cited by von Röder (1886) in Fairchild & León (1986) from Río Cinto, Mindo (Pichincha prov.). (8) *Esenbeckia subvaria* cited by Buestán *et al.* (2007) from Cumbe (Azuay prov.); this specimen deposited in CAS collection is not well preserved and Wilkerson & Fairchild (1983) found great differences from Venezuelan type; Fairchild & Burger (1994) did not record this species to the country. (9) *Fidena atripes* cited by Kröber (1933) in Fairchild & León (1986) is apparently misidentified *sensu* the authors who had never seen any other specimen belonging to that species. (10) *Fidena basilaris* cited by von Röder (1886) in Fairchild & León (1986) and then by Buestán *et al.* (2007) from Río Cinto, Mindo (Pichincha prov.) is not well preserved and there is a confusion at generic level (*Esenbeckia?*). (11) *Scione claripennis* from "Sta. Inez, Ecuador" cited by Kröber (1930) in Fairchild (1942), Fairchild & León (1986), and Buestán *et al.* (2007); Fairchild & Burger (1994) stated this specimen as *costaricana*, but they did not include it in Ecuador. We have never seen voucher specimens of any of both species. (12) *Scione fulva* from "Azogues", cited by Campos (1952), has never been seen by entomologists. (13) A single specimen of *Fidena mattogrossensis* from "Napo, Archidona" is not preserved in BMNH as stated by Kröber (1933) in Fairchild & León (1986). (14) The only *Chrysops laetus* voucher specimen from "Baeza, Napo-Pastaza province" seen by Fairchild & León (1986) is currently lost. (15) *Stenotabanus maculipennis* Kröber 1914 is an invalid name cited in Fairchild & León (1986); we believe they referred to Bolivian *Stypommisa furva* (= *maculipennis*) Kröber 1929, however voucher specimen is lost. (16) "*Esenbeckia arcuata* (Willistion) 1895" has been reported by Buestán *et al.* (2007), by error.

### Subfamily Pangoniinae

#### Tribe Pangoniini

##### Genus *Esenbeckia* Rondani

*Esenbeckia* (*Esenbeckia*) *accincta* Wilkerson & Fairchild 1983

*Esenbeckia* (*Esenbeckia*) *balzapambana* Enderlein 1925

*Esenbeckia* (*Esenbeckia*) *dressleri* Wilkerson & Fairchild 1983

*Esenbeckia* (*Esenbeckia*) *laticlava* Wilkerson & Fairchild 1983

*Esenbeckia* (*Esenbeckia*) *melanogaster* Lutz & Castro 1935

*Esenbeckia* (*Esenbeckia*) *parishi* (Hine 1920)

*Esenbeckia* (*Esenbeckia*) *prasiniventris* (Macquart 1846)

*Esenbeckia* (*Esenbeckia*) *reinburgi* Surcouf 1919

*Esenbeckia (Esenbeckia) testaceiventris* (Macquart 1848)  
*Esenbeckia (Esenbeckia) tigrina* Wilkerson 1979  
*Esenbeckia (Esenbeckia) translucens* (Macquart 1846)  
*Esenbeckia (Esenbeckia) xanthoskela* Wilkerson & Fairchild 1983  
*Esenbeckia (Proboscoides) ecuadorensis* Lutz & Castro 1935  
*Esenbeckia (Proboscoides) geminorum* Fairchild & Wilkerson 1981  
*Esenbeckia (Proboscoides) schlingeri* Philip 1960

### Tribe Scionini

#### Genus *Scaptia* Walker

*Scaptia (Scaptia) aureopygia* Philip 1969  
*Scaptia (Scaptia) rubriventris* Kröber 1930  
*Scaptia (Scaptia) sublata* Philip 1969  
**Genus *Fidena* Walker**  
*Fidena (Fidena) aureopygia* Kröber 1931  
*Fidena (Fidena) auribarba* (Enderlein 1925)  
*Fidena (Fidena) castanea* (Perty 1833)  
*Fidena (Fidena) castaneiventris* Kröber 1934  
*Fidena (Fidena) eriomeroides* (Lutz 1909)  
*Fidena (Fidena) flavipennis* Kröber 1931  
*Fidena (Fidena) laterina* (Rondani 1850)  
*Fidena (Fidena) ochrapogon* Wilkerson 1979  
*Fidena (Fidena) pallidula* Kröber 1933  
*Fidena (Fidena) rhinophora* (Bellardi 1859)  
*Fidena (Fidena) zonalis* Kröber 1931

#### Genus *Scione* Walker

*Scione albifasciata* (Macquart 1846)  
*Scione bilineata* Philip 1969  
*Scione brevibeccus* Wilkerson 1979  
*Scione brevistriga* Enderlein 1925  
*Scione costaricana* Szilády 1926  
*Scione equatoriensis* Surcouf 1919  
*Scione equivexans* Wilkerson 1979  
*Scione flavescens* (Enderlein 1930)  
*Scione flavohirta* Ricardo 1902  
*Scione maculipennis* (Schiner 1868)  
*Scione obscurefemorata* Kröber 1930  
*Scione strigata* (Enderlein 1925)

#### Genus *Pityocera* Giglio-Tos

*Pityocera (Pityocera) festae* Giglio-Tos 1896  
*Pityocera (Elaphella) cervus* (Wiedemann 1828)  
*Pityocera (Pseudelaphella) nana* (Walker 1850)

### Subfamily Chrysopsinae

#### Tribe Chrysopsini

##### Genus *Chrysops* Meigen

\**Chrysops bulbicornis* Lutz 1911  
*Chrysops ecuadorensis* Lutz 1909  
*Chrysops flavipennis* Kröber 1925  
*Chrysops latitibialis* Kröber 1926  
*Chrysops leucospilus* Wiedemann 1828

*Chrysops varians* var. *tardus* Wiedemann 1828  
*Chrysops variegatus* (DeGeer 1776)

### Subfamily Tabaninae

#### Tribe Diachlorini

##### Genus *Acellomyia* González

*Acellomyia lauta* (Hine 1920)

##### Genus *Dasybasis* Macquart

*Dasybasis (Dasybasis) excelsior* Fairchild 1956  
*Dasybasis (Dasybasis) montium* (Surcouf 1919)  
*Dasybasis (Dasybasis) schineri* (Kröber 1931)

##### Genus *Hemichrysops* Kröber

\**Hemichrysops fascipennis* Kröber 1930

##### Genus *Stenotabanus* Lutz

*Stenotabanus (Aegialomyia) aberrans* Philip 1966  
*Stenotabanus (Aegialomyia) bruesi* (Hine 1920)  
*Stenotabanus (Stenotabanus) albilinearis* Philip 1960  
*Stenotabanus (Stenotabanus) detersus* (Walker 1850)  
*Stenotabanus (Stenotabanus) incipiens* (Walker 1860)  
*Stenotabanus (Stenotabanus) obscurus* Kröber 1929  
*Stenotabanus (Stenotabanus) obscurus* var. *flavofemoratus* Kröber 1929  
\**Stenotabanus (Stenotabanus) penai* Chainey 1999

*Stenotabanus (Stenotabanus) peruviensis* Kröber 1929

*Stenotabanus (Stenotabanus) wilkersoni* Chainey 1999

##### Genus *Himantostylus* Lutz

*Himantostylus intermedius* Lutz 1913

##### Genus *Diachlorus* Osten Sacken

*Diachlorus anduzei* Stone 1944  
*Diachlorus bimaculatus* (Wiedemann 1828)  
*Diachlorus curvipes* (Fabricius 1805)  
*Diachlorus fuscistigma* Lutz 1913  
*Diachlorus habecki* Wilkerson & Fairchild 1982  
*Diachlorus jobbinsi* Fairchild 1942  
*Diachlorus leucotibialis* Wilkerson & Fairchild 1982  
*Diachlorus nuneztovari* Fairchild & Ortiz 1955  
\**Diachlorus scutellatus* (Macquart 1838)  
*Diachlorus trevorii* Wilkerson & Fairchild 1982

##### Genus *Bolbodimyia* Bigot

*Bolbodimyia bicolor* Bigot 1892  
*Bolbodimyia celerooides* Stone 1954  
*Bolbodimyia erythrocephala* (Bigot 1892)  
*Bolbodimyia nigra* Stone 1934

##### Genus *Selasoma* Macquart

*Selasoma tibiale* (Fabricius 1805)

##### Genus *Chlorotabanus* Lutz

*Chlorotabanus inanis* (Fabricius 1787)  
*Chlorotabanus mexicanus* (L. 1758)

##### Genus *Phaeotabanus* Lutz

*Phaeotabanus cajennensis* (Fabricius 1787)  
*Phaeotabanus fervens* (L. 1758)

- Phaeotabanus nigriflavus* (Kröber 1930)  
*Phaeotabanus phaeopterus* Fairchild 1964  
*\*Phaeotabanus prasiniventris* (Kröber 1929)  
*Phaeotabanus serenus* (Kröber 1931)
- Genus Spilotabanus** Fairchild  
*Spilotabanus multiguttatus* (Kröber 1930)
- Genus Eutabanus** Kröber  
*Eutabanus pictus* Kröber 1930
- Genus Acanthocera** Macquart  
*Acanthocera (Acanthocera) marginalis* Walker 1854  
*Acanthocera (Querbetia) chaineyi* Fairchild & Burger 1994
- Genus Dichelacera** Macquart  
*Dichelacera (Dichelacera) choocoensis* Fairchild & Philip 1960  
*Dichelacera (Dichelacera) fasciata* Walker 1850  
*Dichelacera (Dichelacera) marginata* Macquart 1847  
*Dichelacera (Dichelacera) regina* Fairchild 1940  
*Dichelacera (Dichelacera) rubrofemorata* Burger 1999  
*Dichelacera (Dichelacera) submarginata* Lutz 1915  
*Dichelacera (Dichelacera) villavoeensis* Fairchild & Philip 1960  
*Dichelacera (Idiochelacera) subcallosa* Fairchild & Philip 1960  
*Dichelacera (Desmatochelacera) albitibialis* Burger 1999  
*Dichelacera (Desmatochelacera) transposita* Walker 1854
- Genus Catachlorops** Lutz  
*Catachlorops (Amphichlorops) vespertinus* (Bequaert & Renjifo-Salcedo 1946)  
*Catachlorops (Psarochlorops) difficilis* (Kröber 1931)  
*Catachlorops (Psarochlorops) ecuadorensis* (Enderlein 1925)  
*Catachlorops (Psalidia) fulmineus* var. *ocellatus* Enderlein 1925
- Genus Dasychela** Enderlein  
*Dasychela (Dasychela) amazonensis* (Barretto 1946)  
*Dasychela (Dasychela) badia* (Kröber 1931)  
*Dasychela (Dasychela) fulvicornis* (Kröber 1931)  
*Dasychela (Dasychela) ocellus* (Walker 1848)  
*Dasychela (Dasychela) peruviana* (Bigot 1892)  
*Dasychela (Triceratomyia) macintyrei* (Bequaert 1937)
- Genus Eristalotabanus** Kröber  
*Eristalotabanus violaceus* Kröber 1931
- Genus Dicladocera** Lutz  
*Dicladocera argenteomaculata* Wilkerson 1979  
*Dicladocera basirufa* (Walker 1850)  
*Dicladocera bellicosa* (Brèthes 1910)  
*Dicladocera clara* (Schiner 1868)  
*Dicladocera distomacula* Wilkerson 1979  
*Dicladocera exilicorne* Fairchild 1958  
*Dicladocera hirsuta* Wilkerson 1979  
*Dicladocera macula* (Macquart 1846)  
*Dicladocera minos* (Schiner 1868)  
*Dicladocera ?neosubmacula* Kröber 1931  
*Dicladocera nigrocoerulea* (Rondani 1850)  
*Dicladocera ornatipenne* (Kröber 1931)  
*Dicladocera pruinosa* Wilkerson 1979  
*Dicladocera riveti* (Surcouf 1919)  
*Dicladocera tribonophora* Fairchild 1958

- Genus Stibasoma** Schiner  
*Stibasoma (Stibasoma) flaviventre* (Macquart 1848)  
*Stibasoma (Stibasoma) fulvohirtum* (Wiedemann 1828)  
*Stibasoma (Stibasoma) panamensis* Curran 1934  
*Stibasoma (Rhabdotylus) venenata* (Osten Sacken 1886)
- Genus Cryptotylus** Lutz  
*Cryptotylus unicolor* (Wiedemann 1828)
- Genus Philopotabanus** Fairchild  
*Philipotabanus (Philipotabanus) magnificus* (Kröber 1934)  
*Philipotabanus (Philipotabanus) nigrinubilus* (Fairchild 1953)  
*Philipotabanus (Philipotabanus) pallidetinctus* (Kröber 1930)  
*Philipotabanus (Philipotabanus) pterographicus* (Fairchild 1943)  
*Philipotabanus (Philipotabanus) tenuifasciatus* (Kröber 1930)  
*Philipotabanus (Mimotabanus) opimus* Fairchild 1975  
*\*Philipotabanus (Mimotabanus) porteri* Fairchild 1975  
*Philipotabanus (Melasmatabanus) criton* (Kröber 1934)  
*Philipotabanus (Melasmatabanus) fascipennis* ssp. *ecuadoriensis* (Kröber 1930)  
*Philipotabanus (Melasmatabanus) nigripennis* Wilkerson 1979
- Genus Styppomissa** Enderlein  
*Styppomissa anoriensis* Fairchild & Wilkerson 1986  
*Styppomissa captiroptera* (Kröber 1930)  
*Styppomissa changena* Fairchild 1986  
*Styppomissa flavescens* (Kröber 1930)  
*Styppomissa glandicolor* (Lutz 1912)  
*Styppomissa hypographa* (Kröber 1930)  
*Styppomissa hypographa* ssp. *neofurva* Philip 1969  
*Styppomissa maruccii* (Fairchild 1947)  
*Styppomissa modica* (Hine 1920)  
*Styppomissa pequeniensis* (Fairchild 1942)  
*Styppomissa venosa* (Bigot 1892)
- Genus Leucotabanus** Lutz  
*Leucotabanus albovarius* (Walker 1854)  
*Leucotabanus cornelianus* Fairchild 1985  
*Leucotabanus exaestuans* (L. 1758)  
*Leucotabanus weyrauchi* Fairchild 1951
- Genus Lepiselaga** Macquart  
*Lepiselaga (Lepiselaga) crassipes* (Fabricius 1805)
- Tribe Tabanini**
- Genus Poeciloderas** Lutz  
*Poeciloderas quadripunctatus* (Fabricius 1805)
- Genus Phorcotabanus** Fairchild  
*Phorcotabanus cinereus* (Wiedemann 1821)
- Genus Tabanus** L.  
*Tabanus albocirculus* Hine 1907  
*Tabanus aniptus* Fairchild 1976  
*Tabanus antarcticus* L. 1758  
*Tabanus argentivittatus* Fairchild 1976  
*Tabanus cicur* Fairchild 1942  
*Tabanus claripennis* (Bigot 1892)  
*Tabanus colombensis* Macquart 1846  
*Tabanus cyclopus* Philip 1961

*Tabanus discifer* Walker 1850  
*Tabanus discus* Wiedemann 1828  
*Tabanus eldridgei* Fairchild 1973  
*Tabanus guyanensis* Macquart 1846  
*Tabanus hirtitibia* Walker 1850  
*Tabanus importunus* Wiedemann 1828  
*Tabanus macquarti* Schiner 1868  
*Tabanus nereus* Fairchild 1943  
*Tabanus occidentalis* L. 1758  
*Tabanus occidentalis* var. *dorsovittatus* Macquart 1855  
*Tabanus occidentalis* var. *modestus* Wiedemann 1828  
*Tabanus pachypalpus* (Bigot 1892)  
*Tabanus pellucidus* Fabricius 1805  
*Tabanus perplexus* Walker 1850  
*Tabanus peruvianus* Macquart 1848  
*Tabanus piceiventris* Rondani 1848  
*Tabanus platycerus* Fairchild 1976  
*Tabanus pseudoculus* Fairchild 1942  
*Tabanus pungens* Wiedemann 1828  
*Tabanus restrepoensis* Fairchild 1942  
*Tabanus rixator* Fairchild 1943  
*Tabanus rubiginipennis* Macquart 1846  
*Tabanus rubripes* Macquart 1838  
*Tabanus sannio* Fairchild 1956  
*Tabanus secundus* Walker 1848  
*Tabanus sorbillans* Wiedemann 1828  
*Tabanus surifer* Fairchild 1964  
*Tabanus thiemeanus* (Enderlein 1925)  
*Tabanus unimaculus* Kröber 1934  
*Tabanus unistriatus* Hine 1906  
*Tabanus vittiger* Thomson 1869  
*Tabanus xuthopogon* Fairchild 1984

### Appendix 3.

#### Acronyms of reference collections

**AMNH:** American Museum of Natural History, New York, USA; **AUEM:** Auburn University, Entomology Museum, Alabama, USA; **BMNH:** British Museum of Natural History, London, UK; **C-JB:** Jaime Buestán Personal Collection, Guayaquil, Ecuador; **CAS:** California Academy of Sciences, San Francisco, USA; **CBP:** Cornelius Becker Philip Personal Collection, Hamilton, USA; **CUIC:** Cornell University Insect Collection, Ithaca, USA; **FIOC:** Fundação Instituto Oswaldo Cruz Entomology Collection, Rio de Janeiro, Brazil; **FSCA:** Florida State Collection of Arthropods, Gainesville, USA; **INPA:** Instituto Nacional de Pesquisas da Amazônia-Coleção Sistemática da Entomologia, Manaus, Brazil; **LACM:** Natural History Museum of Los Angeles County, Los Angeles, USA; **MCZ:** Harvard University Museum of Comparative Zoology, Cambridge, USA; **MEPN:** Museo de la Escuela Politécnica Nacional, Quito, Ecuador; **MLPA:** Universidad Nacional de La Plata-Museo de la Plata, La Plata, Argentina; **MLUH:** Martin-Luther-Universität, Wissenschaftsbereich Zoologie, Halle, Germany; **MHNH:** Muséum National d'Histoire Naturelle, Paris, France; **MPEG:** Museu Paraense Emílio Goeldi, Belém, Brazil; **MTD:** Museum für Tierkunde, Dresden, Germany; **OSUC:** Ohio State University Collection, Columbus, USA; **MZPW:** Warsaw Museum of the Institute of Zoology, Warsaw, Poland; **NHRS:** Naturhistoriska riksmuseet, Stockholm, Sweden; **QCAZ:** Quito Catholic University Zoology Museum, Quito, Ecuador; **UMMZ:** University of Michigan Museum of Zoology, Ann Arbor, USA; **USNM:** Smithsonian National Museum of Natural History, Washington, USA; **ZMBH** (=ZMFHU): Berlin Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; **ZMUH:** Universität von Hamburg Zoologisches Institut und Zoologisches Museum, Hamburg, Germany.

#### On line appendices.

**Appendix 4. Complete catalogue of Ecuadorian species of Tabanidae.**

**Appendix 5. Gazetteer of known localities of Ecuadorian specimens of Tabanidae.**

## Appendix 4.

### Complete catalogue of Ecuadorian species of Tabanidae.

We present a full list of known species localities distribution. We omitted specimens labels information unless they are reported for the first time for Ecuador (marked with \*). Acronyms of reference collections are detailed in Appendix 3. A gazetteer of known localities is provided in Appendix 4. Type-localities have been underlined.

#### SUBFAMILY PANGONIINAE

##### Tribe Pangoniini

*Esenbeckia* (*Esenbeckia*) *accincta* Wilkerson & Fairchild 1983

PICHINCHA: Quito (Carretas) (FSCA in Fairchild & Burger 1994); Pifo (C-JB).  
GUAYAS: Vía a Balao Chico (CUIC *sensu* Fairchild & Burger 1994).

*Esenbeckia* (*Esenbeckia*) *balzapambana* Enderlein 1925

BOLIVAR: Río Cristal (Balzapamba), Km 7 Vía Bucay-Chillanes (C-JB);  
Balzapamba (ZMFHU in Fairchild & Burger 1994). CHIMBORAZO: Río  
Sacramento, Buenos Aires-5 Km O de Cumandá (C-JB). IMBABURA:  
Peñaherrera (Wilkerson & Fairchild 1983). LOJA: Quebrada Chipiango (C-JB).

*Esenbeckia* (*Esenbeckia*) *dressleri* Wilkerson & Fairchild 1983

SANTO DOMINGO: “Santo Domingo to Chiriboga” (FSCA in Wilkerson &  
Fairchild 1983).

*Esenbeckia* (*Esenbeckia*) *laticlava* Wilkerson & Fairchild 1983

GUAYAS: “20 mi West of Guayaquil” (CAS, CUIC in Fairchild & Burger 1994).

*Esenbeckia* (*Esenbeckia*) *melanogaster* Lutz & Castro 1935

LOJA: San Vicente (C-JB).

*Esenbeckia* (*Esenbeckia*) *parishi* (Hine 1920)

CHIMBORAZO: Río Sacramento (C-JB). EL ORO: Bosque Puyango (C-JB).  
LOJA: Catacocha, Quebrada Chipiango (C-JB). LOS RÍOS: EBFD Jauneche (C-  
JB). “Ecuador” as locality datum (OSUC in Fairchild & Burger 1994).

*Esenbeckia* (*Esenbeckia*) *prasiniventris* (Macquart 1846)

LOJA: Sta Rufina (QCAZ).

*Esenbeckia* (*Esenbeckia*) *reinburgi* Surcouf 1919

CHIMBORAZO: Riobamba (Campos 1952). LOJA: Catacocha, San Vicente (C-  
JB). LOJA: Loja (in Fairchild & Burger 1994). PICHINCHA: Quito (MNHN in  
Surcouf 1919); Machachi (Campos 1952).

*Esenbeckia* (*Esenbeckia*) *testaceiventris* (Macquart 1848)

AZUAY: Río Zaracay (C-JB). COTOPAXI: 4 Km al Este de la Esperanza, La  
Gaviota (C-JB); San Fco. de las Pampas (QCAZ); Calupiña (C-JB) (QCAZ).  
IMBABURA: Los Cedros (EC), Los Cedros E1:T,T1 (R.B., B.P.), Los Cedros  
E2:T, T1, T2 (R.B., B.P.), Los Cedros E3:T2, T3 (R.B., B.P.) (QCAZ); Azabí

(Intag) (Wilkerson & Fairchild 1983). LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Arenillas (C-JB). PICHINCHA: Mindo (QCAZ); Hda (Eco) Bomboli (C-JB); Palmeras (QCAZ) (C-JB); Via Quito-Chiriboga (Wilkerson & Fairchild 1983); Nanegal (Fairchild & León 1986); Quito (BMNH in Fairchild & Burger 1994). SANTO DOMINGO: E.C. Río Guajalito (QCAZ), Via Santo Domingo-Chiriboga (Wilkerson & Fairchild 1983). ZAMORA CHINCHIPE: Zamora (Fairchild & León 1986).

*Esenbeckia (Esenbeckia) tigrina* Wilkerson 1979

COTOPAXI: San Fco. De las Pampas (QCAZ). CHIMBORAZO: Río Sacramento (C-JB). SANTA ELENA: 2.6 Km de "Dos Mangas" (C-JB). LOJA: Quebrada Chipiango (C-JB). LOS RÍOS: EBFD Jauneche (C-JB).

*Esenbeckia (Esenbeckia) translucens* (Macquart 1846)

ESMERALDAS: Kumanii Lodge, Kumanii Lodge T, T1,T2,T3, E.C. Río Canandé (Reserva - Jocotoco), E.C. Río Canandé T (Reserva - Jocotoco) (QCAZ); Playa de Oro (Río Santiago), Hda (Eco) Bomboli (C-JB). IMBABURA: Intag (Fraichild & León 1986). MANABÍ: Río Mache (C-JB). SANTO DOMINGO: Santo Domingo (Fraichild & León 1986).

*Esenbeckia (Esenbeckia) xanthoskela* Wilkerson & Fairchild 1983

MORONA SANTIAGO: Cerro Chuark Wihp, Coangos (C-JB). NAPO: Río Hollín (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ); E. C. Tiputini USFQ (TBS) (QCAZ) (MEPN). SUCUMBÍOS: Lumbaqui (QCAZ).

*Esenbeckia (Proboscoides) ecuadorensis* Lutz & Castro 1935

CAÑAR: Cochancay (El chorro; El Chorro, Cochancay), Manuel J.Calle (C-JB). GUAYAS: Naranjal (FIOC in Lutz & Castro 1935); "20 mi West of Guayaquil" (CAS in Philip 1961); Hda. San Joaquín (San Joaquín) (QCAZ); Vía a Balao Chico, Balao-Hacienda Santa Rita (C-JB). LOS RÍOS: "Near Quevedo" (UMMZ in Philip 1960). SUCUMBÍOS: Limoncocha (AUEM in Patrick & Hays 1968).

*Esenbeckia (Proboscoides) geminorum* Fairchild & Wilkerson 1981

SANTA ELENA: Colonche (QCAZ) (C-JB) (FSCA in Fairchild & Wilkerson 1981); Zapotal (C-JB).

*Esenbeckia (Proboscoides) schlingeri* Philip 1960

NAPO: Río Umbuni (C-JB).

**Tribe Scionini**

*Scaptia (Scaptia) aureopygia* Phlip 1969

IMBABURA: Los Cedros E2:T, Los Cedros E3:T2(R.B., B.P.) (QCAZ). MORONA SANTIAGO: Arenillas (C-JB).

*Scaptia (Scaptia) rubriventris* (Kröber 1930)

MORONA SANTIAGO: Arenillas (C-JB).

*Scaptia (Scaptia) sublata* Philip 1969

MORONA SANTIAGO: Arenillas (C-JB).

*Fidena (Fidena) aureopygia* Kröber 1931

BOLIVAR: La Moya (C-JB). CAÑAR: La Carbonería (QCAZ). CHIMBORAZO: Quebrada Bodega Pamba, Río Pangor (C-JB). IMBABURA: Atuntaqui (QCAZ). NAPO: Río Hollín. PICHINCHA: Quito (P. Metropolitano), Quito, Cumbayá, Vía Mindo, Fald. Pichincha, Pululahua, Moraspungo, Palmeras, El Tingo, Yanacocha-Reserva (Pastizal arbolado y BMA) (QCAZ); Conocoto, Quito, San Antonio (Volcán Pululahua), Yaruquí (C-JB). SUCUMBÍOS: El Reventador (QCAZ).

*Fidena (Fidena) auribarba* (Enderlein 1925)

ESMERALDAS: E.C. Río Canandé T, T3 (Reserva - Jocotoco) (QCAZ). MORONA SANTIAGO: Río Pau Grande (Tarapoa) (C-JB).

*Fidena (Fidena) castanea* (Perty 1833)

NAPO:Pozo Daimi, Río Umbuni (C-JB). ORELLANA: Coca (C-JB). SUCUMBÍOS: Shushufindi, Río Aguarico (C-JB).

*Fidena (Fidena) castaneiventris* Kröber 1934

PICHINCHA: Casitagua (MNHN *in* Surcouf 1919), Valle de los Chillos (Fairchild & León 1986).

*Fidena (Fidena) eriomerooides* (Lutz 1909)

NAPO: Río Hollín, Misahualli (QCAZ) MORONA SANTIAGO: Cord. del Cónedor Río Coangos-Río Tsuirin (QCAZ). ORELLANA: Ávila Viejo (QCAZ), Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ) (C-JB). PASTAZA: Villano (QCAZ).

*Fidena (Fidena) flavipennis* Kröber 1931

ESMERALDAS: Caimito (estero salado mangle) (QCAZ). MANABÍ: Río de Mache (C-JB).

*Fidena (Fidena) laterina* (Rondani 1850)

NAPO: Pozo Daimi (QCAZ); Limoncocha (C-JB), Río Napo (*in* Fairchild & Burger 1994). ORELLANA: Est. Chiruisla T, Est. Río Huiririma (QCAZ); Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ) (C-JB); E. C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Villano (QCAZ).

*Fidena (Fidena) ochrapogon* Wilkerson 1979

AZUAY: Cuenca (Wilkerson 1979); Río Zaracay (C-JB). CHIMBORAZO: Quebrada Bodega Pamba (C-JB).

*Fidena (Fidena) pallidula* Kröber 1933

NAPO: Zatzayacu (Fairchild & León 1986).

*Fidena (Fidena) rhinophora* (Bellardi 1859)

CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (QCAZ) (C-JB); Azogues (Azoguez) (Campos 1952). COTOPAXI: San Fco. de las Pampas (QCAZ) (C-JB); B. I. Otonga (El Corcovado) (QCAZ). GUAYAS: Hda. San Joaquín (San Joaquín), Chilcales (Río Chilcales, M. J. Calles) (C-JB). IMBABURA: Los Cedros (EC) (R.B., B.P.) (QCAZ). MORONA SANTIAGO: Indanza, Puerto Yuquianza, Río Pau Grande (Tarapoa), Coangos (C-JB). NAPO: Cascada San Rafael (QCAZ) (C-JB); Río Hollín, Km 6 Vía Narupa - Coca, Vía Loreto-Coca 20.7 Km (Este de Tena) (C-JB). PICHINCHA: Nanegalito, Maquipucuna (QCAZ); Mindo (QCAZ)

(C-JB); Río del Cinto (Mindo) (Fairchild & León 1986). SUCUMBÍOS: El Reventador (QCAZ). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Río Bombuscara, Río Valladolid (C-JB).

*Fidena (Fidena) zonalis* Kröber 1931  
“Ecuador” as locality datum (Fairchild & Burger 1994).

*Scione albifasciata* (Macquart 1846)  
LOJA: Mamanuma (QCAZ); Cord. Sabanilla (C-JB). MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas (C-JB). NAPO: Santa Bárbara de Sucumbíos (Fairchild & León 1986). SUCUMBÍOS: La Fama (QCAZ).

*Scione bilineata* Philip 1969  
MORONA SANTIAGO: “E. Ecuador; Limón” (AMNH, CBP *in* Philip 1969).

*Scione brevibeccus* Wilkerson 1979  
IMBABURA: Los Cedros E3:T, T1,T2 (R.B., B.P.) (QCAZ). LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Arenillas (C-JB).

*Scione brevistriga* Enderlein 1925  
TUNGURAHUA: Baños (Fairchild & León 1986).

*Scione costaricana* Szilády 1926  
“Santa Inez, Ecuador” as locality datum (Kröber 1930 *in* Fairchild 1942 as *claripennis*). Not taken account by Fairchild & Burger (1994).

*Scione equatoriensis* Surcouf 1919  
AZUAY: Maylas (C-JB). CAÑAR: Azogues (Azoguez) (Campos 1952). IMBABURA: Pinular (MNHN *in* Surcouf 1919). MANABÍ: Río Mache (C-JB); Chone (Fairchild & León 1986). PICHINCHA: Quito (Carretas), Pifo 9 Km al este, San Antonio (Volcán Pululahua) (C-JB), Casitagua (MNHN *in* Surcouf 1919). TUNGURAHUA: Ambato (Campos 1952).

*Scione equivexans* Wilkerson 1979  
MORONA SANTIAGO: Potrerillo, Arenillas (C-JB). PICHINCHA: Volcán Pichincha (QCAZ); Quito, Conocoto (QCAZ) (C-JB).

*Scione flavescens* (Enderlein 1930)  
PICHINCHA: Santa Inés (Wilkerson 1979). “Ecuador” as type locality in Fairchild & Burger (1994).

*Scione flavohirta* Ricardo 1902  
AZUAY: Maylas, Río Zaracay, Miguir, Huasipamba (Guasipamba) (C-JB); Valle de Azuay (MLPA *in* Coscarón 2000). BOLIVAR: La Moya, Cerro Pumín (C-JB). MORONA SANTIAGO: Potrerillo (C-JB).

*Scione maculipennis* (Schiner 1868)  
MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas (C-JB).

*Scione obscurefemorata* Kröber 1930  
AZUAY: Maylas (C-JB). IMBABURA: Nangulví (Fairchild & León 1986). LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas,

San Vicente (Límite Azuay prov.), Potrerillo (C-JB). TUNGURAHUA:  
Llanganates (C-JB).

*Scione strigata* (Enderlein 1925)

PICHINCHA: Hda (Eco) Bomboli (C-JB); Santa Inéz (Kröber 1930 *in* Fairchild 1942)

*Pityocera (Pityocera) festae* Giglio-Tos 1896

ESMERALDAS: Kumanii Lodge, Kumanii Lodge T1 (QCAZ); Playa de Oro (Río Santiago (C-JB). SANTO DOMINGO: Santo Domingo (Fairchild & León 1986).

*Pityocera (Elaphella) cervus* (Wiedemann 1828)

NAPO: Río Umbuni (C-JB). SUCUMBÍOS: Limoncocha (AUEM *in* Patrick & Hays 1968). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ). PASTAZA: Villano, Villano (Tarangaro) (QCAZ).

*Pityocera (Pseudelaphella) nana* (Walker 1850)

GUAYAS: San Eduardo (Guayaquil - El Salado) (Campos 1952).

## SUBFAMILY CHRYSOPSINAE

### Tribe Chrysopsini

\**Chrysops bulbicornis* Lutz 1911

ECUADOR, ORELLANA: Vía Coca - Loreto Km 26, 300m., 00°29'42"S  
77°08'00"W, 21.VII.2005, J.M. Vieira Leg., 1f, R. Cárdenas Det. (II.2008),  
QCAZI14816; Dayuma, 290m., 22.III.1996, G. Piedra Leg., 1f, R. Cárdenas det.  
(II.2008), QCAZI44715. Both specimens deposited at QCAZ Museum of Zoology.

*Chrysops ecuadorensis* Lutz 1909

ORELLANA: Chiruisla T1 (QCAZ); PASTAZA: Curaray (San Antonio de Curaray) (Fairchild & León 1986); Lorocachi (QCAZ).

*Chrysops flavipennis* Kröber 1925

“Ecuador, Santa Inez” as locality datum (ZMHB *in* Fairchild & Burger 1994). ZAMORA CHINCHIPE: Zamora (Fairchild & León 1986).

*Chrysops latitibialis* Kröber 1926

“Ecuador, Litoral” as locality datum (MPEG *in* Henriques & Gorayeb 1993) and “Ecuador” as locality datum (INPA *in* Henriques 1995).

*Chrysops leucospilus* Wiedemann 1828

ORELLANA: Est. Chiruisla T3 (QCAZ). LOJA: Cola (Kröber 1925 *in* Fairchild & León 1986).

*Chrysops varians* var. *tardus* Wiedemann 1828

MORONA SANTIAGO: 6.6 Km N vía Limón - Macas, Logroño (QCAZ); Indanza (QCAZ) (C-JB); Kalaglas, Méndez, San Luis de El Hacho, Puerto Yuquianza, Patuca, Unión Río Upano-Paute (C-JB). NAPO: Cascada San Rafael, Archidona, Misahualli, Río Hollín, Aliñahui (cabañas), Jatún Sacha, Jumandi, Joya de los Sachas (QCAZ); Baeza, Río Umbuni, Km 6 Vía Narupa - Coca (C-JB). ORELLANA: Coca, Vía Coca - Loreto Km 26 (QCAZ); Est. Exp. Napo (C-JB); E.

C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Mera, Puyo (El) (QCAZ); Santa Clara, Shell-Mera (C-JB). SANTO DOMINGO: E. C. Río Guajalito (QCAZ). SUCUMBÍOS: Santa Cecilia (AUEM in Patrick & Hays 1968), R. P. F. Cuyabeno (C-JB). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Río Valladolid (C-JB).

*Chrysops variegatus* (DeGeer 1776)

CHIMBORAZO: Buenos Aires (C-JB). EL ORO: Limón Playas-Sta. Rosa (C-JB). ESMERALDAS: E.C. Río Canandé (Reserva - Jocotoco) (QCAZ). GUAYAS: San Carlos, Hda. San Joaquín (San Joaquín) (C-JB). LOS RÍOS: Peniel - Quevedo (QCAZ); EBFD Jauneche, Quevedo (C-JB). SANTO DOMINGO: E. Santo Domingo (QCAZ) (C-JB). SUCUMBÍOS: R. P. F. Cuyabeno (C-JB).

## SUBFAMILY TABANINAE

### Tribe Diachlorini

*Acellomyia lauta* (Hine 1920)

AZUAY: Cumbe (González 1999). SUCUMBÍOS: El Reventador (QCAZ).

*Dasybasis (Dasybasis) excelsior* Fairchild 1956

CHIMBORAZO: Danas (Fairchild & León 1986). LOJA: Catacocha (C-JB).

*Dasybasis (Dasybasis) montium* (Surcouf 1919)

AZUAY: Maylas, Río Zaracay, Miguir (C-JB); Cumbe (Coscarón & Philip 1967). BOLIVAR: Salinas (QCAZ) (C-JB); Cerro Pumín, La Moya (C-JB). CAÑAR: Río Yanacachi (C-JB). CHIMBORAZO: Quebrada Bodega Pamba (C-JB). COTOPAXI: Rumiñahui faldas volcán (QCAZ). LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: San Vicente (Límite Azuay prov.), Arenillas (C-JB). PICHINCHA: Casitagua (MNHN in Surcouf 1919); R.B. Yanacocha, Yanacocha-Reserva (Pastizal arbolado y BMA), Lloa (QCAZ); Pifo, Hda (Eco) Bomboli (C-JB); TUNGURAHUA: Llanganates (C-JB).

*Dasybasis (Dasybasis) schineri* (Kröber 1931)

AZUAY: Maylas, Río Zaracay, Miguir (C-JB); Cumbe (Coscarón & Philip 1967). BOLIVAR: Cerro Pumín (C-JB). CAÑAR: Río Yanacachi (C-JB). IMBABURA: Machetes (Fairchild & León 1986). MORONA SANTIAGO: San Vicente (Límite Azuay prov.) (C-JB).

\**Hemichrystops fascipennis* Kröber 1930

ECUADOR, IMBABURA, 10 Km W Santa Rosa, 700m., 00°19'51''N  
78°55'55''W, 21-25.VII.2008, D. Chávez Leg., 1♂, R. Cárdenas Det. (VIII.2008).  
Ojos bicolores en vida, verde abajo y negro arriba. QCAZI44767. Deposited at  
QCAZ Museum of Zoology.

*Stenotabanus (Aegialomyia) aberrans* Philip 1966

SANTA ELENA: Santa Elena (CAS in Fairchild & Burger 1994).

*Stenotabanus (Aegialomyia) bruesi* (Hine 1920)

BOLIVAR: Río Cristal (Balzapamba) (C-JB). CHIMBORAZO: Buenos Aires (C-JB). LOJA: Quebrada Chipiango, Río Catamayo (C-JB). MANABÍ: Julcuy, Río Mache (C-JB).

*Stenotabanus (Stenotabanus) albilinearis* Phliph 1960

MORONA SANTIAGO: San Luis de El Hacho (C-JB). NAPO: Río Umbuni (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ). PASTAZA: Shell-Mera (C-JB). TUNGURAHUA: El Topo (C-JB).

*Stenotabanus (Stenotabanus) detersus* (Walker 1850)

CHIMBORAZO: Río Sacramento (C-JB). LOJA: San Vicente (C-JB). MORONA SANTIAGO: Kalaglas, Indanza, Arenillas (C-JB). SANTO DOMINGO: Mindo, Alluriquín (C-JB).

*Stenotabanus (Stenotabanus) incipiens* (Walker 1860)

ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (C-JB).

*Stenotabanus (Stenotabanus) obscurus* Kröber 1929

MORONA SANTIAGO: Puerto Yuquianza (C-JB). NAPO: Río Hollín (QCAZ); Río Umbuni, Km 6 Vía Narupa - Coca, Cocodrilo (C-JB). PAZTASA: Shell-Mera (C-JB). TUNGURAHUA: El Topo (QCAZ) (C-JB). ZAMORA CHINCHIPE: Río Bombuscara, Río Valladolid (C-JB).

*Stenotabanus (Stenotabanus) obscurus* var. *flavofemoratus* Kröber 1929

NAPO: Río Hollín (QCAZ).

\**Stenotabanus (Stenotabanus) penai* Chainey 1999

ECUADOR, ESMERALDAS: Caimito, 5m., 00°42'07.26''N 80°05'50.82''W, 06.IV.2007, R. Cárdenas Leg., 11££, R. Cárdenas Det. (IX.2008). Dos líneas verdes transversales en ojos. QCAZI44703, QCAZ44704, QCAZI44706–QCAZI44714; Caimito, 50m., 00°41'56.88''N 80°05'34.02''W, 07.IV.2007, R. Cárdenas Leg., 1£, R. Cárdenas Det. (IX.2008). QCAZI44704. Deposited at QCAZ Museum of Zoology.

*Stenotabanus (Stenotabanus) peruviensis* Kröber 1929

SUCUMBÍOS: “Santa Cecilia” (AUEM in Patrick & Hays 1968). “Ecuador” as locality datum in Fairchild & Burger 1994 (as *pallidicornis*).

*Stenotabanus (Stenotabanus) wilkersoni* Chainey 1999

ESMERALDAS: Playa de Oro (Río Santiago) (C-JB).

*Himantostylus intermedius* Lutz 1913

From “Panama to Bolivia” in Fairchild & Burger (1994).

*Diachlorus anduzei* Stone 1944

SUCUMBÍOS: Limoncocha (Wilkerson & Fairchild 1982).

*Diachlorus bimaculatus* (Wiedemann 1828)

LOJA: La Toma (Fairchild & León 1986). MORONA SANTIAGO: Mayaico (Fairchild & León 1986). ORELLANA: Nuevo Rocafuerte (Fairchild & León 1986). PASTAZA: Curaray (San Antonio de) (Fairchild & León 1986). SUCUMBÍOS: Santa Cecilia (AUEM in Patrick & Hays 1968). ZAMORA CHINCHIPE: Río Nangaritza, Zamora (Fairchild & León 1986).

*Diachlorus curvipes* (Fabricius 1805)

ESMERALDAS: Playa de Oro (Río Santiago) (C-JB). NAPO: Río Umbuni (C-JB).

ORELLANA: Est. Chiruisla T1,T2, Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ); Coca (C-JB). PASTAZA: Shell (QCAZ), Shell-Mera (C-JB).

*Diachlorus fuscistigma* Lutz 1913

“Ecuador” as locality datum (Henriques & Rafael 1999).

*Diachlorus habecki* Wilkerson & Fairchild 1982

SUCUMBÍOS: R. P. F. Cuyabeno (C-JB); Limoncocha (Playaco river) (FSCA *in* Wilkerson & Fairchild 1982).

*Diachlorus jobbinsi* Fairchild 1942

ESMERALDAS: Limones (Fairchild & León 1986).

*Diachlorus leucotibialis* Wilkerson & Fairchild 1982

ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ); E. C. Tiputini USFQ (TBS) (MEPN); Primavera (La) (FSCA *in* Wilkerson & Fairchild 1982).

*Diachlorus nuneztovari* Fairchild & Ortiz 1955

ORELLANA: Est. Chiruisla T (QCAZ). SUCUMBÍOS: Sacha Lodge (QCAZ). “East of Ecuador” as locality datum in Fairchild & Burger (1994).

\**Diachlorus scutellatus* (Macquart 1838)

ECUADOR, ORELLANA, Est. Chiruisla T, 204m., 00°41'09"S 75°56'27"W, 25.II.2006, R. Cárdenas Leg., 1♂, R. Cárdenas Det. (III.2006). QCAZI36299.  
Deposited at QCAZ Museum of Zoology.

*Diachlorus trevori* Wilkerson & Fairchild 1982

SUCUMBÍOS: Limoncocha (Playaco river) (FSCA *in* Wilkerson & Fairchild 1982).

*Bolbodimyia bicolor* Bigot 1892

IMBABURA: Los Cedros E1:T,T1 (R.B., B.P.) (QCAZ). MANABÍ: Río Mache (C-JB).

*Bolbodimyia celeroides* Stone 1954

IMBABURA: Los Cedros (EC) (R.B., B.P.) (QCAZ). MORONA SANTIAGO: Unión Río Upano-Paute, Puerto Yuquianza (C-JB). NAPO: Aliñahui (cabañas) (QCAZ).

*Bolbodimyia erythrocephala* (Bigot 1892)

ESMERALDAS: Playa de Oro (Río Santiago) (C-JB).

*Bolbodimyia nigra* Stone 1934

BOLIVAR: Km 7 Vía Bucay - Chillanes (C-JB). GUAYAS: Guayaquil (USNM *in* Stone 1934). NAPO: Cascada San Rafael (QCAZ).

*Selasoma tibiale* (Fabricius 1805)

From “Mexico (Oaxaca) to n. Argentina” *in* Fairchild & Burger (1994).

*Chlorotabanus inanis* (Fabricius 1787)

ESMERALDAS: Kumanii Lodge, Kumanii Lodge T, T2 (QCAZ). GUAYAS: Hda. Santa Rita (Balao) (C-JB). NAPO: Aliñahui (cabañas) (QCAZ); Río Napo, Río

Umbuni, Misahuallí, Juturi (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE), Est. Chiruisla T (QCAZ); Est. Exp. Napo (C-JB); E. C. Tiputini USFQ (TBS) (MEPN). SANTO DOMINGO: Santo Domingo (C-JB). SUCUMBÍOS: Lago Agrio (QCAZ) (C-JB), Limoncocha (AUDEM in Patrick & Hays 1968).

*Chlorotabanus mexicanus* (L. 1758)

ESMERALDAS: Quinindé, San Francisco (Muisne), Mayronga (La) (QCAZ); Alto Cayapa (C-JB); San Lorenzo (QCAZ) (C-JB). GUAYAS: Balao Chico, Hda. Santa Rita (Balao), Bucay (1 Km NO Cumandá), El Empalme (C-JB). LOS RÍOS: Hda. Clementina, Pichilingue, EPFD Jauneche (C-JB).

*Phaeotabanus cajennensis* (Fabricius 1787)

ORELLANA: Est. Exp. Napo (C-JB); Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ). SUCUMBÍOS: "Limoncocha" (AUDEM in Patrick & Hays 1968).

*Phaeotabanus fervens* (L. 1758)

From "Venezuela to Argentina" in Fairchild & Burger (1994).

*Phaeotabanus nigriflavus* (Kröber 1930)

ORELLANA: Est. Río Huiririma, Coca (C-JB). SUCUMBÍOS: "Limoncocha" (AUDEM in Patrick & Hays 1968).

*Phaeotabanus phaeopterus* Fairchild 1964

PICHINCHA: Tandapi (Manuel Cornejo Astorga) (C-JB).

\**Phaeotabanus prasiniventris* (Kröber 1929)

ECUADOR, SUCUMBÍOS, Nueva Loja, 450m., 00°05'00" N 76°52'00" W, 11.IV.2007, J. Prado Leg., 1f, K. M. Bayless Det. (2009). QCAZI36347. Deposited at QCAZ Museum of Zoology.

*Phaeotabanus serenus* (Kröber 1931)

NAPO: Río Umbuni (C-JB). MORONA SANTIAGO: Puerto Yuquianza (C-JB).

*Spilotabanus multiguttatus* (Kröber 1930)

COTOPAXI: Vía Salcedo-Tena (QCAZ). LOJA: Vía Zamora Puerto, P. N. Podocarpus (QCAZ); Cord. Sabanilla (C-JB). MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas, Potrerillo (C-JB); San Vicente (QCAZ) (C-JB). NAPO: La Alegría (C-JB). PICHINCHA: R. B. Yanacocha. (QCAZ). SUCUMBÍOS: Vía La Bonita - La Fama (QCAZ). TUNGURAHUA: Runtún (C-JB).

*Eutabanus pictus* Kröber 1930

"Ecuador" as locality datum in Fairchild & Burger (1994).

*Acanthocera (Acanthocera) marginalis* Walker 1854

NAPO: Río Umbuni, Jatún Sacha (C-JB). ORELLANA: Bloque 31, Estación Huiririma, Yasuní (SC - Res. Sta. - EC - PUCE), (QCAZ). MORONA SANTIAGO: Puerto Yuquianza (C-JB).

*Acanthocera (Querbetia) chaineyi* Fairchild & Burger 1994

NAPO: Río Umbuni (C-JB).

*Dichelacera (Dichelacera) chocoensis* Fairchild & Philip 1960

ESMERALDAS: Playa de Oro (Río Santiago) (C-JB). GUAYAS: Balao Chico (C-JB); Hda. San Joaquín (San Joaquín) (C-JB) (QCAZ). MANABÍ: Río Mache (C-JB).

*Dichelacera (Dichelacera) fasciata* Walker 1850

ESMERALDAS: Kumanii Lodge, Kumanii Lodge T, T1, T2, T3, E.C. Río Canandé T, T1, T3 (Reserva - Jocotoco) (QCAZ); Playa de Oro (Río Santiago) (C-JB). MANABÍ: Río Mache (C-JB). NAPO: Latas (Misahualli) (QCAZ); Río Umbuni (C-JB). SANTO DOMINGO: Santo Domingo (C-JB) (Fairchild & León 1986). ZAMORA CHINCHIPE: Río Valladolid (C-JB).

*Dichelacera (Dichelacera) marginata* Macquart 1847

ESMERALDAS: Alto Cayapa (C-JB). MANABÍ: Palmar (C-JB). NAPO: Río Umbuni, Jatún Sacha (C-JB). ORELLANA: Coca, Payamino, Est. Exp. Napo (C-JB). PASTAZA: Villano (Tarangaro, Kurintza) (QCAZ); Shell-Mera (C-JB). SUCUMBÍOS: Limoncocha (C-JB), Santa Cecilia (AUEM in Patrick & Hays 1968).

*Dichelacera (Dichelacera) regina* Fairchild 1940

From "Honduras to Ecuador" in Wilkerson (1979) and Burger & Fairchild (1994).

*Dichelacera (Dichelacera) rubrofemorata* Burger 1999

NAPO: Misahualli (QCAZ), Latas (Misahualli) (FSCA in Burger 1999); La Selva (E. of Limoncocha) (FSCA in Burger 1999). ORELLANA: Coca (FSCA in Burger 1999). PASTAZA: Villano (QCAZ). SUCUMBÍOS: Sacha Lodge (LACM in Burger 1999), Limoncocha, 8 Km W Lago Agrio (FSCA in Burger 1999).

*Dichelacera (Dichelacera) submarginata* Lutz 1915

CAÑAR: Chilcales (Río Chilcales, M. J. Calles), Joyapal (Joyapal - Cochancay), Cochancay (El chorro; El Chorro, Cochancay) (C-JB). MORONA SANTIAGO: Río Pau Grande (Tarapoa) (QCAZ), Unión Río Upano-Paute (C-JB). NAPO: Vía Puyo-Tena, Río Umbuni (C-JB). ORELLANA: E. C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Santa Clara (C-JB); Puyo C. E. Fátima (MEPN). SANTO DOMINGO: Tinalandia(C-JB). SUCUMBÍOS: R. P. F. Cuyabeno (QCAZ) (C-JB). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Palanda (C-JB).

*Dichelacera (Dichelacera) villavoensis* Fairchild & Philip 1960

MORONA SANTIAGO: Puerto Yuquianza (C-JB). NAPO: Misahualli (QCAZ); Río Umbuni, Jatún Sacha (C-JB). SUCUMBÍOS: R. P. F. Cuyabeno (C-JB). TUNGURAHUA: El Topo (C-JB).

*Dichelacera (Idiochelacera) subcallosa* Fairchild & Philip 1960

GUAYAS: Hda. San Joaquín (San Joaquín) (QCAZ).

*Dichelacera (Desmatochelacera) albitibialis* Burger 1999

NAPO: Misahualli (QCAZ); Río Umbuni, Jatún Sacha (C-JB). MORONA SANTIAGO: Puerto Yuquianza (C-JB). PASTAZA: Villano (Tarangaro, Kurintza), Shell (LACM in Burger 1999).

*Dichelacera (Desmatochelacera) transposita* Walker 1854

BOLIVAR: Km 7 Vía Bucay - Chillanes (C-JB). ESMERALDAS: Playa de Oro (Río Santiago) (C-JB). NAPO: Daimi (QCAZ).

*Catachlorops (Amphichlorops) vespertinus* (Bequaert & Renjifo-Salcedo 1946)

MORONA SANTIAGO: Puerto Yuquianza (C-JB). PASTAZA: Abitagua (Fairchild & León 1986). TUNGURAHUA: El Topo (QCAZ) (C-JB); Baños (Fairchild & León 1986). ZAMORA CHINCHIPE: Río Bombuscara, El Pangui (C-JB); Zamora (Fairchild & León 1986).

*Catachlorops (Psarochlorops) difficilis* (Kröber 1931)

ORELLANA: Est. Chiruisla T1, T2, T3 (QCAZ). SUCUMBÍOS (PASTAZA in error): Limoncocha (MPEG in Henriques & Gorayeb 1993).

*Catachlorops (Psarochlorops) ecuadoriensis* (Enderlein 1925)

MORONA SANTIAGO: Puerto Yuquianza (C-JB). NAPO: Baeza (in Fairchild 1966), Río Hollín, Cascada San Rafael, Vía Jondachi-Loreto Río Hollín, Hollín-Loreto (QCAZ); El Salado, Cocodrilo (C-JB); Campanacocha (QCAZ) (C-JB); Baeza, Boyayaco (Panyagacu) (Fairchild & León 1986). PASTAZA: Shell, Puyo (El) (C-JB). PICHINCHA: Santa Inéz (ZMHB in Fairchild & Burger 1994). SANTO DOMINGO: Santo Domingo (Fairchild & León 1986). TUNGURAHUA: El Topo, Río Negro (C-JB).

*Catachlorops (Psalidia) fulmineus* var. *ocellatus* Enderlein 1925

ESMERALDAS: Kumanii Lodge T2, T3, E.C. Río Canandé T (Reserva - Jocotoco) (QCAZ); Playa de Oro (Río Santiago) (C-JB).

*Dasychela (Dasychela) amazonensis* (Barretto 1946)

ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ); E. C. Tiputini USFQ (TBS) (MEPN).

*Dasychela (Dasychela) badia* (Kröber 1931)

BOLIVAR: Guaranda (Fairchild & León 1986). IMBABURA: Azabí (Intag) (Wilkerson & Fairchild 1983)

*Dasychela (Dasychela) fulvicornis* (Kröber 1931)

PICHINCHA: Santa Inez (Kröber 1931a). TUNGURAHUA: Baños (Kröber 1931a).

*Dasychela (Dasychela) ocellus* (Walker 1848)

COTOPAXI: San Fco. de las Pampas (C-JB). IMBABURA: Los Cedros (EC) (R.B., B.P.), Los Cedros E2:T, T2 (R.B., B.P.), Los Cedros E3:T1, T2, (R.B., B.P.), García Moreno, 10 Km W Santa Rosa (QCAZ). MANABÍ: Chone (Fairchild & León 1986). PICHINCHA: Quito (Fairchild & León 1986).

*Dasychela (Dasychela) peruviana* (Bigot 1892)

IMBABURA: Peñaherrera (Fairchild & León 1986). PICHINCHA: Mindo (Nambillo) (QCAZ); Mindo (C-JB). TUNGURAGUA: Baños (Fairchild & León 1986).

*Dasychela (Triceratomyia) macintyreai* (Bequaert 1937)

NAPO: Latas (Misahualli), Misahualli (QCAZ); Río Napo – Jatun Yacu (MCZ in

Fairchild & Burger 1994), Río Umbuni (C-JB); Bloque 16 Yasuní (MEPN). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ). PASTAZA: Villano (QCAZ).

*Eristalotabanus violaceus* Kröber 1931

AZUAY: Maylas (C-JB), Pucay-W Cordillere (ZMUH in Chainey 1986). BOLIVAR: Arrayán, carretera Salinas a Arrayán (Burger 1999). CAÑAR: Río Yanacachi (C-JB). LOJA: (Loja locality?) (QCAZ); Cord. Sabanilla (C-JB). MORONA SANTIAGO: San Vicente (Límite Azuay prov.), Potrerillo (C-JB). PICHINCHA: Yanacocha-Reserva (Pastizal arbolado y BMA) (QCAZ); Hda (Eco) Bomboli (C-JB). TUNGURAHUA: Patate (QCAZ); Runtún (C-JB); Baños (BMNH in Chainey 1986).

*Dicladocera argenteomaculata* Wilkerson 1979

CHIMBORAZO: Río Sacramento (C-JB). IMBABURA: Los Cedros (EC) (R.B., B.P.), Los Cedros E1:T, T1, T2 (R.B., B.P.) (QCAZ). PICHINCHA: Cabecera Río Pachijal (7.3 Km S Nanegalito), Mindo (QCAZ).

*Dicladocera basirufa* (Walker 1850)

LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Arenillas (C-JB).

*Dicladocera bellicosa* (Brèthes 1910)

AZUAY: Guarumales (Guarumales-Paute) (QCAZ) (C-JB).

*Dicladocera clara* (Schiner 1868)

CHIMBORAZO: Río Sacramento (C-JB). COTOPAXI: San Fco. de las Pampas (QCAZ); El Tingo (C-JB). IMBABURA: Los Cedros E1:T1, T2 (R.B., B.P.) (QCAZ). MORONA SANTIAGO: Tinajillas (QCAZ), Arenillas (C-JB).

*Dicladocera distomacula* Wilkerson 1979

LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas (C-JB). TUNGURAHUA: Runtún (C-JB).

*Dicladocera exilicorne* Fairchild 1958

COTOPAXI: B. I. Otonga (El Corcovado) (C-JB). IMBABURA: Machetes (Fairchild 1958, MCZ in Fairchild & Burger 1994). PICHINCHA: Palmeras (QCAZ); Cordero (C-JB).

*Dicladocera hirsuta* Wilkerson 1979

AZUAY: Maylas (C-JB). MORONA SANTIAGO: Loja (QCAZ); Potrerillo, San Vicente (C-JB).

*Dicladocera macula* (Macquart 1846)

AZUAY: Maylas, Río Zaracay (C-JB). BOLIVAR: Totoras (QCAZ); Santiago, Cerro Pumín (C-JB). CARCHI: San Gabriel (Surcouf 1919). COTOPAXI: Pilaló (C-JB). IMBABURA: Los Cedros E3:T1 (R.B., B.P.) (QCAZ). LOJA: Saraguro (QCAZ); Cord. Sabanilla (C-JB); PN Podocarpus (Cajanuma) (MEPN). MORONA SANTIAGO: Arenillas, Potrerillo, San Vicente (Límite Azuay prov.), Tinajillas (C-JB). NAPO: Papallacta (QCAZ); La Alegría (C-JB). PICHINCHA: Nanegalito, Yanacocha-Reserva (300m Sur del PC) (QCAZ); Nono, Quito (C-JB); Paschoa (QCAZ) (C-JB); Hda (Eco) Bomboli (C-JB). SUCUMBÍOS: Vía La Bonita - La

Fama (QCAZ). TUNGURAHUA: Runtún (C-JB).

*Dicladocera minos* (Schiner 1868)

TUNGURAHUA: Baños (Fairchild & León 1986).

*Dicladocera ?neosubmacula* Kröber 1931

See discussion of its status in Fairchild & Burger (1994). CAÑAR: *in* Kröber (1931a). GUAYAS: Bucay (Kröber 1931a). PICHINCHA: Río del Cinto (Mindo) (Kröber 1931a).

*Dicladocera nigrocoerulea* (Rondani 1850)

COTOPAXI: La Esperanza (C-JB). LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas, Potrerillo (C-JB). TUNGURAHUA: Runtún (C-JB).

*Dicladocera ornatipenne* (Kröber 1931)

From “Ecuador” in Kröber (1931b) (MTD); LOJA: *in* Fairchild & Burger (1994).

*Dicladocera pruinosa* Wilkerson 1979

IMBABURA: Los Cedros E2:T, T1 (R.B., B.P.), Los Cedros E3:T2, T3 (R.B., B.P.) (QCAZ). LOJA: San Vicente, Card. Sabanilla (C-BJ). MORONA SANTIAGO: Tinajillas (QCAZ); Arenillas (C-JB). NAPO: Cocodrilo (C-JB).

*Dicladocera riveti* (Surcouf 1919)

PICHINCHA: Mindo (QCAZ); “Faldas del Volcán Corazón-Oeste” (Surcouf 1919). SANTO DOMINGO: Santo Domingo (Surcouf 1919). GUAYAS: “Chemin entre Guanasilla et San Nicolás” (MNHN *in* Surcouf 1919).

*Dicladocera tribonophora* Fairchild 1958

“Río Blanco-Oriente” (TUNGURAHUA?, MCZ *in* Fairchild 1958).

CHIMBORAZO: Río Sacramento (QCAZ) (C-JB). IMBABURA: Nangulví (FSCA *in* Fairchild 1958). PICHINCHA: Bellavista (Reserva Biológica, Ecológica-Est. Científica) (QCAZ).

*Stibasoma (Stibasoma) flaviventre* (Macquart 1848)

ESMERALDAS: Kumanii Lodge T2 (QCAZ).

*Stibasoma (Stibasoma) fulvohirtum* (Wiedemann 1828)

SUCUMBÍOS: “Limoncocha” (AUEM *in* Patrick & Hays 1968).

*Stibasoma (Stibasoma) panamensis* Curran 1934

From “Honduras to Ecuador” in Burger & Fairchild (1994). ESMERALDAS: Quinindé (QCAZ).

*Stibasoma (Rhabdotylus) venenata* (Osten Sacken 1886)

BOLIVAR: Río Cristal (Balzapamba), Km 7 Vía Bucay - Chillanes (C-JB). EL ORO: Río Calera (C-JB). NAPO: Río Hollín (QCAZ). PICHINCHA: Palmeras, Puerto Quito, Km Vía Nanegalito R. Maquip., Nanegalito, Maquipucuna, Río Umachaca, Aloag-Sto. Domingo Km 40 (QCAZ); Río Cambugán (MEPN); Mindo (QCAZ) (MEPN).

*Cryptotylus unicolor* (Wiedemann 1828)

ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE), Est. Chiruisla T (QCAZ).  
SUCUMBÍOS: Limoncocha (AUEM in Patrick & Hays 1968).

*Philipotabanus (Philipotabanus) magnificus* (Kröber 1934)

BOLIVAR: Balzapamba, Km 7 Vía Bucay - Chillanes (C-JB). CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (QCAZ); Joyapal (Joyapal - Cochancay), Chilcales (Río Chilcales, M. J. Calles) (C-JB). ESMERALDAS: Kumanii Lodge T1, T2, T3, E.C. Río Canandé (Reserva - Jocotoco), E.C. Río Canandé T, T3 (Reserva - Jocotoco), Caimito (estero salado mangle) (QCAZ); Playa de Oro (Río Santiago) (C-JB); Alto Cayapa (Fairchild & León 1986). GUAYAS: Balao Chico, Hda. San Joaquín (San Joaquín) (C-JB); Guayaquil (Fairchild & León 1986). IMBABURA: 10 Km W Santa Rosa (QCAZ). LOJA: Loja, Vía Catamayo (QCAZ). MANABÍ: Río Mache (C-JB). PICHINCHA: Chiriboga (QCAZ). PICHINCHA?: “Pucay-Santo Domingo” (Holotype lost in Fairchild & Burger 1994). SANTO DOMINGO: La Unión del Toachi, Otongachi (QCAZ); Santo Domingo (Fairchild & León 1986). SUCUMBÍOS: “Limoncocha” (AUEM in Patrick & Hays 1968).

*Philipotabanus (Philipotabanus) nigrinubilus* (Fairchild 1953)

CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (C-JB). ESMERALDAS: E.C. Río Canandé (Reserva - Jocotoco) (QCAZ); Playa de Oro (Río Santiago) (C-JB).

*Philipotabanus (Philipotabanus) pallidetinctus* (Kröber 1930)

“Ecuador as locality datum” in Fairchild & Burger (1994).

*Philipotabanus (Philipotabanus) pterographicus* (Fairchild 1943)

CHIMBORAZO: Río Sacramento (C-JB). GUAYAS: Hda. San Joaquín (San Joaquín) (QCAZ).

*Philipotabanus (Philipotabanus) tenuifasciatus* (Kröber 1930)

MORONA SANTIAGO: Puerto Yuquianza, Río Pau Grande (Tarapoa) (C-JB). NAPO: Misahuallí, Aliñahui (cabañas) (QCAZ); Jatún Sacha, Río Umbuni (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ). “East of Ecuador as locality datum” in Fairchild & Burger (1994) and Henriques (2006). C-JB specimens as *P. nigrinubilus* in Cárdenas & Vieira (2005). PASTAZA: Villano, Villano (Tarangaro) (QCAZ).

*Philipotabanus (Mimotabanus) opimus* Fairchild 1975

BOLIVAR: Balzapamba (Fairchild 1975a).

\**Philipotabanus (Mimotabanus) porteri* Fairchild 1975

ECUADOR, ESMERALDAS, Kumanii Lodge: 59m., 00°45'23"N 78°55'01,4"W, 14.IV.2006, 15.IV.2006, R. Cárdenas Leg., 2♂, R. Cárdenas Det. (III.2007), QCAZI35819, QCAZI35815; 38m., 00°45'19,8"N 78°55'06"W, 14.IV.2006, R. Cárdenas Leg., 2♂, R. Cárdenas Det. (III.2007), QCAZI35814, QCAZI35816; 41m., 00°45'14"N 78°55'15"W, 14.IV.2006, R. Cárdenas Leg., 1♂, R. Cárdenas Det. (III.2007), QCAZI35817; 69m., 00°45'21,9"N 78°54'59,4"W, 14.IV.2006, R. Cárdenas Leg., 1♂, R. Cárdenas Det. (III.2007), QCAZI35818. All specimens deposited at QCAZ Museum of Zoology.

*Philipotabanus (Melasmatabanus) criton* (Kröber 1934)  
From “e. Ecuador” in Fairchild & Burger (1994)

*Philipotabanus (Melasmatabanus) fascipennis* ssp. *ecuadoriensis* (Kröber 1930)  
AZUAY: Cordillera-Pucay (Holotype lost? MLUH in Fairchild & Burger 1994).  
BOLIVAR: Balzapamba (MZPW in Fairchild 1975b). EL ORO: Zaruma-Machala  
(L. L. Pechuman collection, *in* CUIC?, Fairchild 1975b). PICHINCHA: Mindo  
(QCAZ). SANTO DOMINGO: Otongachi, Unión del Toachi (QCAZ).

*Philipotabanus (Melasmatabanus) nigripennis* Wilkerson 1979  
From “Ecuador” and “Ecuador e. of Andes” as locality data in Wilkerson (1979)  
and Fairchild & Burger (1994) respectively.

*Stypommisa anoriensis* Fairchild & Wilkerson 1986  
ZAMORA CHINCHIPE: Río Bombuscara (C-JB).

*Stypommisa captiroptera* (Kröber 1930)  
ESMERALDAS: Kumanii Lodge (QCAZ). MANABÍ: Río Mache (C-JB). NAPO:  
Río Umbuni (C-JB); Río Hollín (QCAZ). PASTAZA: Shell-Mera (C-JB).  
PICHINCHA: Quito (Fairchild & Wilkerson 1986). SUCUMBÍOS: “Limoncocha”  
(AUEM *in* Patrick & Hays 1968).

*Stypommisa changena* Fairchild 1986  
CARACHI: Cabecera del Río Baboso (C-JB). PICHINCHA: Mindo (C-JB).

*Stypommisa flavescens* (Kröber 1930)  
AZUAY: Guarumales (Guarumales-Paute) (C-JB). PASTAZA: 17.2 Km SE Puyo  
(Fairchild & Wilkerson 1986). PICHINCHA: Sta. Inéz (MZPW *in* Fairchild  
1975b). ZAMORA CHINCHIPE: 12 Km S Zamora (Fairchild & Wilkerson 1986).

*Stypommisa glandicolor* (Lutz 1912)  
CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (C-JB).

*Stypommisa hypographa* (Kröber 1930)  
TUNGURAHUA: El Topo (C-JB). NAPO: Río Umbuni, Km 6 Vía Narupa - Coca  
(C-JB).

*Stypommisa hypographa* ssp. *neofurva* Philip 1969  
From “Ecuador, no further data (L. Leon)” in Fairchild & Wilkerson (1986).

*Stypommisa maruccii* (Fairchild 1947)  
From “Nicaragua to Ecuador” in Fairchild & Wilkerson (1986) and confirmed by  
Fairchild & Burger (1994).

*Stypommisa modica* (Hine 1920)  
MORONA SANTIAGO: Unión Río Upano-Paute, Río Pau Grande (Tarapoa),  
Yunkumas-Centro Shua (C-JB). NAPO: Río Hollín (QCAZ); Río Umbuni (C-JB).  
ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ) PASTAZA: Río  
Liquino (QCAZ). SANTO DOMINGO: E. C. Río Guajalito (QCAZ).  
SUCUMBÍOS: “Santa Cecilia” (AUEM *in* Patrick & Hays 1968).

*Stypommisa pequeniensis* (Fairchild 1942)

ESMERALDAS: Playa de Oro (Río Santiago) (C-JB). GUAYAS: Hda. San Joaquín (San Joaquín) (C-JB). MORANA SANTIAGO: Puerto Yuquianza, Río Yananas (C-JB). NAPO: Latas (Misahualli), Misahualli (QCAZ); Río Umbuni, Jatún Sacha, Km 6 Vía Narupa - Coca, Cocodrilo (C-JB). ORELLANA: Est. Exp. Napo (C-JB). PASTAZA: Villano (Tarangaro) (QCAZ); Shell-Mera (C-JB). SUCUMBÍOS: “Santa Cecilia” (AUEM in Patrick & Hays 1968).

*Stypommisa venosa* (Bigot 1892)

CAÑAR: Javín (C-JB). CHIMBORAZO: Río Sacramento (QCAZ)(C-JB). COTOPAXI: San Fco. de las Pampas (C-JB). NAPO: Río Hollín (C-JB). PASTAZA: Shell-Mera (C-JB). PICHINCHA: Quito, Palmeras (C-JB). TUNGURAHUA: Patate (C-JB).

*Leucotabanus albovarius* (Walker 1854)

NAPO: Latas (Misahualli) (QCAZ); Río Umbuni (C-JB). ORELLANA: E. C. Yasuní (QCAZ) ; Est. Exp. Napo (C-JB); E. C. Tiputini USFQ (TBS) (MEPN).

*Leucotabanus cornelianus* Fairchild 1985

SANTO DOMINGO: “Río Mulaute 15 Km NE Sto. Domingo” (CUIC in Fairchild 1985).

*Leucotabanus exaestuans* (L. 1758)

ESMERALDAS: Mayronga (La), Kumanii Lodge (QCAZ). GUAYAS: Hda. Santa Rita (Balao), Hda. San Joaquín (San Joaquín) (C-JB). LOS RÍOS: EBFD Jauneche (C-JB). MANABÍ: Pedernales (QCAZ); Río Mache (C-JB). MORANA SANTIAGO: Puerto Yuquianza (C-JB). NAPO: Aliñahui (cabañas) (QCAZ); Río Umbuni, Misahualli (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ), Coca (QCAZ) (C-JB); Est. Exp. Napo (C-JB); E. C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Villano (QCAZ). SUCUMBÍOS: El Eno (QCAZ); Limoncocha, Santa Cecilia (AUEM in Patrick & Hays 1968).

*Leucotabanus weyrauchi* Fairchild 1951

MORANA SANTIAGO: Río Yananás (C-JB). NAPO: Misahualli (C-JB). ZAMORA CHINCHIPE: Río Bombuscara (C-JB); Zamora (MCZ in Fairchild & Burger 1994).

*Lepiselaga (Lepiselaga) crassipes* (Fabricius 1805)

GUAYAS: Nobol (QCAZ) (C-JB); Hda. Santa Rita (Balao), San Carlos, Cerecita (C-JB). LOS RÍOS: EBFD- Jauneche (C-JB). ORELLANA: Primavera (La) (QCAZ); Est. Exp. Napo (C-JB). SUCUMBÍOS: Limoncocha (AUEM in Patrick & Hays 1968).

### Tribe Tabanini

*Poeciloderas quadripunctatus* (Fabricius 1805)

AZUAY: Huasipamba (Guasipamba) (C-JB). BOLIVAR: Río Cristal (Balzapamba) (C-JB). CHIMBORAZO: Río Sacramento (C-JB). ESMERALDAS: Mayronga (La) (QCAZ). GUAYAS: Hda. San Joaquín (San Joaquín) (C-JB). LOJA: Loja locality? (QCAZ); San Vicente (C-JB). MORANA SANTIAGO: Puerto Yuquianza (C-JB). NAPO: Río Hollín, Aliñahui (cabañas) (QCAZ); Río Umbuni, Km 6 Vía

Narupa - Coca (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ), Est. Exp. Napo (C-JB); E. C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Shell-Mera (C-JB). SUCUMBÍOS: "Santa Cecilia" (AUEM in Patrick & Hays 1968). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Río Bombuscara, Río Valladolid (C-JB).

*Phorcotabanus cinereus* (Wiedemann 1821)  
From "Ecuador" as locality datum in Fairchild & Burger (1994).

*Tabanus albocirculus* Hine 1907  
ESMERALDAS: Kumanii Lodge (QCAZ); Playa de Oro (Río Santiago) (C-JB). GUAYAS: Balao Chico (QCAZ); Hda. Santa Rita (Balao), Hda. La María-25 Km N Guayaquil (C-JB). LOS RÍOS: EBFD Jauneche, Hda. Clementina (C-JB).

*Tabanus aniptus* Fairchild 1976  
From "Ecuador" as locality datum in Wilkerson (1979).

*Tabanus antarcticus* L. 1758  
GUAYAS: Reserva Churute (C-JB).

*Tabanus argentivittatus* Fairchild 1976  
NAPO: Archidona, Jatún Sacha, Río Umbuni (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE), Est. Chiruisla T (QCAZ). PASTAZA: Diez de Agosto (C-JB).

*Tabanus cicur* Fairchild 1942  
NAPO: Latas (Misahualli) (QCAZ); Río Umbuni (C-JB). ORELLANA: Est. Exp. Napo (C-JB). PASTAZA: Shell-Mera (C-JB).

*Tabanus claripennis* (Bigot 1892)  
PICHINCHA: Santa Inez (Fairchild 1942).

*Tabanus colombensis* Macquart 1846  
CAÑAR: Cochancay (El chorro; El Chorro, Cochancay), La Troncal (C-JB). CHIMBORAZO: Buenos Aires, Río Sacramento (C-JB). GUAYAS: Balao Chico, Hda. Santa Rita (Balao), Hda. La María-25 Km N Guayaquil, Milagro, Nobol, Hda. San Joaquín (San Joaquín) (C-JB). LOJA: Quebrada Chipiango, Río Catamayo (C-JB). LOS RÍOS: Hda. Clementina, Pichilingue (C-JB). MANABÍ: Julcuy (C-JB). NAPO: Río Umbuni (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (C-JB). PASTAZA: Shell-Mera (C-JB). SANTA ELENA: 2.6 Km de "Dos Mangas" (C-JB). SANTO DOMINGO: Santo Domingo (C-JB).

*Tabanus cyclopus* Philip 1961  
GUAYAS: "20 mi West of Guayaquil" (CAS in Philip 1961).

*Tabanus discifer* Walker 1850  
ORELLANA: Est. Chiruisla T, Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ); Nuevo Rocafuerte (Fairchild & León 1986). PASTAZA: Lorocachi (QCAZ). PASTAZA: Villano (QCAZ). SUCUMBÍOS: "Limoncocha" (AUEM in Patrick & Hays 1968).

*Tabanus discus* Wiedemann 1828

ORELLANA: Est. Exp. Napo (C-JB).

*Tabanus eldridgei* Fairchild 1973

ESMERALDAS: Esmeraldas (Fairchild 1973).

*Tabanus guyanensis* Macquart 1846

ORELLANA: Est. Exp. Napo (C-JB); “Nuevo Rocafuerte” (Fairchild & León 1986). SUCUMBÍOS: “Limoncocha” (AUEM in Patrick & Hays 1968 and Fairchild 1984).

*Tabanus hirtitibia* Walker 1850

MORONA SANTIAGO: Río Yananás, Río Pau Grande (Tarapoa), Puerto Yuquianza (C-JB). NAPO: Cascada San Rafael, Cercanías Río Aguarico, Misahualli, Latas (Misahualli) (QCAZ), Río Umbuni, Jatún Sacha, Cocodrilo, Km 6 Vía Narupa - Coca (C-JB). ORELLANA: Coca, Pozo Ishpingo (QCAZ). PASTAZA: Puyo, Villano (Tarangaro) (QCAZ); Santa Clara, Shell-Mera (C-JB). SUCUMBÍOS: “Limoncocha” (AUEM in Patrick & Hays 1968). Shushufindi (QCAZ). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Río Bombuscara, Río Valladolid (C-JB).

*Tabanus importunus* Wiedemann 1828

From “Panama to Brazil” in Fairchild & Burger (1994).

*Tabanus macquarti* Schiner 1868

MORONA SANTIAGO: Río Yananás, Puerto Yuquianza (C-JB). NAPO: Misahualli (QCAZ); Río Umbuni, Jatún Sacha (C-JB). ORELLANA: Est. Exp. Napo (C-JB). PASTAZA: Santa Clara, Shell-Mera (C-JB). SUCUMBÍOS: “Limoncocha” (AUEM in Patrick & Hays 1968). ZAMORA CHINCHIPE: Río Bombuscara (C-JB).

*Tabanus nereus* Fairchild 1943

GUAYAS: Guayaquil (Fairchild 1973); “Ecuador in coastal mangrove habitats” (Fairchild 1983).

*Tabanus occidentalis* L. 1758

BOLIVAR: Río Cristal (Balzapamba) (C-JB). CHMBORAZO: Río Sacramento (C-JB). EL ORO: Buenos Aires, Los Rosales de Machay (C-JB). ESMERALDAS: Playa de Oro (Río Santiago). GUAYAS: Daule, La Toma, Guayaquil, Guayaquil (Cerro Blanco), Hda. San Joaquín (San Joaquín). LOJA: Quebrada Chipiango, San Vicente (C-JB). LOS RÍOS: EBFD Jauneche (C-JB). MANABÍ: Río Mache (C-JB). MORONA SANTIAGO: Indanza, Río Pau Grande (Tarapoa), Puerto Yuquianza. NAPO: Archidona, Jatun Sacha, Km. 6 Vía Narupa-Coca, Río Umbuni (C-JB). ORELLANA: Coca, Est. Exp. Napo (C-JB); E. C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Costa Azul, Santa Clara, Shell-Mera (C-JB). PICHINCHA: Mindo (C-JB). SUCUMBÍOS: “Limoncocha” (AUEM in Patrick & Hays 1968). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Río Valladolid (C-JB).

*Tabanus occidentalis* var. *dorsovittatus* Macquart 1855

CARCHI: Maldonado (QCAZ). NAPO: Río Hollín (QCAZ). ORELLANA: Coca,

Yasuní (SC - Res. Sta. - EC - PUCE), Taracoa (QCAZ). PASTAZA: Lorocachi, Villano (QCAZ). PICHINCHA: Puerto Quito (QCAZ). SANTO DOMINGO: Santo Domingo (QCAZ). SUCUMBÍOS: Tarapoa (QCAZ).

*Tabanus occidentalis* var. *modestus* Wiedemann 1828

BOLIVAR: Río Cristal (Balzapamba) (C-JB). CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (C-JB). CHIMBORAZO: Río Sacramento (C-JB). COTOPAXI: San Fco. de las Pampas (QCAZ). ESMERALDAS: Kumanii Lodge (QCAZ); Playa de Oro (Río Santiago) (C-JB). GUAYAS: Hda. San Joaquín (San Joaquín) (C-JB). LOJA: Virgen del Cisne, Quebrada Chipiango (C-JB). MORONA SANTIAGO: Río Pau Grande (Tarapoa), Puerto Yuquianza (C-JB). NAPO: Río Umbuni (C-JB). ORELLANA: Taracoa, Est. Chiruisla T, Vía Coca - Loreto Km 26, Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ); Est. Exp. Napo (C-JB). PASTAZA: Villano (Tarangaro, Kurintza) (QCAZ); Santa Clara, Shell-Mera, Diez de Agosto (C-JB). SANTO DOMINGO: Unión del Toachi (QCAZ); Tandapi (Manuel Cornejo Astorga), Mindo (C-JB). SUCUMBÍOS: R. P. F. Cuyabeno (QCAZ).

*Tabanus pachypalpus* (Bigot 1892)

PICHINCHA: Mindo (Fairchild & León 1986). ZAMORA CHINCHIPE: Zamora (Fairchild & León 1986).

*Tabanus pellucidus* Fabricius 1805

ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (C-JB). PASTAZA: Puyo (C-JB). SUCUMBÍOS: R. P. F. Cuyabeno, Limoncocha (C-JB).

*Tabanus perplexus* Walker 1850

IMBABURA: Azabí (Intag), Nangulví (Fairchild & León 1986). ORELLANA: Nuevo Rocafuerte (Fairchild & León 1986).

*Tabanus peruvianus* Macquart 1848

IMBABURA: Nangulví, “Cord. Intag” (Fairchild & León 1986). PICHINCHA: Quito (BMNH in Macquart 1848).

*Tabanus piceiventris* Rondani 1848

NAPO: Aliñahui (cabañas), (QCAZ); Río Umbuni (C-JB). ORELLANA: Est. Chiruisla T, Yasuní (SC - Res. Sta. - EC - PUCE), PNY Yasuní Bloque 31 Pozo petrolero PSCA 2, Río Yasuní Línea 10 y Sub base Bloque 31, Coca-Primavera (QCAZ); Coca (C-JB). PASTAZA: Villano (Tarangaro, Kurintza) (QCAZ). SUCUMBÍOS: R. P. F. Cuyabeno (QCAZ) (C-JB); Limoncocha, Tarapoa (C-JB).

*Tabanus platycerus* Fairchild 1976

NAPO: Río Umbuni, Misahualli (C-JB). ORELLANA: Est. Chiruisla T (QCAZ); E. C. Tiputini USFQ (TBS) (MEPN). PASTAZA: Santa Clara, Shell-Mera (C-JB).

*Tabanus pseudoculus* Fairchild 1942

MORONA SANTIAGO: Unión Río Upano-Paute, Puerto Yuquianza, Río Pau Grande (Tarapoa) (C-JB). NAPO: Río Umbuni, Jatún Sacha (C-JB). ORELLANA: Yasuní (SC - Res. Sta. - EC - PUCE) (QCAZ)

*Tabanus pungens* Wiedemann 1828

AZUAY: Yunguilla (QCAZ). CAÑAR: Cochancay (El chorro; El Chorro, Cochancay), La Troncal (C-JB). CHIMBORAZO: Buenos Aires, Río Sacramento (C-JB). ESMERALDAS: Quinindé (QCAZ) (C-JB). GUAYAS: Guayaquil (QCAZ) (C-JB); Balao Chico, Cerecita, Guayaquil (Cerro Azul), Hda. Santa Rita (Balao), Hda. La María 25 Km N Guayaquil, Milagro, Nobol, Samborondón, San Carlos, San Eduardo (Guayaquil - El Salado), Hda. San Joaquín (San Joaquín), Santa Lucía (C-JB). IMBABURA: "Nangulví-Cord. Intag" (Fairchild & León 1986). LOJA: San Vicente (C-JB). LOS RÍOS: Hda. Clemencita, Mt. Pichincha, Pichilingue (C-JB). MANABÍ: Julcuy, Río Mache (C-JB). NAPO: Río Umbuni (C-JB). PASTAZA: Shell-Mera (C-JB). SANTA ELENA: 2.6 Km de "Dos Mangas", Colonche (C-JB).

*Tabanus restrepoensis* Fairchild 1942

NAPO: Río Umbuni, Jatún Sacha (C-JB).

*Tabanus rixator* Fairchild 1943

ESMERALDAS: Esmeraldas, Limones (Fairchild & León 1986)

*Tabanus rubiginipennis* Macquart 1846

LOJA: Cord. Sabanilla (C-JB). MORONA SANTIAGO: Arenillas, Potrerillo (C-JB). NAPO: Km 6 Vía Narupa - Coca, Cocodrilo (C-JB). PASTAZA: Shell-Mera (C-JB). TUNGURAHUA: El Topo, Runtún (C-JB).

*Tabanus rubripes* Macquart 1838

From "Panama to Paraguay" in Fairchild & Burger (1994).

*Tabanus sannio* Fairchild 1956

SUCUMBÍOS: "Santa Cecilia" (AUEM in Patrick & Hays 1968), Shushufindi (C-JB).

*Tabanus secundus* Walker 1848

CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (C-JB). GUAYAS: Hda. San Joaquín (San Joaquín) (C-JB). LOS RÍOS: EBFD Jauneche (C-JB). LOJA: Virgen del Cisne (C-JB). MORONA SANTIAGO: Indanza, Río Yananás, Puerto Yuquianza (C-JB). NAPO: Río Umbuni, Km 6 Vía Narupa - Coca, Cocodrilo (C-JB). ORELLANA: Est. Chiruisla T (QCAZ); Est. Exp. Napo (C-JB). PASTAZA: Shell (QCAZ); Diez de Agosto, Puyo, Nuevo Mundo, Santa Clara (C-JB). PICHINCHA: Mindo (C-JB). TUNGURAHUA: El Topo (C-JB). ZAMORA CHINCHIPE: Río Valladolid (C-JB).

*Tabanus sorbillans* Wiedemann 1828

ORELLANA: Est. Chiruisla T3 (QCAZ); Est. Exp. Napo, Yasuní (SC - Res. Sta. - EC - PUCE) (C-JB). SUCUMBÍOS: "Limoncocha" (AUEM in Patrick & Hays 1968).

*Tabanus surifer* Fairchild 1964

ESMERALDAS: Playa de Oro (Río Santiago) (C-JB).

*Tabanus thiemeanus* (Enderlein 1925)

CAÑAR: Cochancay (El chorro; El Chorro, Cochancay) (QCAZ). IMBABURA:

Los Cedros (EC) (R.B., B.P.), Los Cedros E1:T, T1, T2 (R.B., B.P.), Los Cedros E2:T, T1, T2 (R.B., B.P.), Los Cedros E2-E3 (R.B., B.P.) (QCAZ). PASTAZA: Puyo (QCAZ). SUCUMBÍOS: “Limoncocha” (AUEM *in* Patrick & Hays 1968), R. P. F. Cuyabeno (QCAZ).

*Tabanus unimaculus* Kröber 1934

From “Ecuador” as locality datum in Fairchild & Burger (1994).

*Tabanus unistriatus* Hine 1906

ESMERALDAS: E.C. Río Canandé T, T1, T3 (Reserva - Jocotoco), Kumanii Lodge T, T1, T2 (QCAZ); Playa de Oro (Río Santiago) (C-JB). GUAYAS: Hda. San Joaquín (San Joaquín) (C-JB). MANABÍ: Río Mache (C-JB).

*Tabanus vittiger* Thomson 1869

GALÁPAGOS: “Galápagos Islands” (NHRS *in* Fairchild & Burger 1994), Santa Cruz-Playa (QCAZ) (C-JB), Isla San Cristóbal, Puerto Ayora (QCAZ).

*Tabanus xuthopogon* Fairchild 1984

NAPO: Río Umbuni, Misahualli (C-JB). ORELLANA: Est. Exp. Napo, Yasuní (SC - Res. Sta. - EC - PUCE) (C-JB). SUCUMBÍOS: “Alrededores de Limoncocha”, Limoncocha (Playaco river) (Fairchild 1984) and (MPEG) *in* Henriques & Gorayeb (1993).

## Appendix 5.

### Gazetteer of known localities of Ecuadorian specimens of Tabanidae.

Georeferenced error (mean  $\pm$  SD) =  $2.85 \pm 4.07$  Km. Datum: WGS84; coordinates system: decimal degrees.

Locality	Province	Altitude (m)	Longitude	Latitude	Error (Km)
10 Km W Santa Rosa	IMBABURA	700	-78.93194	0.33083	0
12 Km S Zamora	ZAMORA CHINCHIPE	1200	-78.94139	-4.14300	14.707
17,2 Km SE Puyo	PASTAZA	1000	-77.86400	-1.57900	19.807
2.6 Km de "Dos Mangas"	SANTA ELENA	60	-80.71556	-1.83333	5.78
6,6 Km N vía Limón - Macas	MORONA SANTIAGO	1013	-78.40701	-2.92665	9.636
8 Km W Lago Agrio	SUCUMBÍOS	311	-76.97900	0.08500	10.58
Abitagua	PASTAZA	1200	-78.17639	-1.44306	1.974
Aliñahui (cabañas)	NAPO	410	-77.60194	-1.04861	0
Alluriquín	SANTO DOMINGO	750	-78.99347	-0.32031	1.875
Aloag	PICHINCHA	2900	-78.58333	-0.45139	1.841
Alto Cayapa	ESMERALDAS	11	-78.95833	0.86667	2.215
Amaguaña	PICHINCHA	2620	-78.50389	-0.37278	4.167
Ambato	TUNGURAHUA	2540	-78.62250	-1.23667	8.369
Archidona	NAPO	600	-77.80683	-0.90627	3.624
Arenillas	MORONA SANTIAGO	2200	-78.61389	-3.01556	3.135
Arrayán, carretera Salinas a Arrayán	BOLIVAR	3600	-79.05889	-1.37194	1.977
Atuntaqui	IMBABURA	2500	-78.21402	0.33311	2.479
Ávila Viejo	ORELLANA	750	-77.43278	-0.63639	0
Azabí (Intag)	IMBABURA	2200	-78.46532	0.32986	1.581
Azogues (Azoguez)	CAÑAR	2520	-78.84500	-2.73667	1.612
B. I. Otonga (El Corcovado)	COTOPAXI	2000	-79.00020	-0.41673	2.68
Baeza	NAPO	1900	-77.88500	-0.46000	1.579
Balao Chico	GUAYAS	30	-79.69444	-2.73833	1.583
Balzapamba (Balzpambana)	BOLIVAR	750	-79.17600	-1.76600	1.874
Baños	TUNGURAHUA	1843	-78.42333	-1.39444	1.857
Bellavista (Reserva Biológica)	PICHINCHA	2200	-78.70833	-0.01278	0
Bellavista (Reserva Ecológica-Est. Científica)	PICHINCHA	2287	-78.68794	-0.01083	0
Bosque Puyango	LOJA	300	-80.07905	-3.88281	2.255
Boyayaco (Panyagacu)	NAPO	980	-77.81667	-0.80000	1.813
Bucay (1 Km NO Cumandá)	GUAYAS	300	-79.14100	-2.20200	1.648

Buenos Aires	CHIMBORAZO	300	-79.19528	-2.20361	2.689
Buenos Aires, 5 Km O de Cumandá	CHIMBORAZO	300	-79.19528	-2.20361	6.59
Cabecera del Río Baboso	CARCHI	1500	-78.38200	0.96100	10.069
Cabecera Río Pachijal (7,3 Km S Nanegalito)	PICHINCHA	2050	-78.68389	-0.00028	1.581
Caimito (estero salado mangle)	ESMERALDAS	5	-80.09722	0.70194	0
Caimito (ladera)	ESMERALDAS	50	-80.09278	0.69889	0
Calacalí	PICHINCHA	2800	-78.51111	0.00083	1.761
Calupiña	COTOPAXI	1500	-78.92583	-0.53833	1.588
Campanacocha	NAPO	350	-77.50167	-1.02500	4.674
Casitagua	PICHINCHA	3500	-78.47667	-0.03000	1.655
Catacocha	LOJA	1930	-79.64677	-4.04661	1.632
Cerecita	GUAYAS	20	-80.26694	-2.33000	1.606
Cerro Pumín	BOLIVAR	3400	-79.03556	-1.44028	2.346
Cerro Toledo	LOJA	3484	-79.10861	-4.40139	1.601
Chachimbiro	IMBABURA	1600	-78.08910	0.49465	0
Chilcales (Río Chilcales, M. J. Calles)	CAÑAR	680	-79.22333	-2.20667	1.824
Chiriboga	PICHINCHA	1900	-78.76500	-0.22833	1.898
Chone	MANABÍ	20	-80.09167	-0.69444	7.269
Coangos	MORONA SANTIAGO	670	-78.21406	-3.04337	2.507
Coca	ORELLANA	260	-76.98333	-0.46250	1.683
Cochancay (El chorro; El Chorro, Cochancay)	CAÑAR	500	-79.29444	-2.46389	1.735
Cocodrilo	NAPO	1700	-77.78944	-0.64583	1.746
Cola	LOJA	1320	-79.86957	-4.09771	1.62
Colonche	SANTA ELENA	8	-80.66750	-2.01750	2.326
Conocoto	PICHINCHA	2530	-78.47444	-0.29028	10.169
Cord. Sabanilla	LOJA	2700	-79.15000	-4.44889	1.774
Costa Azul	PASTAZA	490	-77.81021	-1.12151	1.753
Cuenca	AZUAY	2527	-79.00111	-2.89278	12.868
Cumbayá	PICHINCHA	2400	-78.42667	-0.19806	6.969
Cumbe	AZUAY	2700	-79.00889	-3.08361	1.874
Curaray (San Antonio de)	PASTAZA	310	-76.96667	-1.37361	30.469
Cuyabeno (Reserva de Producción Faunística)	SUCUMBÍOS	200	-76.18028	0.01806	4.818
Danas	CHIMBORAZO	3300	-78.88333	-2.13333	2.301
Daule	GUAYAS	20	-79.97722	-1.85722	4.216
Dayuma	ORELLANA	260	-76.87910	-0.66658	1.616
Diez de Agosto	PASTAZA	1000	-77.90341	-1.45410	2.003
E. C. Río Guajalito	SANTO DOMINGO	1800	-78.81670	-0.23330	2.18

E. C. Tiputini USFQ (TBS)	ORELLANA	240	-76.14944	-0.63639	1.739
E. Santo Domingo	SANTO DOMINGO	600	-79.16222	-0.25333	1.681
E.C. Río Canandé (Reserva - Jocotoco)	ESMERALDAS	389	-79.20111	0.48472	0
E.C. Río Canandé T (Reserva - Jocotoco)	ESMERALDAS	400	-79.19694	0.47917	0
E.C. Río Canandé T1 (Reserva - Jocotoco)	ESMERALDAS	400	-79.19833	0.47833	0
E.C. Río Canandé T3 (Reserva - Jocotoco)	ESMERALDAS	400	-79.19750	0.47889	0
EBFD Jauneche	LOS RIOS	50	-79.58333	-1.58333	2.967
El Empalme	GUAYAS	60	-79.61667	-1.05000	2.075
El Eno	SUCUMBIOS	293	-76.87846	-0.06635	0.64
El Pangui	ZAMORA CHINCHIPE	800	-78.58651	-3.62449	1.817
El Reventador	SUCUMBÍOS	1700	-77.55000	-0.03333	2.904
El Salado	NAPO	1280	-77.68846	-0.20097	1.862
El Salado	GUAYAS	6	-79.90556	-2.21722	2.535
El Tingo	PICHINCHA	2600	-78.43426	-0.28276	1.882
El Tingo	COTOPAXI	1400	-79.05659	-0.91474	1.595
El Topo	TUNGURAHUA	1245	-78.19444	-1.40833	1.909
Est. Chiruisla T	ORELLANA	204	-75.94083	-0.68583	0
Est. Chiruisla T1	ORELLANA	204	-75.94167	-0.68583	0
Est. Chiruisla T2	ORELLANA	204	-75.94208	-0.68528	0
Est. Chiruisla T3	ORELLANA	204	-75.94250	-0.68500	0
Est. Exp. Napo	ORELLANA	250	-77.02167	-0.43083	3.408
Est. Río Huiririmá	ORELLANA	220	-75.78400	-0.06610	5.214
García Moreno	IMBABURA	1420	-78.62624	0.23415	1.671
Guaranda	BOLIVAR	3670	-79.00000	-1.59056	1.661
Guarumales (Guarumales-Paute)	AZUAY	1860	-78.52252	-2.61065	4.017
Guayaquil	GUAYAS	5	-79.89361	-2.19861	31.568
Guayaquil (Cerro Azul)	GUAYAS	230	-79.97528	-2.15611	3.993
Guayaquil (Cerro Blanco)	GUAYAS	240	-80.08333	-2.11667	3.735
Guayllabamba	PICHINCHA	2140	-78.34028	-0.05556	2.985
Hda (Eco) Bomboli	PICHINCHA	3000	-78.68167	-0.46361	0
Hda. Clementina	LOS RIOS	20	-79.38750	-1.71028	1.593
Hda. La Julia	LOS RIOS	9	-79.55166	-1.70334	1.642
Hda. San Joaquín (San Joaquín)	GUAYAS	290	-79.16667	-2.22222	1.632
Hda. Santa Rita (Balao)	GUAYAS	30	-79.81250	-2.90667	2.167
Huasipamba (Guasipamba)	AZUAY	2879	-79.32673	-3.19655	0
Ibarra	IMBABURA	2200	-78.12635	0.36035	9.269
Indanza	MORONA SANTIAGO	1220	-78.47397	-3.05550	1.874

Inga	PICHINCHA	2700	-78.33333	-0.30000	1.654
Jatún Sacha	NAPO	400	-77.61667	-1.06667	1.825
Javín	CAÑAR	1500	-79.17876	-2.46756	1.728
Jerusalén	PICHINCHA	2280	-78.35667	0.00056	0
Joya de los Sachas	NAPO	270	-76.85255	-0.29296	1.824
Joyapal (Joyapal - Cochancay)	CAÑAR	700	-79.19722	-2.45694	1.584
Julcuy	MANABÍ	300	-80.62406	-1.47559	2.669
Jumandi	NAPO	620	-77.79694	-0.88833	1.698
Kalaglas	MORONA SANTIAGO	1350	-78.53194	-3.24000	1.873
Km 6 Vía Narupa - Coca	NAPO	1300	-77.74100	-0.71800	1.619
Km 7 Vía Bucay - Chillanes	BOLIVAR	850	-79.12250	-2.13444	10.007
Km 9 Vía Bucay - Chillanes	BOLIVAR	300	-79.12250	-2.13444	12.002
Kumanii Lodge	ESMERALDAS	43	-78.92083	0.75389	0
Kumanii Lodge T	ESMERALDAS	38	-78.91833	0.75550	0
Kumanii Lodge T1	ESMERALDAS	59	-78.91706	0.75639	0
Kumanii Lodge T2	ESMERALDAS	69	-78.91650	0.75608	0
Kumanii Lodge T3	ESMERALDAS	95	-78.91389	0.75556	0
La Carbonería	CAÑAR	2850	-79.00299	-2.51707	1.836
La Fama	SUCUMBÍOS	2120	-77.48956	0.59914	0.5303
La Moya	BOLIVAR	3350	-79.03556	-1.46639	1.817
La Sabana (200m de Bachillero)	MANABÍ	4	-80.17111	-0.72222	0
La Selva (E. of Limoncocha)	NAPO	235	-76.37349	-0.49839	0
La Toma	GUAYAS	100	-79.97917	-1.99778	1.815
La Toma	LOJA	1360	-79.35000	-3.98278	1.66
La Troncal	CAÑAR	150	-79.33611	-2.42222	1.697
Lago Agrio	SUCUMBÍOS	300	-76.88778	0.09278	10.669
Latas (Misahualli)	NAPO	500	-77.73306	-1.03278	1.985
Limón Playas, Sta. Rosa	EL ORO	170	-79.93567	-3.57567	1.902
Limoncocha	SUCUMBÍOS	300	-76.61667	-0.40000	10.969
Limones	ESMERALDAS	15	-78.77167	1.12333	1.636
Lloa	PICHINCHA	3060	-78.5757	-0.24791	0
Logroño	MORONA SANTIAGO	625	-78.17833	-2.61500	1.644
Loja	LOJA	2060	-79.19861	-4.00000	10.567
Loja, Vía Catamayo	LOJA	2064	-79.19944	-3.99583	10.567
Lorocachi	PASTAZA	220	-75.96667	-1.61639	1.969
Los Cedros (EC) (R.B., B.P.)	IMBABURA	1350	-78.77938	0.30879	0
Los Cedros E1:T (R.B., B.P.)	IMBABURA	1180	-78.77750	0.30528	0
Los Cedros E1:T1 (R.B., B.P.)	IMBABURA	1180	-78.77722	0.30528	0
Los Cedros E1:T2 (R.B., B.P.)	IMBABURA	1180	-78.77694	0.30528	0

Los Cedros E2:T (R.B., B.P.)	IMBABURA	1680	-78.78111	0.32167	0
Los Cedros E2:T1 (R.B., B.P.)	IMBABURA	1680	-78.78111	0.32139	0
Los Cedros E2:T3 (R.B., B.P.)	IMBABURA	1680	-78.78111	0.32194	0
Los Cedros E3:T (R.B., B.P.)	IMBABURA	2180	-78.79194	0.33778	0
Los Cedros E3:T1 (R.B., B.P.)	IMBABURA	2180	-78.79194	0.33750	0
Los Cedros E3:T2 (R.B., B.P.)	IMBABURA	2180	-78.79194	0.33722	0
Los Cedros E3:T3 (R.B., B.P.)	IMBABURA	2180	-78.79194	0.33778	0
Los Cedros E2-E3 (R.B., B.P.)	IMBABURA	1920	-78.78676	0.32959	0
Lumbaqui	SUCUMBÍOS	480	-77.32939	0.04922	1.875
Machachi	PICHINCHA	2900	-78.57722	-0.50694	3.361
Machay	TUNGURAHUA	1650	-78.27982	-1.39622	1.913
Maldonado	CARCHI	1580	-78.10833	0.91083	2.091
Mamanuma	LOJA	2400	-79.20833	-3.88778	3.381
Mangahuanta (Mangaguanta)	PICHINCHA	2400	-78.36833	-0.16833	1.895
Manuel J. Calle	CAÑAR	50	-79.39522	-2.35322	1.874
Maquipucuna	PICHINCHA	1600	-78.62160	0.11531	2.378
Mayaico	MORONA SANTIAGO	1000	-78.61972	-3.98333	3.447
Maylas	AZUAY	3000	-78.68306	-2.98806	1.994
Mayronga (La)	ESMERALDAS	100	-79.21722	0.89083	2.162
Méndez	MORONA SANTIAGO	420	-78.31536	-2.71452	1.874
Mera	PASTAZA	1170	-78.11861	-1.45000	2.302
Miguir	AZUAY	3560	-79.30056	-2.79917	1.606
Milagro	GUAYAS	13	-79.58833	-2.13139	7.269
Mindo	PICHINCHA	1250	-78.77806	-0.05000	1.947
Mindo (Nambillo)	PICHINCHA	1880	-78.73833	-0.12500	7.469
Misahualli	NAPO	400	-77.66528	-1.04139	2.373
Montalvo	LOS RIOS	70	-79.28611	-1.78972	2.793
Moraspungo	PICHINCHA	2915	-78.51000	0.03167	1.814
Nanegal	PICHINCHA	1100	-78.67667	0.14333	1.769
Nanegalito	PICHINCHA	1630	-78.68056	0.06667	2.376
Nangulví	IMBABURA	1390	-78.54691	0.32789	0
Naranjal	GUAYAS	30	-79.60833	-2.67500	3.377
Nobol	GUAYAS	10	-80.00861	-1.90778	1.709
Nono	PICHINCHA	2700	-78.57421	-0.06114	1.875
Nueva Loja	SUCUMBÍOS	300	-76.88505	0.09143	6.2
Nuevo Mundo	PASTAZA	850	-77.90714	-1.58083	2.222
Nuevo Rocafuerte	ORELLANA	265	-75.40417	-0.92500	1.752
Otongachi	SANTO DOMINGO	960	-78.94800	-0.31667	1.994

Palanda	ZAMORA CHINCHIPE	1044	-79.13233	-4.64367	1.607
Palmar	MANABÍ	114	-79.95150	-0.03835	1.602
Palmeras	PICHINCHA	1000	-78.92861	-0.30833	1.653
Papallacta	NAPO	3300	-78.14648	-0.36516	2.061
Pasochoa	PICHINCHA	3350	-78.45861	-0.43083	1.875
Patate	TUNGURAHUA	2000	-78.50417	-1.30889	3.719
Patuca	MORONA SANTIAGO	720	-78.25998	-2.75302	1.874
Payamino	NAPO	270	-77.02800	-0.44700	1.886
Pedernales	MANABI	5	-80.05000	0.08306	2.247
Peñaherrera	IMBABURA	1750	-78.53139	0.35750	1.594
Peniel - Quevedo	LOS RÍOS	40	-79.45000	-1.10000	2.57
Pichilingue	LOS RIOS	73	-79.46028	-1.03167	2.33
Pifo	PICHINCHA	2550	-78.34444	-0.22250	3.447
Pilaló	COTOPAXI	2560	-78.99202	-0.94028	1.875
Playa de Oro (Río Santiago)	ESMERALDAS	70	-78.80000	0.88333	2.365
PN Podocarpus (Cajanuma)	LOJA	2450	-79.20000	-4.08333	1.856
Potrerillo	MORONA SANTIAGO	3230	-78.65444	-3.00333	2.318
Pozo Daimi	NAPO	250	-76.18600	-1.01400	1.61
Pozo Ishpingo	ORELLANA	240	-75.63639	-0.91639	5.14
Primavera (La)	ORELLANA	270	-76.76111	-0.41806	7.569
Pucay	AZUAY	2220	-79.25000	-3.20000	2.502
Puerto Ayora	GALÁPAGOS	30	-90.31286	-0.74313	2.67
Puerto Quito	PICHINCHA	180	-79.25242	0.12618	2.586
Puerto Yuquianza	MORONA SANTIAGO	920	-78.23028	-2.93944	1.756
Pululahua	PICHINCHA	2100	-78.51708	0.06685	1.692
Puyo (El)	PASTAZA	950	-77.99111	-1.48861	5.129
Quebrada Bodega Pamba	CHIMBORAZO	3200	-78.89861	-1.84944	2.232
Quebrada Chipiango	LOJA	750	-79.72972	-3.84750	1.968
Quevedo	LOS RIOS	54	-79.46167	-1.03167	6.769
Quinindé	ESMERALDAS	80	-79.46667	0.33306	3.655
Quito	PICHINCHA	2800	-78.50000	-0.16667	38.069
Quito (Carretas)	PICHINCHA	3680	-78.45167	-0.10333	3.292
Quito (El Batán)	PICHINCHA	2800	-78.46879	-0.16903	3.622
Quito (P. Metropolitano)	PICHINCHA	2960	-78.46417	-0.18376	3.392
R. B. Yanacocha	PICHINCHA	3521	-78.5847	-0.11155	0
R. P. F. Cuyabeno	SUCUMBÍOS	200	-76.18169	-0.00976	1.909
Reserva Churute	GUAYAS	7	-79.72000	-2.48000	6.433
Río Bombuscara	ZAMORA CHINCHIPE	980	-78.96056	-4.11361	1.799

Río Calera	EL ORO	300	-79.63100	-3.70300	1.601
Río Catamayo	LOJA	660	-79.87222	-4.18917	1.677
Río Cristal (Balzapamba)	BOLIVAR	810	-79.18778	-1.77333	2.208
Río del Cinto (Mindo)	PICHINCHA	1500	-78.80694	-0.10778	2.158
Río Hollín	NAPO	1100	-77.59040	-0.71502	2.079
Río Liquino	PASTAZA	475	-77.48444	-1.44222	0
Río Mache	MANABÍ	5	-79.88472	0.21500	1.654
Río Mulaute 15 Km NE Sto. Domingo	SANTO DOMINGO	480	-79.11600	-0.08200	1.59
Río Nangaritza	ZAMORA CHINCHIPE	950	-78.67389	-3.92944	1.877
Río Napo (not <i>Fidena laterina</i> )	NAPO	450	-77.80278	-1.05833	1.661
Río Negro	TUNGURAHUA	1300	-78.20722	-1.40278	1.777
Río Pangor	CHIMBORAZO	2085	-78.97900	-1.93333	1.824
Río Pau Grande (Tarapoa)	MORONA SANTIAGO	720	-78.23556	-2.83278	2.099
Río Pucuno	NAPO	1250	-77.61400	-0.67191	2.003
Río Sacramento	CHIMBORAZO	1150	-78.02800	-2.14600	1.696
Rio Tendales	AZUAY	880	-79.51018	-3.31285	0
Río Umachaca	PICHINCHA	1300	-78.62700	0.12600	1.629
Río Umbuni	NAPO	460	-77.73167	-1.03194	1.679
Río Valladolid	ZAMORA CHINCHIPE	1100	-79.12861	-4.62111	2.115
Río Yanacachi	CAÑAR	2700	-79.00750	-2.45444	1.626
Río Zaracay	AZUAY	2400	-79.40917	-2.72556	1.663
Riobamba	CHIMBORAZO	2796	-78.64583	-1.66667	10.369
Rumiñahui faldas volcán	COTOPAXI	1820	-78.52167	0.60500	0
Runtún	TUNGURAHUA	2270	-78.41600	-1.40700	2.55
Sacha Lodge	SUCUMBÍOS	230	-76.45938	-0.47081	2.319
Salinas	BOLIVAR	3500	-79.01611	-1.40222	1.874
Samborondón	GUAYAS	20	-79.72306	-1.95889	2.901
San Antonio (Volcán Pululahua)	PICHINCHA	2430	-78.44444	-0.00694	4.058
San Carlos	LOS RÍOS	60	-79.43333	-1.11667	2.612
San Eduardo (Guayaquil - El Salado)	GUAYAS	10	-79.89444	-2.19583	1.894
San Fco. de las Pampas	COTOPAXI	1500	-78.96806	-0.42333	1.875
San Francisco (Muisne)	ESMERALDAS	50	-80.06278	0.65583	1.875
San Gabriel	CARCHI	2842	-77.82798	0.58947	4.14
San Isidro	CARCHI	3050	-77.98691	0.60404	1.875
San Juan	PICHINCHA	2900	-78.62361	-0.28500	2.429
San Lorenzo	ESMERALDAS	5	-78.83522	1.28698	3.756
San Lorenzo (La Boca 16m)	ESMERALDAS	5	-78.83500	1.29139	3.756

San Luis de El Hacho	MORONA SANTIAGO	500	-78.30000	-2.74167	2.433
San Rafael	PICHINCHA	2500	-78.44194	-0.30583	1.649
Cascada San Rafael	NAPO	1500	-77.55833	-0.04556	2.32
San Vicente (Límite Azuay prov.)	MORONA SANTIAGO	2770	-78.58333	-3.03056	3.559
San Vicente	LOJA	1750	-79.44972	-3.94944	2.056
Santa Cecilia	SUCUMBÍOS	317	-76.95419	0.08539	1.692
Santa Clara	PASTAZA	500	-77.89167	-1.29722	2.2
Santa Cruz-Playa	GALÁPAGOS	0	-90.41639	-0.75611	1.157
Santa Elena	SANTA ELENA	10	-80.85611	-2.22167	5.64
Santa Lucía	GUAYAS	30	-79.98639	-1.71306	2.863
Santiago	BOLIVAR	2500	-78.99735	-1.69758	2.25
Santo Domingo (Sto. Domingo)	SANTO DOMINGO	600	-79.17269	-0.25441	6.455
Saraguro	LOJA	2520	-79.24333	-3.62167	2.163
Shell	PASTAZA	1000	-78.05670	-1.49805	2.949
Shell-Mera	PASTAZA	1000	-78.09214	-1.47791	2.863
Shushufindi	SUCUMBÍOS	260	-76.64650	-0.18278	4.248
Sta Rufina	LOJA	850	-79.75968	-3.84648	1.873
Tandapi (Manuel Cornejo Astorga)	PICHINCHA	1470	-78.79667	-0.41444	1.875
Taracoa	ORELLANA	260	-76.77274	-0.49018	1.6
Tarapoa	SUCUMBÍOS	230	-76.33753	-0.11617	2
Tinajillas	MORONA SANTIAGO	2915	-78.55667	-3.03333	2.549
Tinalandia	SANTO DOMINGO	850	-79.05000	-0.30944	1.736
Totoras	BOLIVAR	2800	-78.98058	-1.72553	2.942
Unión del Toachi	SANTO DOMINGO	850	-78.95441	-0.31383	1.686
Unión Río Upano-Paute	MORONA SANTIAGO	420	-78.27500	-2.75300	1.569
Valle de los Chillos	PICHINCHA	2900	-78.53333	-0.31667	1.766
Vía a Balao Chico	GUAYAS	30	-79.69444	-2.73833	1.713
Vía Coca - Loreto Km 26	ORELLANA	300	-77.18304	-0.54295	1.652
Vía La Bonita - La Fama	SUCUMBÍOS	2200	-77.53333	0.53333	2.261
Villano	PASTAZA	552	-77.67812	-1.42180	0
Villano (Kurintza)	PASTAZA	350	-77.51308	-1.50630	0
Villano (Tarangaro)	PASTAZA	340	-77.38208	-1.39552	0
Virgen del Cisne	LOJA	2250	-79.41690	-3.84603	1.873
Yanacocha-Reserva (300m Sur del PC)	PICHINCHA	3520	-78.58442	-0.11309	0
Yanacocha-Reserva (Pastizal arbolado y BMA)	PICHINCHA	3530	-78.58989	-0.11715	0
Yaruquí	PICHINCHA	2570	-78.31667	-0.15806	2.924

Yasuní (SC - Res. Sta. - EC - PUCE)	ORELLANA	250	-76.40050	-0.67131	2.026
Yunkumas, Centro Shuar	MORONA SANTIAGO	1150	-78.24639	-3.06250	3.75
Zamora	ZAMORA CHINCHIPE	970	-78.95226	-4.06643	3.89
Zapotal	SANTA ELENA	30	-80.56335	-2.31770	1.673

**The following localities could not be georeferenced because of uncertainty of the data or lack of voucher material**

Cercanías Río Aguarico	NAPO
Cerro Chuark Wihp	MORONA SANTIAGO
Chemin entre Guanasilla et San Nicolás	GUAYAS
Coca-Primavera	ORELLANA
Cord. del Cóndor Río Coangos-Río Tsuirin	MORONA SANTIAGO
Cordillera Pucay	AZUAY
Hda. La María 25 Km N Guayaquil	GUAYAS
Hda. La María-25 Km N Guayaquil	GUAYAS
Isla San Cristóbal	GALÁPAGOS
Juturi	NAPO
Limoncocha (Playaco river)	SUCUMBÍOS
Llanganates	TUNGURAHUA
Loja	MORONA SANTIAGO?
Los Rosales de Machay	CHIMBORAZO
Machetes	IMBABURA
Peñaherrera	IMBABURA
Pifo 9 Km al este	PICHINCHA
Pinular (Pinnlar, Pinullar)	IMBABURA
Plataforma Villano	PASTAZA
PNY Yasuní Bloque 31 Pozo petrolero PSCA 2	ORELLANA
Pucay-W Cordillere	AZUAY
Pucay-Santo Domingo	PICHINCHA?
Río Napo ( <i>Fidena laterina</i> )	NAPO?
Río Napo - Jatun Yacu	NAPO
Río Yananás	MORONA SANTIAGO
Río Yasuní Línea 10 y Sub base Bloque 31	ORELLANA
San Carlos	GUAYAS
Santa Bárbara de Sucumbíos	NAPO
Santa Inés	PICHINCHA
Santa Inéz	PICHINCHA

Santo Domingo to Chiriboga	SANTO DOMINGO
Valle de Azuay	AZUAY
Vía Loreto-Coca 20.7 Km (Este de Tena)	NAPO
Vía Puyo-Tena	NAPO
Volcán Pichincha	PICHINCHA
Yunguilla	AZUAY
Zaruma-Machala	EL ORO

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# Termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of Ecuador

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**Abstract.** Termites are an abundant and diverse group in the Neotropics with about 500 species representing 83 genera. The paucity of the termite fauna recorded from Ecuador is due, in part, to a lack of deliberate surveys. We revise the termite fauna of Ecuador and raise the number of species from 25 species to 72 based on our recent termite surveys. Of the 72 species, 18 could not be conclusively identified and are likely new species. Given the limited area that has been covered in surveys of the Ecuadorian termite fauna, there are undoubtedly many more species to be recorded for Ecuador, primarily in the eastern lowland areas, cloud forests on both the eastern and western slopes of the Andes, and the Amazonian lowland forests.

**Résumé. Les termites (Isoptera : Kalotermitidae, Rhinotermitidae, Termitidae) de l'Équateur.** Dans la zone néotropicale, le groupe des termites est abondant et diversifié avec environ 500 espèces représentées en 83 genres. Le manque de connaissance actuel sur la faune de termites en Equateur est lié à un manque d'inventaire. Dans cet article, nous révisons la faune équatorienne de termites dont la diversité est augmentée de 25 à 72 espèces. De ces 72 espèces, 18 n'ont pu être identifiées de façon concluante et sont probablement de nouvelles espèces. En raison de l'aire limitée couverte par l'ensemble des inventaires réalisés sur la faune de termites en Equateur, il existe indubitablement plus d'espèces à répertorier pour le pays, principalement dans les régions orientales de basses altitude ainsi que dans les forêts de nuages sur les flancs orientaux et occidentaux de la cordillère des Andes.

**Keywords:** Termites, Diversity, Ecuador, Galapagos.

Termites are an abundant and diverse, yet often cryptic order of insects in the Neotropics, especially in the savannas and rainforests of mainland. There are currently about 500 species in 83 genera recorded from the Neotropics (Constantino 1998). Currently, the Neotropical region has the second highest termite diversity behind the Ethiopian termite fauna (Constantino 1992) but the diversity of the former may ultimately surpass all other regions. Knowledge of the termite fauna of Ecuador is incomplete due to lack of deliberate surveys. The most recent termite description from Ecuador is that of *Caetetermes taquarussu* Fontes 1981 and *Dolichorhinotermes lanciaris* Engel & Krishna 2007 and the most updated New World catalog is that of Constantino 1998, which includes Araújo's 1977 Ecuadorian list. Araújo (1977) recorded

12 species in three different families from Ecuador that include *Rugitermes* sp. (Kalotermitidae), *Coptotermes testaceus* (L. 1758) (Rhinotermitidae), *Constrictotermes latinotus* (Holmgren 1910), *Cornitermes acignathus* (Silvestri 1901), *Embiratermes transandinus* Araújo 1977, *Nasutitermes corniger* (Motschulsky 1855), *Na. dendrophilus* (Desneux 1906), *Na. ecuadorianus* (Holmgren 1910), *Na. peruanus* (Holmgren 1910), *Na. tredecimarticulatus* (Holmgren 1910), *Neocapritermes talpoides* Krishna & Araújo 1968 and *Rhynchotermes perarmatus* (Snyder 1925) (Termitidae).

The aim of this paper is to summarize the currently known termite fauna of Ecuador based on literature records and recent expeditions by Křeček & Warner collected in 2001 and Bahder in 2006 and 2007.

## Materials and Methods

From 16 to 28 December 2001, 186 termite samples were collected by Křeček & Warner from 37 different locations in western Ecuador (Fig. 1). Specimens collected in this survey were discovered by chopping dead wood, fence poles, and collecting from under rocks using an aspirator. Many

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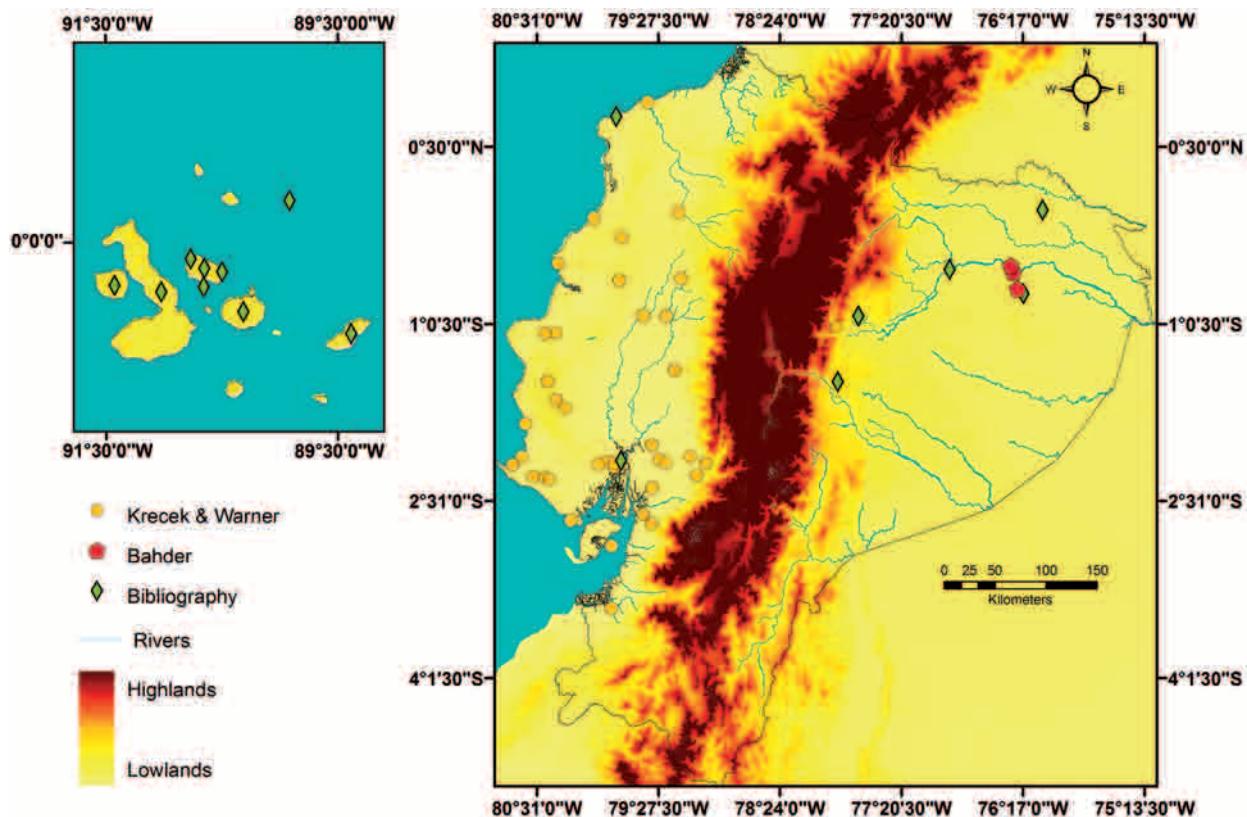
specimens were collected directly from nests and mud tubes. From 13 February to 16 April 2006, 144 termite samples were collected by Bahder from one location in eastern Ecuador, Yasuni Research Station of the Pontifical Catholic University of Ecuador ( $0^{\circ} 41' S$  latitude,  $76^{\circ} 24' W$  longitude, Fig. 1). This area is approximately 3,300 meters by 1,100 meters in size. At Yasuni, specimens were primarily taken from nests. When nests high on the boles or branches of trees were visible from the ground, the trees were climbed and termites were collected from the nests and foraging tubes. From 14 – 19 August 2007, 53 additional samples were collected by Bahder in three different locations at the Yasuni Research Station, Ecuador. Additional samples were collected from the Napo Wildlife Center, and at Sacha Lodge ( $0^{\circ} 28' 15'' S$  latitude,  $76^{\circ} 27' 35'' W$  longitude Fig. 1) using the same techniques as in the 2006 survey except trees were not climbed. Additionally, freshly fallen, dry branches from the canopy were searched. Sacha Lodge was included in the 2007 survey because it is on the north side of the Napo River, essentially an extensive flood plain reaching to the Colombian border including the drainages of the Aguarico and Putumayo Rivers. The area on the south side of the Napo River, Yasuni National Park, rises to a series of low hills dissected by smaller rivers. The areas surveyed at the Yasuni Research Station included both terra firma and varzea, seasonally flooded forests. All termites were collected and stored in 85% ethanol.

Termites were identified using the keys provided by Constantino

(2002), the reference collection at the University of Florida, and additional authors as cited in the text and table. The specimens collected during these studies were deposited at the University of Florida Termite Collection at the Fort Lauderdale Research and Education Center and in the Museum of Invertebrates in the School of Biological Sciences of the Pontifical Catholic University of Ecuador, Quito, Ecuador.

## Results

The survey by Křeček & Warner yielded 18 species in 12 genera included in three families, Kalotermitidae, Rhinotermitidae, and Termitidae. Species recorded from this collection include *Calcaritermes* cf. *temnocephalus* (Silvestri 1901), *Cr. brevis* (Walker 1853), *Cr. fatulus* (Light 1935), *I. immigrans* (Snyder 1922), *Neotermes holmgreni* Banks 1918, *Ru. panamae* (Fig. 2a) (Snyder 1925) from the Kalotermitidae, *Co. testaceus* (L. 1758), *Heterotermes tenuis* (Hagen 1858) (Fig. 2b) from the Rhinotermitidae, *Amitermes* cf. *amifier* Silvestri 1901, two different undetermined species of *Anoplotermes* s. l. (soldierless termites) morphotyped by worker enteric valve armature as sp. 1 and sp. 5, an unidentified species of *Cylindrotermes* labeled sp. 1,



**Figure 1**

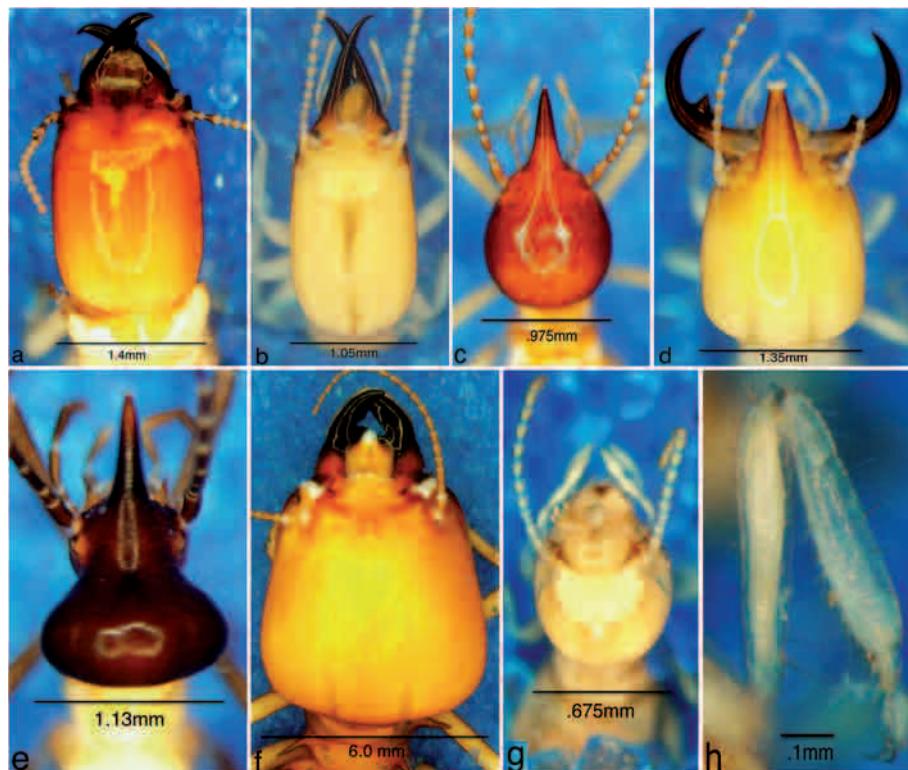
Collection sites (red and orange) represented in the surveys done by Křeček & Warner and Bahder, and literature records from previous papers (green).

*Microcerotermes exiguus* (Hagen 1858), *Na. glabritergus* (Snyder & Emerson in Snyder 1949), *Na. guayanae* (Holmgren 1910), and *Na. nigriceps* (Haldeman 1853) and two undetermined *Nasutitermes* in the Termitidae. These species were designated species 1 and 2.

The survey by Bahder from 13 February 2006 to 16 April 2006 focused on nest building species in one location in Amazonia and yielded 34 species in 18 different genera from two families, Rhinotermitidae and Termitidae (Table 1). Species newly recorded for Ecuador from this survey include *Dolichorhinotermes longilabius* (Emerson 1925), *Rhinotermes nasutus* (Perity 1853) in the Rhinotermitidae, *An. cf. banksi* Emerson 1925, *An. parvus* Snyder 1923, six unidentified species of *Anoplotermes*, *Armitermes cf. holmgreni* Snyder 1926, *Ar. teevani*, *Ar. minutus* (Emerson 1925), *Cavitermes tuberosus* (Emerson 1925), *Constrictotermes cavifrons* (Holmgren 1910) (Fig. 2e), *Co. pugnax* Emerson 1925, *Cylindrotermes parvignathus* Emerson in Snyder 1949, *Em. neotenicus* (Holmgren 1910) (Fig. 2d), *Ereymatermes cf. rotundiceps* Constantino 1991, cf. *Grigiotermes* Mathews 1977, *Labiotermes labralis*

(Holmgren 1910), cf. *Paraconvexitermes* (Cancello and Noirot 2003) sp. 1, *Rotunditermes bragantinus* (Fontes and Bandeira 1979), and *Syntermes spinosus* (Latreille 1804) (Fig. 2f) in the Termitidae. There were six additional species of *Nasutitermes* that could not be identified and were designated species 2–7 based on morphological differences. Three other *Nasutitermes* were also found in this survey; *Na. ephratae* (Holmgren 1910), *Na. guayanae* (Holmgren 1910), and *Na. surinamensis* (Holmgren 1910) (Termitidae).

The survey by Bahder from 14 August 2007 to 19 August 2007 yielded 12 species of termites from three families. Species collected during this survey included one undetermined kalotermitid species, *Co. testaceus*, *He. tenuis*, and *Rhinotermes marginalis* (L. 1758) from the family Rhinotermitidae. Species in the Termitidae included *Armitermes cf. holmgreni*, *Cornitermes pugnax*, *Cylindrotermes* sp. 1, *Em. neotenicus*, *Na. sp. 1*, *Na. sp. 2*, *Na. corniger*, and *Na. ephratae*. Four species of termites were found both west of the Andes and east of the Andes; *Na. guayanae*, *Na. corniger*, *Co. testaceus*, and *He. tenuis*. Species present only in the western part



**Figure 2**

Examples of termite soldiers found in Ecuador: **a**, *Rugitermes panamae* (western Ecuador); **b**, *Heterotermes tenuis* (eastern and western Ecuador); **c**, *Nasutitermes cf. corniger* (eastern and western Ecuador); **d**, *Embiratermes neotenicus* (eastern Ecuador); **e**, *Constrictotermes cavifrons* (eastern Ecuador); **f**, *Syntermes spinosus* (eastern Ecuador); **g**, *Anoplotermes* sp 3 (eastern Ecuador); **h**, dilated foretibia of *Anoplotermes* sp. 3.

**Table 1.** Termite species from Ecuador listed alphabetically by family, subfamily, and genus. Taxa followed by asterisk are new mainland country records.

TAXON	ECUADOR DISTRIBUTION	PREVIOUS NEAREST LOCALITY	PREVIOUS LOCALITY REFERENCE
<b>Kalotermitidae</b>			
<i>cf. Calcaritermes</i> sp. <sup>4</sup> Snyder 1949 (workers only)*	Eastern, Lowland Tropical Rainforest		
<i>Calcaritermes</i> cf. <i>temnocephalus</i> <sup>2</sup> (Silvestri 1901)*	Western Ecuador (coastal)	Venezuela	Silvestri 1901
<i>Cryptotermes brevis</i> <sup>2</sup> (Walker 1853)*	Structures only, pest species (non-endemic)	Endemic to Chile, Peru	Scheffrahn <i>et al.</i> 2008
<i>Cryptotermes darwini</i> <sup>5</sup> (Light 1935)	Endemic to Galapagos		Light 1935
<i>Cryptotermes fatalis</i> <sup>2</sup> (Light 1935)*	Galapagos and coastal mainland		Light 1935
<i>Incisitermes galapagoensis</i> <sup>7</sup> (Banks 1901)	Galapagos		Banks 1901
<i>Incisitermes immigrans</i> <sup>2</sup> (Snyder 1922)*	West of the Andes		Constantino 1998
<i>Incisitermes pacificus</i> <sup>5</sup> (Banks 1901)	Galapagos	El Salvador	Banks 1901
<i>Neotermes holmgreni</i> <sup>2</sup> Banks 1918*	West of the Andes	Guyana	Emerson 1925
<i>Rugitermes panamae</i> <sup>2</sup> (Snyder 1925)*	West of the Andes	Panama	Snyder 1925
<b>Rhinotermitidae</b>			
<i>Coptotermes testaceus</i> <sup>1,2,3,4</sup> (L. 1758)	Western and Eastern Ecuador	Amazonia	Constantino 1998
<i>Dolichorhinotermes lanciarius</i> <sup>9</sup> Engel & Krishna 2007	Eastern slopes of the Andes		
<i>Dolichorhinotermes longilabius</i> <sup>3</sup> (Emerson 1925)*	Eastern, Lowland Tropical Rainforest	Guyana	Emerson 1925
<i>Heterotermes convexinotatus</i> <sup>5</sup> (Snyder 1924)	Western Ecuador	Panama	Constantino 2001
<i>Heterotermes tenuis</i> <sup>2,3,4</sup> (Hagen 1858)	Western and Eastern Ecuador	widespread	Constantino 2001
<i>Rhinotermes marginalis</i> <sup>4</sup> (L. 1758)*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1991
<i>Rhinotermes nasutus</i> <sup>3</sup> (Perty 1833)*	Eastern, Lowland Tropical Rainforest	Peru	Constantino 1998
<b>Termitidae</b>			
<b>Apicotermatinae</b>			
<i>Anoplotermes</i> cf. <i>banksi</i> <sup>3</sup> Emerson 1925*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1991
<i>Anoplotermes parvus</i> <sup>3</sup> Snyder 1923*	Eastern, Lowland Tropical Rainforest	Panama	Snyder 1923
<i>Anoplotermes</i> sp. 1 <sup>2*</sup>	West of the Andes		
<i>Anoplotermes</i> sp. 2 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Anoplotermes</i> sp. 3 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Anoplotermes</i> sp. 4 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Anoplotermes</i> sp. 5 <sup>2*</sup>	Eastern, Lowland Tropical Rainforest		
cf. <i>Grigiotermes</i> <sup>3</sup> Mathews 1977*	Eastern, Lowland Tropical Rainforest	Central Brazil	Constantino 1998
<b>Nasutitermitinae</b>			
<i>Caetetermes taquarussu</i> <sup>13</sup> Fontes 1981	Eastern, Lowland Tropical Rainforest		Fontes 1981
<i>Constrictotermes cavifrons</i> <sup>3</sup> (Holmgren 1910)*	Eastern, Lowland Tropical Rainforest	Peru	Constantino 1998
<i>Constrictotermes latinotus</i> <sup>1</sup> (Holmgren 1910)	"Ecuador" (all surrounding regions)		Holmgren 1910
<i>Ereymatertes</i> cf. <i>rotundiceps</i> <sup>3</sup> Constantino 1991*	Eastern, Lowland Ecuador	Colombia	Constantino 1991
<i>Nasutitermes</i> cf. <i>brevipilus</i> <sup>2</sup> Emerson 1925*	Lowland Tropical Rainforest	Guyana	Emerson 1925
<i>Nasutitermes corniger</i> <sup>1,3,4</sup> (Motschulsky 1855)	Eastern and Western		Scheffrahn <i>et al.</i> 2006
<i>Nasutitermes dendrophilus</i> <sup>1</sup> (Desneux 1906)	West of the Andes		
<i>Nasutitermes ecuadorianus</i> <sup>1</sup> (Holmgren 1910)	West of the Andes		
<i>Nasutitermes ephratiae</i> <sup>3,4</sup> (Holmgren 1910)*	Eastern, Lowland Tropical Rainforest	Neotropical	Constantino 1998
<i>Nasutitermes glabritergus</i> <sup>2</sup> Snyder & Emerson in Snyder 1949			
<i>Nasutitermes guayanae</i> <sup>2,3</sup> (Holmgren 1910)*	Eastern and Western	Neotropical	Holmgren 1910
<i>Nasutitermes minor</i> <sup>12</sup> (Holmgren 1906)	Lowland Tropical Rainforest		Fontes & Filho 1998
<i>Nasutitermes nigriceps</i> <sup>2</sup> (Haldeman 1853)*	West of the Andes	Colombia	Holmgren 1910
<i>Nasutitermes peruanus</i> <sup>1</sup> (Holmgren 1910)	West of the Andes		
<i>Nasutitermes</i> sp. 1 <sup>2,4*</sup>	West of the Andes		
<i>Nasutitermes</i> sp. 2 <sup>3,4*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 3 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 4 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 5 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 6 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		

TAXON	ECUADOR DISTRIBUTION	PREVIOUS NEAREST LOCALITY	PREVIOUS LOCALITY REFERENCE
<i>Nasutitermes</i> sp. 7 <sup>3*</sup>	Western Ecuador		
<i>Nasutitermes surinamensis</i> <sup>3</sup> (Holmgren 1910)*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1991
<i>Nasutitermes tredecimarticulatus</i> <sup>1</sup> (Holmgren 1910)	West of the Andes		
cf. <i>Paraconvexitermes</i> (Cancello & Noirot 2003) sp. 1 <sup>3*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Rotunditermes bragantinus</i> <sup>3</sup> (Roonwal & Rathore 1976)*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1998
<b>Syntermiteinae</b>			
<i>Armitermes</i> cf. <i>holmgreni</i> <sup>3</sup> Snyder 1926*	Eastern, Lowland Tropical Rainforest	Brazil	Snyder 1926
<i>Armitermes minutus</i> <sup>3</sup> Emerson 1925*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1998
<i>Armitermes teevani</i> <sup>3</sup> Emerson 1925*	Eastern, Lowland Tropical Rainforest	Bolivia	Constantino 1998
<i>Cornitermes acignathus</i> <sup>1</sup> Silvestri 1901	West of the Andes		Silvestri 1901
<i>Cornitermes pugnax</i> <sup>3,4</sup> Emerson 1925*	Eastern, Lowland Tropical Rainforest	Colombia	Constantino 1998
<i>Embiratermes neotenicus</i> <sup>3,4</sup> (Holmgren 1906)*	Eastern, Lowland Tropical Rainforest	Peru	Fontes 1985
<i>Embiratermes transandinus</i> <sup>1</sup> (Araujo 1977)	Eastern, Lowland Tropical Rainforest		
<i>Labiotermes labralis</i> <sup>3</sup> (Holmgren 1906)*	Eastern, Lowland Tropical Rainforest	Peru	Holmgren 1906
<i>Rhynchotermes perarmatus</i> <sup>1</sup> (Snyder 1925)	Eastern, Lowland Tropical Rainforest		
<i>Syntermes chaquimayensis</i> <sup>11</sup> (Holmgren 1906)	Eastern, Lowland Tropical Rainforest		
<i>Syntermes molestus</i> <sup>11</sup> (Burmeister 1839)	Lowland Tropical Rainforest	Brazil	Constantino 1995
<i>Syntermes spinosus</i> <sup>3</sup> (Latreille 1804)	Eastern, Lowland Tropical Rainforest	Colombia	Emerson 1965
<b>Termitinae</b>			
<i>Amiatermes</i> n sp cf. <i>amiger</i> <sup>3</sup> (Silvestri 1901)*	West of the Andes	Brazil	Silvestri 1901
<i>Cavitermes tuberosus</i> <sup>3</sup> (Emerson in Snyder 1949)*	Eastern, Lowland Tropical Rainforest	Brazil	Emerson 1925
<i>Cylindrotermes parvignathus</i> <sup>3</sup> (Emerson in Snyder 1949)*	Eastern, Lowland Tropical Rainforest	Brazil	Snyder 1949
<i>Cylindrotermes</i> sp. 1 <sup>4*</sup>	Eastern, Lowland Tropical Rainforest		
<i>Cylindrotermes</i> sp. 2 <sup>2*</sup>	West of the Andes	Panama	Snyder 1929
<i>Microcerotermes arboreus</i> <sup>2</sup> Emerson 1925*	“Ecuador”	Guyana	Constantino 1998
<i>Microcerotermes exiguis</i> <sup>2</sup> (Hagen 1858)*	West of the Andes	Colombia	Holmgren 1912
<i>Neocapritermes opacus</i> <sup>8</sup> (Hagen 1858)	Eastern Andean slopes	Brazil	Krishna & Araujo 1968
<i>Neocapritermes talpoides</i> <sup>1</sup> Krishna & Araujo 1968	Lowland Tropical Rainforest		
<i>Neocapritermes villosus</i> <sup>6</sup> (Holmgren 1906)	Lowland Tropical Rainforest	Peru	Krishna & Araujo 1968

<sup>1</sup>Araujo (1977)<sup>2</sup>Křeček & Warner expedition, 16 December 2001-28 December 2001<sup>3</sup>Bahder, 3 February 2006 – 15 May 2006<sup>4</sup>Bahder, 14 – 19 August 2007<sup>5</sup>Light (1935)<sup>6</sup>Krishna & Araujo (1968)<sup>7</sup>Banks (1901)<sup>8</sup>Constantino (1991)<sup>9</sup>Engel & Krishna (2007)<sup>10</sup>Snyder (1924)<sup>11</sup>Constantino (1995)<sup>12</sup>Fontes (1996)<sup>13</sup>Fontes (1981)

of the country, not including species endemic to the Galapagos Islands, were *Cryptotermes brevis*, *Cr. fatalis*, *In. immigrans*, *Ne. holmgreni*, *Ru. panamae* (Fig. 2a), one unidentified species of *Anoplotermes* labeled sp. 1, *Con. latinotus*, *Cor. acignathus*, *Na. dendrophilus*, *Na. ecuadorianus*, *Na. nigriceps*, *Na. peruanus*, *Na. tredecimarticulatus*, *Amiatermes amiger*, *Cy. parvignathus*, *Microcerotermes exiguis*, and *Neo. talpoides*. In the

surveys done by Bahder in eastern Ecuador, two species were collected at Sacha Lodge north of the Napo River, which were not collected in Yasuni south of the Napo River. One was an unidentified species of *Cylindrotermes* and the other was *Rhinotermes marginalis*. All other species collected north of the Napo River had been previously been collected south of the Napo River.

## Discussion

Many regions and a variety of habitats in Ecuador remain either significantly underrepresented in museum collections or have not been collected adequately for termites. Undoubtedly, there are more species that have yet to be recorded for Ecuador and probably, there are some that have yet to be discovered and described, particularly in Amazonian Ecuador and the eastern and western cloud forests to an elevation of about 1,500 meters. In this report, we list a *Calcaritermes* that could not be identified to species, six undetermined species of *Anoplotermes* s. l., seven undetermined *Nasutitermes*, an unknown species of *Paraconvexitermes*, an unidentified species of *Grigiotermes*, an unidentified species of *Rhynchotermes*, and two unidentified *Cylindrotermes*. These specimens represent potentially 19 species new to science and perhaps a new genus if examined more closely. A recent list of the termites of Colombia (Madrigal 2003) contained references to 45 species of termites from 29 genera representative of only one family, Termitidae. We collected two species reported from Colombia, *Syntermes spinosus* (Latreille 1804) (Constantino 1995) and *Cornitermes pugnax* (Emerson 1945) (Constantino 1998) but not listed by Madrigal (2003).

Between the 77 species listed in this report from Ecuador and the 45 from Colombia, there are only seven species that overlap, *Co. testaceus*, *He. tenuis*, *Cor. acignathus*, *Na. brevissimus*, *Na. nigriceps*, and *Micr. exiguis*. Madrigal (2003) concentrated on pests and insects in forestry practice while Bahder, Křeček, and Warner collected in pristine, or less disturbed ecosystems.

Ecuadorian Amazonia has several records that were collected incidentally (Table 1) but the Bahder 2006 and 2007 surveys were done in restricted, small areas that do not fully represent the entire region. These Amazonian surveys also focused on nest building groups so that taxa living in wood or that forage underground are underrepresented. Even though the surveys by Bahder overlooked certain taxa, 34 species in 18 different genera were recorded in a small area (3300 meters long by 1100 meters wide). Clearly, there is high diversity of termites in the eastern lowland forest of Ecuador and Yasuni in particular. The abundance of termite species in a relatively restricted area demands an explanation. There are a number of factors that may contribute to the high diversity of termites found in the Amazon region of Ecuador. First, there is a high diversity of woody plants from a variety of families. In a 50-hectare plot at the Yasuni Scientific Station, over 1,200 woody plants, trees, shrubs and lianas have been

counted in a systematic survey (Valencia *et al.* 2004). It is easy to imagine a similar array of herbivorous insects specializing on various plant species, genera or families and a range of feeding sites and styles. Consumption of dead wood is a different matter as many of the differences in leaf, flower, and even woody tissue chemistry and morphology that drive specialization by herbivores are no longer a factor after the death of the woody plant. Nevertheless, this diversity of woody plants has a large variety of structural and chemical differences in their woody tissue that may lead to specialization by termites. One of the basic dichotomies is palm vs. dicotyledonous trees. While in general, wood from palms is harder and more resistant to decay than other trees, palm trunks are clearly degraded slowly over time in the forest and termites play a role in this degradation. The potential specialization of separate groups of termites on palm wood must be confirmed with field observations and laboratory studies. Recent work suggests that traits of individual plant species play a significant role in the rate of litter decomposition in forests (Cornwell *et al.* 2008). Termites are important members of the decomposer community and are likely to be differentially affected by the species composition of coarse woody litter. Further, termites are known to feed on a variety of substrates in addition to wood in varying degrees of decay. This includes sound wood, leaf litter, lichen, humus, soil and perhaps even herbaceous growth (Traniello & Leuthold 2000).

Tropical forests can be classified on a continuum from dry to wet with seasonal inundations. Soils are typically fine textured sediments but are also classified into a variety of types. Especially for those termites that nest or forage underground, these differences in hydrology and soil may result in delineation of species. The subterranean species are not well-represented in the collections reported in this paper. Tropical forests have multiple levels of canopy and it is conceivable that different species may construct nests at different levels in the canopy. Our sampling in this paper did not reach much higher than 25m but it is possible that we captured foragers from nests higher than those we sampled directly (Roison *et al.* 2006). Agonistic interactions with ants may also drive specialization in tropical termites. Predatory foraging by ants is a major factor in the ecology of tropical forests (Hölldobler & Wilson 1990). The abundance of the *Nasutitermes* group (15 species or about 25% of the species list) is probably due in large part to their ability to chemically defend their large nests against attack by foraging ants. It is not unreasonable to hypothesize that pressure from foraging ants has resulted in differing adaptations and diversification in other termite groups.

Perhaps the most important factor driving termite diversity is the interaction between the diversity of wood types and the microorganisms colonizing the wood as the decomposition process begins. The complex interactions between the type of wood, the environment, and the diversity of competing microorganisms that colonize this wood in successive waves can be a significant factor driving termite diversity. Some microorganisms might be completely refractory or repellent to virtually all termites while others are likely to be completely compatible with termite feeding. The diverse microorganism community is likely to form a gradient between these extremes. This gradient will vary for each species and their associated hind gut microbial symbionts. The complexity and importance of soil and litter microbial communities in nutrient cycling and productivity has recently become more apparent (Van de Heijden *et al.* 2008). The influence of these microorganism communities on wood degradation and termite foraging in tropical systems is likely to be significant.

There is also evidence for classic geographic isolating mechanisms promoting species diversity. The two definite endemic species listed for Ecuador are kalotermitids from the Galápagos Islands. These oceanic islands were formed by volcanism about 3-5 millions years ago and are isolated from the mainland by 1000 km of open ocean. The degree of endemism in these islands is well known (Kricher 2002). These species are similar to mainland species, eg. *Cr. brevis* on the mainland and *Cr. darwini* in the Galápagos (Scheffran *et al.* 2008). The dominant physiographic feature of Ecuador is the Andes Mountains running north – south and separating the country into 3 zones, the Andean Highlands with a series of interandean valleys, the Western Coast, and in the east, Amazonia. The Andes represent a formidable barrier to gene flow between the east and the west for insect populations in general. Only 4 species of termites were found both east and west of the Andes. Not counting the Galapagos endemic species, 18 termite species are found exclusively in the west of the Andes. There are 27 species that occur exclusively east of the Andes in Amazonia. Despite significant collecting effort south of the Napo, there were two species collected north of the river that were not found in the south. This is possibly due to the region north of the Napo River being a large flood plain. The other 10 species collected north of the Napo were collected in the south as well. It is likely that this discontinuity may result from changes in physiography, flood plain north of the river and upland habitat south of the Napo, as opposed to a barrier formed by the river itself.

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**Paulian R. 1988.** *Biologie des Coléoptères*. Lechevalier, Paris, 719 p.

Thèse / Thesis:

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Partie d'un travail collectif / Part of a collective publication:

**Bontems C. 1988.** Localization of spermatozoa inside viviparous and oviparous females of Chrysomelinae, p. 299-316 in: **Jolivet P., Petitpierre E., Hsiao T. H. (eds.), Biology of Chrysomelidae**. Kluwer, Dordrecht.

Livre inclu dans une collection numérotée / Part of a book serial:

**Brindle A. 1969.** *Insectes Dermaptères. Faune de Madagascar*, 30, ORSTOM-CNRS, Paris, 112 p.

Comptes-rendus / Proceedings:

**Medvedev L.N. 1971.** The ways of evolution and phylogeny of Chrysomelidae (Coleoptera). *Proceedings of the 13th International Congress of Entomology* 1: 271.

Article dans une revue / Paper in a serial:

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