

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'Equateur.

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 flanc 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 lanciarius* Engel & Krishna 2007 and the most updated New World catalog is that of Constantino 1998, which includes Araujo's 1977 Ecuadorian list. Araujo (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* Araujo 1977, *Nasutitermes corniger* (Motschulsky 1855), *Na. dendrophilus* (Desneux 1906), *Na. ecuadorianus* (Holmgren 1910), *Na. peruanus* (Holmgren 1910), *Na. tredecimarticulatus* (Holmgren 1910), *Neocapritermes talpoides* Krishna & Araujo 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° 41' S latitude, 76° 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° 28' 15" S latitude, 76° 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 Putomayo 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. *amifer* 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,

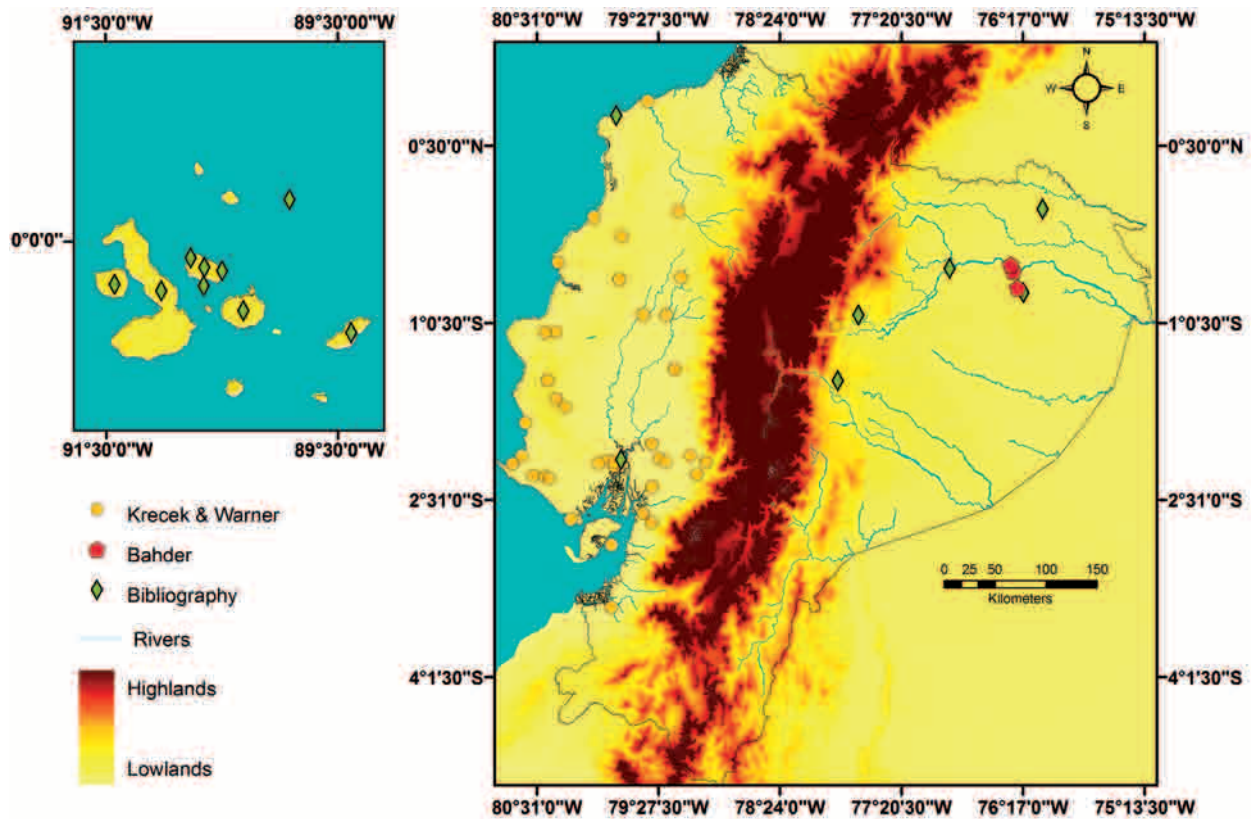


Figure 1

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* (Perty 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* (Canello and Noiro 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

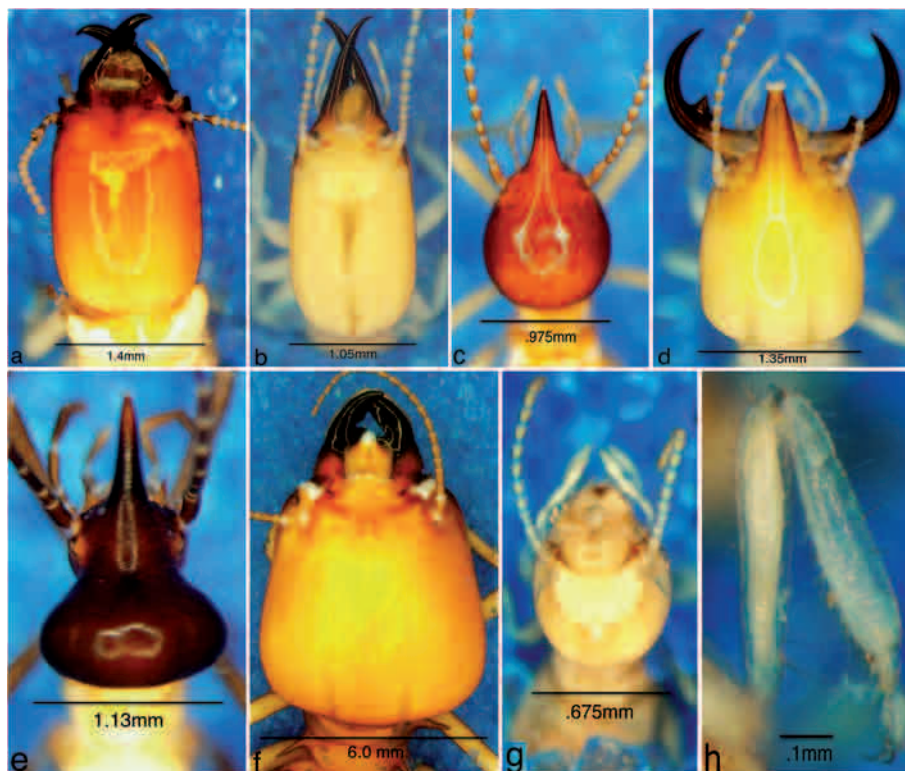


Figure 2

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
Kalotermitidae			
cf. <i>Calcaritermes</i> sp. ⁴ Snyder 1949 (workers only)*	Eastern, Lowland Tropical Rainforest		
<i>Calcaritermes</i> cf. <i>temnocephalus</i> ² (Silvestri 1901)*	Western Ecuador (coastal)	Venezuela	Silvestri 1901
<i>Cryptotermes brevis</i> ² (Walker 1853)*	Structures only, pest species (non-endemic)	Endemic to Chile, Peru	Scheffrahn <i>et al.</i> 2008
<i>Cryptotermes darwini</i> ⁵ (Light 1935)	Endemic to Galapagos		Light 1935
<i>Cryptotermes fatalus</i> ² (Light 1935)*	Galapagos and coastal mainland		Light 1935
<i>Incisitermes galapagoensis</i> ⁷ (Banks 1901)	Galapagos		Banks 1901
<i>Incisitermes immigrans</i> ² (Snyder 1922)*	West of the Andes		Constantino 1998
<i>Incisitermes pacificus</i> ⁵ (Banks 1901)	Galapagos	El Salvador	Banks 1901
<i>Neotermes holmgreni</i> ² Banks 1918*	West of the Andes	Guyana	Emerson 1925
<i>Rugitermes panamae</i> ² (Snyder 1925)*	West of the Andes	Panama	Snyder 1925
Rhinotermitidae			
<i>Coptotermes testaceus</i> ^{1,2,3,4} (L. 1758)	Western and Eastern Ecuador	Amazonia	Constantino 1998
<i>Dolichorhinotermes lanciarius</i> ⁹ Engel & Krishna 2007	Eastern slopes of the Andes		
<i>Dolichorhinotermes longilabius</i> ³ (Emerson 1925)*	Eastern, Lowland Tropical Rainforest	Guyana	Emerson 1925
<i>Heterotermes convexinotatus</i> ⁵ (Snyder 1924)	Western Ecuador	Panama	Constantino 2001
<i>Heterotermes tenuis</i> ^{2,3,4} (Hagen 1858)	Western and Eastern Ecuador	widespread	Constantino 2001
<i>Rhinotermes marginalis</i> ⁴ (L. 1758)*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1991
<i>Rhinotermes nasutus</i> ³ (Perty 1833)*	Eastern, Lowland Tropical Rainforest	Peru	Constantino 1998
Termitidae			
Apicotermitinae			
<i>Anoplotermes</i> cf. <i>banksi</i> ³ Emerson 1925*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1991
<i>Anoplotermes parvus</i> ³ Snyder 1923*	Eastern, Lowland Tropical Rainforest	Panama	Snyder 1923
<i>Anoplotermes</i> sp. 1 ^{2*}	West of the Andes		
<i>Anoplotermes</i> sp. 2 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Anoplotermes</i> sp. 3 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Anoplotermes</i> sp. 4 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Anoplotermes</i> sp. 5 ^{2*}	Eastern, Lowland Tropical Rainforest		
cf. <i>Grigiotermes</i> ³ Mathews 1977*	Eastern, Lowland Tropical Rainforest	Central Brazil	Constantino 1998
Nasutitermitinae			
<i>Caetetermes taquarussu</i> ¹³ Fontes 1981	Eastern, Lowland Tropical Rainforest		Fontes 1981
<i>Constrictotermes cavifrons</i> ³ (Holmgren 1910)*	Eastern, Lowland Tropical Rainforest	Peru	Constantino 1998
<i>Constrictotermes latinotus</i> ¹ (Holmgren 1910)	“Ecuador” (all surrounding regions)		Holmgren 1910
<i>Ereymatermes</i> cf. <i>rotundiceps</i> ³ Constantino 1991*	Eastern, Lowland Ecuador	Colombia	Constantino 1991
<i>Nasutitermes</i> cf. <i>brevipilus</i> ² Emerson 1925*	Lowland Tropical Rainforest	Guyana	Emerson 1925
<i>Nasutitermes corniger</i> ^{1,3,4} (Motschulsky 1855)	Eastern and Western		Scheffrahn <i>et al.</i> 2006
<i>Nasutitermes dendrophilus</i> ¹ (Desneux 1906)	West of the Andes		
<i>Nasutitermes ecuadorianus</i> ¹ (Holmgren 1910)	West of the Andes		
<i>Nasutitermes ephratae</i> ^{3,4} (Holmgren 1910)*	Eastern, Lowland Tropical Rainforest	Neotropical	Constantino 1998
<i>Nasutitermes glabritergus</i> ² Snyder & Emerson in Snyder 1949			
<i>Nasutitermes guayanae</i> ^{2,3} (Holmgren 1910)*	Eastern and Western	Neotropical	Holmgren 1910
<i>Nasutitermes minor</i> ¹² (Holmgren 1906)	Lowland Tropical Rainforest		Fontes & Filho 1998
<i>Nasutitermes nigriceps</i> ² (Haldeman 1853)*	West of the Andes	Colombia	Holmgren 1910
<i>Nasutitermes peruanus</i> ¹ (Holmgren 1910)	West of the Andes		
<i>Nasutitermes</i> sp. 1 ^{2,4*}	West of the Andes		
<i>Nasutitermes</i> sp. 2 ^{3,4*}	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 3 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 4 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 5 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Nasutitermes</i> sp. 6 ^{3*}	Eastern, Lowland Tropical Rainforest		

Taxon	Ecuador Distribution	Previous Nearest Locality	Previous Locality Reference
<i>Nasutitermes</i> sp. 7 ^{3*}	Western Ecuador		
<i>Nasutitermes surinamensis</i> ³ (Holmgren 1910)*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1991
<i>Nasutitermes tredecimarticulatus</i> ¹ (Holmgren 1910)	West of the Andes		
cf. <i>Paraconvexitermes</i> (Cancellato & Noirot 2003) sp. 1 ^{3*}	Eastern, Lowland Tropical Rainforest		
<i>Rotunditermes bragantinus</i> ³ (Roonwal & Rathore 1976)*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1998
Syntermitinae			
<i>Armitermes</i> cf. <i>holmgreni</i> ³ Snyder 1926*	Eastern, Lowland Tropical Rainforest	Brazil	Snyder 1926
<i>Armitermes minutus</i> ³ Emerson 1925*	Eastern, Lowland Tropical Rainforest	Brazil	Constantino 1998
<i>Armitermes teevani</i> ³ Emerson 1925*	Eastern, Lowland Tropical Rainforest	Bolivia	Constantino 1998
<i>Cornitermes acignathus</i> ¹ Silvestri 1901	West of the Andes		Silvestri 1901
<i>Cornitermes pugnax</i> ^{3,4} Emerson 1925*	Eastern, Lowland Tropical Rainforest	Colombia	Constantino 1998
<i>Embiratermes neotenicus</i> ^{3,4} (Holmgren 1906)*	Eastern, Lowland Tropical Rainforest	Peru	Fontes 1985
<i>Embiratermes transandinus</i> ¹ (Araujo 1977)	Eastern, Lowland Tropical Rainforest		
<i>Labiotermes labralis</i> ³ (Holmgren 1906)*	Eastern, Lowland Tropical Rainforest	Peru	Holmgren 1906
<i>Rhynchotermes perarmatus</i> ¹ (Snyder 1925)	Eastern, Lowland Tropical Rainforest		
<i>Syntermes chaquimayensis</i> ¹¹ (Holmgren 1906)	Eastern, Lowland Tropical Rainforest		
<i>Syntermes molestus</i> ¹¹ (Burmeister 1839)	Lowland Tropical Rainforest	Brazil	Constantino 1995
<i>Syntermes spinosus</i> ³ (Latreille 1804)	Eastern, Lowland Tropical Rainforest	Colombia	Emerson 1965
Termitinae			
<i>Amitermes</i> n sp cf. <i>amifer</i> ³ (Silvestri 1901)*	West of the Andes	Brazil	Silvestri 1901
<i>Cavitermes tuberosus</i> ³ (Emerson in Snyder 1949)*	Eastern, Lowland Tropical Rainforest	Brazil	Emerson 1925
<i>Cylindrotermes parvignathus</i> ³ (Emerson in Snyder 1949)*	Eastern, Lowland Tropical Rainforest	Brazil	Snyder 1949
<i>Cylindrotermes</i> sp. 1 ^{4*}	Eastern, Lowland Tropical Rainforest		
<i>Cylindrotermes</i> sp. 2 ^{2*}	West of the Andes	Panama	Snyder 1929
<i>Microcerotermes arboreus</i> ² Emerson 1925*	“Ecuador”	Guyana	Constantino 1998
<i>Microcerotermes exiguus</i> ² (Hagen 1858)*	West of the Andes	Colombia	Holmgren 1912
<i>Neocapritermes opacus</i> ⁸ (Hagen 1858)	Eastern Andean slopes	Brazil	Krishna & Araujo 1968
<i>Neocapritermes talpoides</i> ¹ Krishna & Araujo 1968	Lowland Tropical Rainforest		
<i>Neocapritermes villosus</i> ⁶ (Holmgren 1906)	Lowland Tropical Rainforest	Peru	Krishna & Araujo 1968

¹ Araujo (1977)² Křeček & Warner expedition, 16 December 2001–28 December 2001³ Bahder, 3 February 2006 – 15 May 2006⁴ Bahder, 14 – 19 August 2007⁵ Light (1935)⁶ Krishna & Araujo (1968)⁷ Banks (1901)⁸ Constantino (1991)⁹ Engel & Krishna (2007)¹⁰ Snyder (1924)¹¹ Constantino (1995)¹² Fontes (1996)¹³ Fontes (1981)

of the country, not including species endemic to the Galapagos Islands, were *Cryptotermes brevis*, *Cr. fatalus*, *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*, *Amitermes amiger*, *Cy. parvignathus*, *Microcerotermes exiguus*, 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 probable, 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. exiguus*. 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 symbiotes. 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. darwinii* 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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