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Ongoing invasions of old-growth tropical forests: establishment of three incestuous beetle species in southern Central America (Curculionidae: Scolytinae)

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Abstract

Old-growth tropical forests are widely believed to be immune to the establishment of alien species. Collections from tropical regions throughout the world, however, have established that this generalization does not apply to inbreeding host generalist bark and ambrosia beetles. Scolytine saproxylophages are readily spread by shipping, inbreeders can easily establish new populations, and host generalists readily find new breeding material, apparently regardless of stage of forest succession. Consequently, many inbreeding scolytines are globally distributed and abundant in all forest types, often being among the dominant species in their wood-borer communities. We report the recent introductions to lower Central America of two Old World inbreeding ambrosia beetles: *Xylosandrus crassiusculus,* which breeds primarily in smaller diameter trunks, small branches, and twigs, and *Xyleborinus exiguus,* which is apparently not size selective. We also document the establishment of *Euwallacea fornicatus* in the region, known previously from a single collection in Panama. *Xylosandrus crassiusculus* and *E. fornicatus* are notorious agricultural and forestry pests, as are several previously established alien species in the region. Studying the spread of species such as these three new arrivals into millions of years-old faunas could help us to understand if the saproxylic communities of old-growth tropical forests are peculiarly vulnerable to invasion.

Key words: tropical ecology, alien species, bark beetle, community ecology, biodiversity, inbreeding

Resumen

Los bosques tropicales primarios se consideran generalmente inmunes al establecimiento de especies exóticas. Sin embargo, las colecciones de las regiones tropicales del mundo demuestran que esta generalización no es válida en el caso de los escarabajos ambrosiales endógamos y generalistas con respecto a los huéspedes. Los saproxylofagos Scolytinae son comúnmente dispersados por el embarque, las especies autógamas pueden establecer poblaciones nuevas fácilmente, y los generalistas pueden sin dificultad encontrar nuevo material para reproducirse, al parecer independientemente del estado sucesional del bosque. Consecuentemente, muchas especies de Scolytinae endógamos tienen una distribución global, abundan en todos los tipos de bosque, y dominan usualmente las comunidades de insectos barrenadores de la madera. En este estudio presentamos unas introducciones recientes del Viejo Mundo en Centro América baja de dos escarabajos ambrosiales endógamos y de *Xylosandrus crassiusculus* los cuales se reproducen en primer lugar en troncos de poco diámetro y en ramas, y de *Xyleborinus exiguus*, el cual aparentemente no tiene preferencia por un tamaño en particular. También documentamos el establecimiento en la región de *Euwallacea fornicatus*, conocida previamente por una única colección en Panamá. *Xylosandrus crassiusculus* y *E. fornicatus*, así como varias especies exóticas establecidas previamente en la región, son plagas notorias de la agricultura y de la silvicultura. El estudio de la dispersión de especies como las de estos tres nuevos introducciones en faunas de millones de años de antigüedad puede ayudar a entender si las comunidades de barrenadores de la madera en los bosques primarios tropicales son particularmente vulnerables a la invasión.

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Introduction

We live in exciting times, with respect to the exploration of life on our planet. Intensive biodiversity surveys have been or are being carried out in many of the world's most species rich ecosystems, in unprecedented number and scope. Besides detailing the native fauna (much of which is undescribed), the intensive taxonomic scrutiny afforded by such inventories regularly reveals previously unrecorded alien species—testimony to the prescience of one of the founders of the field of ecology, Charles Elton, who half a century ago predicted today's explosion of invasive plant and animal pests (Elton, 1958).

Bark- and wood-boring beetles readily survive transglobal shipping while esconced within wood packing materials, logs or sawn timber (Brockerhoff *et al.*, 2006; Haack, 2006). Intercontinental transport of forest insects is considered a major threat to forest sustainability worldwide (Chornesky *et al.*, 2005), but research has focused on introductions to temperate countries (e.g. Brockerhoff *et al.*, 2006; Haack, 2001; 2006; Humble & Allen, 2006). We document thriving populations of two new scolytine ambrosia beetle (Curculionidae: Scolytinae) colonizations and confirm the establishment of a species previously known from a single collection in the Panama Canal Zone.

Methods

We did not sample specifically for these taxa. Rather, the bulk of specimens were found in arthropod inventory samples made by either the ongoing insect biodiversity survey of Costa Rica being conducted by INBio (12 of 18 drawers of unsorted bark beetles were searched, for the three species), the ALAS (Arthropods of La Selva) survey of lowland tropical forest biodiversity patterns (Colwell & Longino, 2006), or the IBISCA (Investigating Biodiversity of Soil and Canopy Arthropods) survey of tropical lowland moist forest in Panama during 2003 and 2004 (Leponce & Basset, 2006; Springate & Basset, 2004). These projects are among the first large scale mass samplings of arthropods from tropical forests which enlist a broad array of collecting methods. Other collections from Costa Rica and Panama were made in conjunction with smaller research projects or made during routine hand-sampling for wood-boring beetles. The exact sampling methods (where known) are given in the specimen data for each species, and mass sampling methods are detailed in the publications cited above. In addition, Kirkendall examined 150 scolytines from flight intercept trap collections made by Chris Lyal and Jane Beard (Natural History Museum, London) in Belize between Aug. 1994 and Jan. 1995, and 190 scolytines collected between 1989 and 1992 from Nicaragua (hand collecting and black light traps). The three species treated here were not found in those collections.

Results

***Xylosandrus crassiusculus* (Motschulsky)**
(Fig. 1a–c)

Records. New to Neotropics, recently established in North America. **COSTA RICA**, Heredia, Cariari, Pocosí, Finca Prima Vera, 0–100 m, Mar. 1996, trunk of standing *Tectona grandis* (teak, Verbenaceae), M. Arguedas (2 beetles), 29 July 1997, 15–20 cm dbh 6 years-old standing teak killed by *Nectria nauriticola* fungus, L. R. Kirkendall (1); Heredia, La Selva Biological Station 10° 26' N, 84° 01' W, 50–150 m elevation, 26 July 1996, trunk of felled *Vochysia ferruginea* (Vochysiaceae) L. R. Kirkendall (1); La Selva, ground-level UV light traps in second growth forest, 4 Aug. (1) and 24 Sept. (2), 11 Nov. (1), 1998, and 8 Feb. and 29 Mar. 1999 (1 each); La Selva, canopy UV light trap in old-growth forest, 2 Feb. 1999, ALAS project (1); La Selva, Malaise traps near treefalls not far from a forest edge, Nov. 1998 and Aug. 1999, ALAS project (1 each date); La Selva, 7 July 1999, 8 cm dia. broken branch of *Pourouma bicolor* (Urticaceae) (1) and 1 cm dia. broken branch of *Protium pittieri* (Burseraceae), L. R. Kirkendall (1); La Selva, 8, 17 & 19 Dec. 2003, 8 Mar. 2004, woody petiole of fallen leaf of *Cecropia insignis* (Urticaceae; not breeding), old growth forest, Justin Calabrese (1 each date); La Selva, 26–27 Mar. 2004, canopy UV light 30 m up *Lecythis ampla* (Lecythidaceae) tree at CCL 350 in old-growth forest ca. 300 m from secondary forest (abandoned plantation), Gunther Brehm (1); La Selva, 27–28 Mar. 2004, ground-level UV light at SUR 900 in old-growth forest near border with secondary-growth forest, Gunther Brehm (1); La Selva, 27 Mar. 2004, 1.5 cm branch with green leaves of cut-up, fallen *Topobea maurofernandeziana* (Melastomataceae) at CEN 565, L. R. Kirkendall (2); La Selva (ALAS project), 16 Feb.–18 April 2004, 5 combined Malaise/flight intercept traps, secondary forest (402); same place and period, 5 combined Malaise/flight intercept traps, primary forest (134); La Selva, 24 June–11 July 2006, secondary forest and forest edges, 21 collections from 13 thin, fallen *Castilla elastica* (Moraceae) branches, 1 from fallen *Cecropia* leaf, Hanne Andersen; Prov. Alajeula, Canõ Negro, 49 m, 1–5 Sept. 2005, J. Azofeifa, Y. Cárdenas, M. Moraga, ecotono, INBio collection #84533 (1); Prov. Limón, La Suerte Biological Station, 10° 26' 30" N, 83 ° 46' 15" W, pitfall traps in secondary forest and a grove of exotic bamboo, 14 May 2005 (22) and 16 Sept. 2006 (10), light trap in secondary forest 12 April 2006 (1), Erica McAlister.

PANAMA, Colon Prov. San Lorenzo Protected Area, 917'N 79º58'W 130 m elevation, old-growth forest, 22 Sept. 2003 to 30 Oct. 2004, ground level UV light traps, R. Kitching (149), ground level flight intercept traps, A. Tishechkin (76), flight intercept traps at different heights, R. K. Didham, L. L. Fagan & M. Rapp, 0 m (136), 1.3 m (61), 7 m (119), 14 m (27), 21 m (3), 28 m (1), pit fall traps, E. Medianero (7), Malaise traps, S. Pinzon & N. D. Springate (2); same site, beating 2 cm dia. recently dead branches of *Calliandra* sp. (Fabaceae) 15 Oct. 2003, F. Ødegaard (1), beating 3 cm dia. recently dead branches of *Poulsenia armata* (Moraceae) 28 May 2004, F. Ødegaard (1).

Diagnosis. Among xyleborine ambrosia beetles, *Xylosandrus crassiusculus* is easily recognizable by the combination of shape (Fig. 1a,b), separated procoxae (placing it in *Xylosandrus*), size (2.2–2.5 mm), and characteristic declivity with its dull surface and dense, scattered fine granules (Fig. 1c; see also Rabaglia *et al.*, 2006).

Comments. Like many other xyleborines, this stout, medium-sized Oriental species has been transported through commerce to many parts of the world (CAB International, 2005b). First detected in North America in 1974, it has rapidly spread throughout the southeastern U. S., westwards as far as Texas and northwards as far as Maryland (Atkinson *et al.*, 1988; Bright & Skidmore, 2002; Rabaglia, 2003; Rabaglia *et al.*, 2006; Wood & Bright, 1992). Small populations have recently become established in Oregon as well, introduced via hardwood railroad ties (CAB International, 2005b; LaBonte *et al.*, 2005). This aggressive species is considered a high-risk quarantine pest, and is recorded as killing otherwise healthy nursery stock and saplings (especially transplants) where it has been introduced in Africa and the U.S. (Atkinson *et al.*, 1988; Browne, 1963; CAB International, 2005b; Roberts, 1969; Schedl, 1962). For example, *X. crassiusculus* has caused considerable mortality to *Cinchona* planted in Java (Kalshoven, 1924), to *Aucoumea kleiniana* and *Khaya ivoriensis* plantations in Ghana (Browne, 1963), to peach orchards in South Carolina (Kovach & Gorsuch, 1985), and to potted *Quercus shumardii* and *Ulmus parviflora* in a nursery in Florida (Atkinson *et al.*, 2005). It is not known if the species can kill healthy plants or branches in natural forests. Local populations are known to have spread successfully into native tropical forests on Hawaii (Samuelson, 1981) and in peninsular Malaysia (Maeto *et al.*, 1999). The species normally breeds in smaller diameter stems or branches of a wide variety of host plant families; in Costa Rica it has been also collected several times from the woody petioles of fallen *Cecropia* leaves, though no breeding activity has been observed in them. Although common in small diameter breeding material, *X. crassiusculus* has also been collected from larger trunks and from timber (Atkinson *et al.*, 1988). The stratification data from flight intercept traps in the Panama study, suggest that this species normally flies at heights under 10 m above the ground.

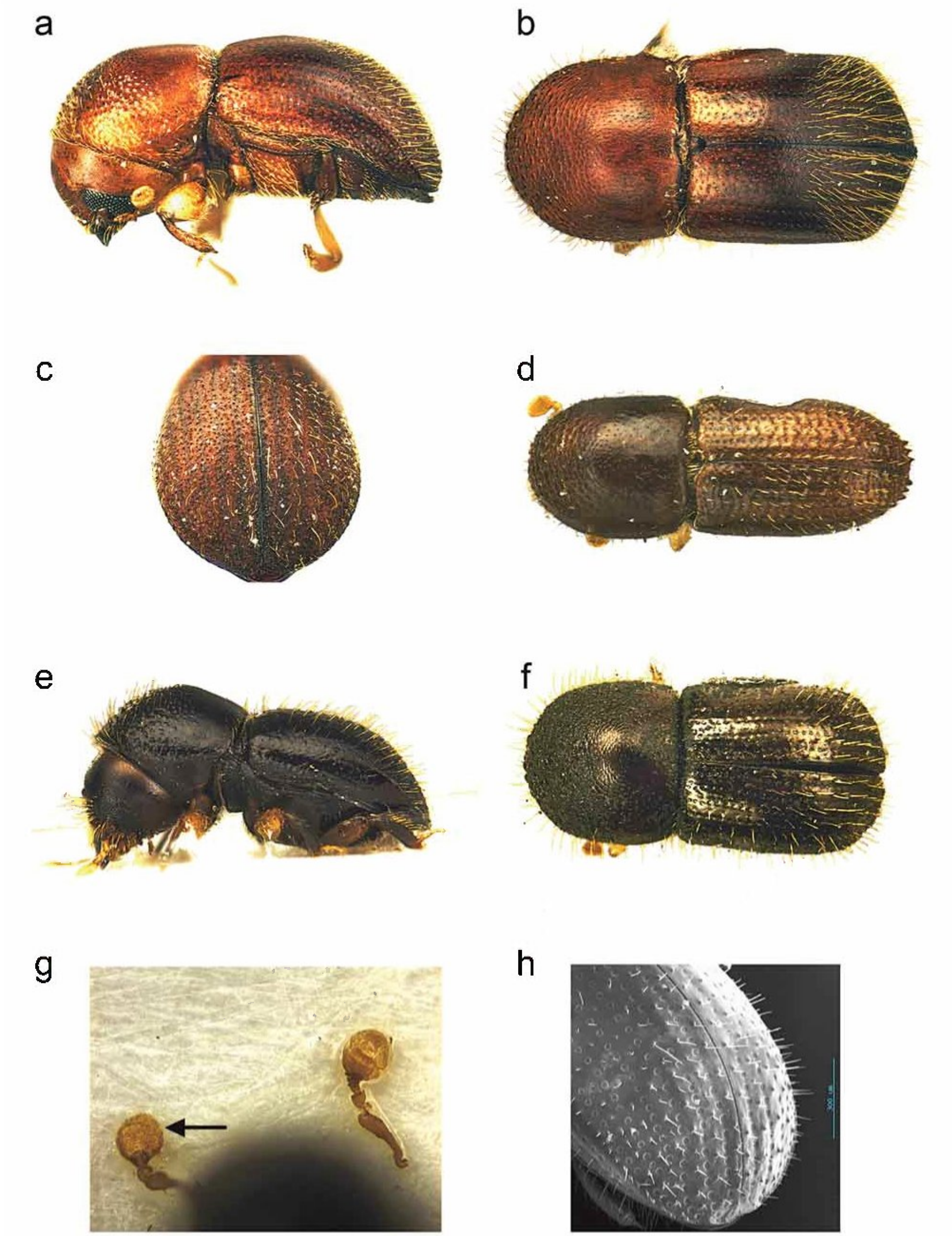

FIGURE 1. Invasive Asian xyleborine ambrosia beetles in Central American forests. (a–c) *Xylosandrus crassiusculus*: the shape (a), size (2.2–2.5 mm), and dull declivity with dense long setae and dense, scattered granules (c) are characteristic. (d) *Xyleborinus exiguus*: note the plain, convex declivity with a distinctive border of large teeth at the apex. (e–h) *Euwallacea fornicatus*: arrow (g) indicates suture on the posterior face of the antennal club (upper antenna in figure shows anterior face).

The earliest neotropical records are from a teak plantation and from La Selva Biological Research Station, both near the Caribbean port of Limón, northeast Costa Rica. The specimens from teak were taken from one of several trees which had apparently been initially weakened or killed by a lightning strike. The ambrosia beetles attacking the affected trees were primarily *Euplatypus parallelus* (Fabricius) and *Xyleborus affinis* Eichhoff, and included *X. ferrugineus* (Fabricius), *X. volvulus* (Fabricius) and the platypodines *Megaplatypus latreillei* (Chapuis) and *M. liratus* (Blandford).

La Suerte Biological Station is located 22 km E of La Selva, and less than 10 km NW of the teak plantations. The pitfall traps were baited with feces (monkey, human, cow, or chicken) and contained ethanol as a preservative. (Many scolytine beetles were found in the traps, presumably attracted by the ethanol.)

If *X. crassiusculus* had been established much earlier in northeast Costa Rica, specimens would certainly have been collected. Before 1996, no *X. crassiusculus* were collected by J. Saunders in the 1960s during thesis research on a cacao farm only about 40 km SE of La Selva; at La Selva in Malaise traps run by P. E. Hanson and helpers (1991–1993, as part of a country-wide Malaise trap network); or during extensive trapping and hand-sampling associated with the ALAS arthropod survey in the early and mid-1990s.

Some of the above records are from old-growth (primary) forest, though all of these are from sites less than 1 km from secondary-growth forest and almost all were sampled along or very close to established trails.This species is now the second most frequently collected scolytine breeding in small branches at La Selva Biological Station, after *Xylosandrus morigerus*—another well-established Asian exotic. Curiously, the two native central American congeners [*X. curtulus* (Eichhoff), *X. zimmermanni* (Hopkins)] are rarely collected by hand or in traps in Costa Rica–Panama, and native genera of ambrosia beetles specialized to small branches, such as *Coptoborus* and *Theoborus,* are infrequently encountered and uncommon in traps.

Many hundreds of individuals of *X. crassiusculus* have been collected from La Selva Biological Station since 1996. The single specimen found by the nation-wide insect inventory being conducted by INBio is from Caño Negro Wildlife Refuge, located approximately 90 km NW of La Selva and ca 15 km S of Lake Nicaragua. Taken together, these finds suggest that the species is now well established and widespread in the north and east of Costa Rica; it is also likely that it has spread into southern Nicaragua as well.

The large numbers of this species collected in the old growth forest in the Colón region of Panama indicate a well-established population there as well, but lack of earlier research in the region means that the age of the population is unknown. Since there has not been any other intensive collecting of wood-breeding insects along the Caribbean coast of southern Central America, we cannot say whether the collections from Heredia and Colón represent separate introductions or two samples from one continuous population. However, there are no specimens from southeastern Costa Rica in the country-wide general insect collections of the national biodiversity institute INBio. Nor has the species been found in flight intercept trap, Malaise, or UV light collections from Belize or Nicaragua conducted in the 1990s (Kirkendall, unpublished data). The species is not yet known from South America (Wood, 2007).

Xyleborinus exiguus (Walker)

(Fig. 1d)

Records: New to Americas. **COSTA RICA**, Puntarenas, Osa Conservation Area, Estación Esquinas, 200 m, coll. #2273, July 1993, INBio specimen barcode CRI001839038; same locality, Malaise trap, coll. #3087, June 1994, J. F. Quesada & M. Segura, INBIO barcode INB0003504987; Puntarenas, Golfito, Estación Agujas, Sendero Ajo, 250–350 m elevation, coll. #57259, 18 July 1999, large diameter *Brosimum utile* (Moraceae), R. Gonzalez Manual, INBio barcodes INB0003310007, INB0003310009, INB0003310010, INB0003310011, INB0003310012, INB0003310014; Puntarenas, Golfito, Estación Agujas, Sendero Homo, 300 m elevation, coll. #61424, 12 Aug. 2000, in trunk, A. Azofeifa, INB0003127510.

PANAMA, Panama Prov., Gamboa , 99'N 79º44'W, 50 m elevation, 28 Dec. 1995, at lights in second growth forest, F. Ødegaard (1); Darien Prov., Darien National Park, Pirre, Rancho Frio, 30 July 2002, Malaise trap, A. Santos & R. Miranda (1); Colon Prov., San Lorenzo Protected Area, 9º17'N 79º58'W, 130 m elevation, old-growth forest, 22 Sept. 2003–30 Oct. 2004, ground level UV light traps, R. Kitching (2), ground level flight intercept traps, A. Tishechkin (19), sticky traps, Y. Basset (14), pit fall traps, E. Medianero (1), canopy fogging, J. Schmidl & J. Bail (1), flight intercept traps at different heights, R. K. Didham, L. L. Fagan & M. Rapp, 0 m (53), 1.3 m (61), 7 m (33), 14 m (91), 21 m (115), 28 m (84), 35 m (26); Panamá Prov, Alto de Espave, 100 m elevation, 19 Dec. 2003, flight intercept trap, L. Guerra (1); Panama Prov., Cerro Azul, 800 m elevation, 4 Mar. 2004, flight intercept trap, L. Guerra (1). In addition, there are many specimens of this species in vials of unidentified Scolytinae collected by Hector Barrios (Univ. Panamá) from flight intercept traps in the dry tropical forest of Parque Natural Metropolitano (Panamá Prov., close to Panama City) in 1996–1997 (Kirkendall, unpublished identifications).

Diagnosis. This species was identified by direct comparison with Sri Lanka specimens determined by Karl E. Schedl and Malaysian specimens determined by Roger A. Beaver. The overall shape, conical scutellum (diagnostic for *Xyleborinus*), and pattern of teeth on the declivital margin (Fig. 1d) are characteristic.

Comments. This small, slender Oriental ambrosia beetle occurs naturally from Sri Lanka to Southeast Asia, and Indonesia to Sulawesi (Beaver, 2005). In what was the first report of the species from West Africa (from Gabon), *Xyleborinus exiguus* was one of the most numerous of the scolytines collected during intensive insect trapping from Jan.–Mar. 1999 (Basset *et al.*, 2001; Beaver, 2005).

Multiple specimens have been collected from two localities in southwest Costa Rica (Osa Peninsula and Golfito), and hundreds from scattered localities in central Panama, plus one from Darien National Park in southern Panama. Based on these records, it is probable that there is one continuous population in southern Central America, stretching from southwestern Costa Rica to (at least) the border between Panama and Colombia, but this needs to be corroborated by further collecting. It is only a matter of time before this species becomes established in South America; S. L. Wood did not see specimens of this species during his preparation of a monograph of the bark beetles of South America (Wood, 2007). It seems likely that this population was introduced to Panama via shipping from Asia, though a West African origin cannot be ruled out.

Xyleborinus exiguus does not seem to be size-selective in host use (Browne, 1961). Data from Panama indicate that this is a dominant scolytine in the canopy, but unlike *X. crassiusculus* it shows no height preferences. It is not considered to be an aggressive species (Browne, 1961); however, all ambrosia beetles are considered potential vectors for introducing pathogenic fungi (Beaver, 1988; Kühnholz *et al.*, 2001).

***Euwallacea fornicatus* (Eichhoff)**
(Fig. 1e–h)

Records. Recently discovered in North America (Rabaglia *et al.*, 2006; Thomas, 2005); one previous record for Neotropics, a single specimen from an unidentified branch in the Panama Canal Zone in July 1979 (Wood 1980)**. COSTA RICA**, Heredia, La Selva Biological Station 10º 26' N, 84º 01' W, 50–150 m elevation, 8 April 1982 (1) & 7 April 1983 (1), H. A. Hespenheide; La Selva, 12 July 1996 (1), 2 cm branch of *Protium panamense*, and 31 July 1997, 3 cm branch of *Cedrela odorata* (1), L. Kirkendall; La Selva, Project ALAS Malaise traps in old-growth forest emptied on 15 Feb. 1993 (1), 1 May 1993 (1), 2 May 1993 (1), 1 July 1993 (1), 15 Feb. 1994 (1), one in secondary growth forest, 2 April 1993 (2). The Malaise traps in old-growth forest are within 500 m of more disturbed habitats with the exception of a trap (M/08) which is ca 1100 m inside old-growth forest.

PANAMA, multiple collections from old-growth forest in Prov. Colón, San Lorenzo Protected Area: 1. Feb. 2002, beating dead branches of *Brosimum utile* in the understory, F. Ødegaard (1); 1–13 Oct. 2003, flight intercept trap at 14 m height, R. Didham & L Fagan (1); 11–15 Oct. 2003, sticky trap, Y. Basset (1); 31 May 2004, beating dead branches of *Tocoyena pittieri* (Rubiaceae), F. Ødegaard (1).

Diagnosis. This species was identified by direct comparison with authenticated specimens in The Natural History Museum (London). This species was sorted for several years as an unidentified species in the endemic genus *Theoborus*, in the ALAS collections. Though *Euwallacea* and *Theoborus* are not closely related (Jordal, 2002), these taxa are quite similar; *E. fornicatus* and most described and undescribed *Theoborus* from Central America have a carinate posterolateral declivital margin which extends from interstriae 7 or striae 7 on the disc (Fig. 1e, h), and *E. fornicatus* and *Theoborus* have similar body proportions, a suture on the antennal club continued on the posterior face (Fig. 1g, arrow), and a crenulate margin of the pronotum. This species can be identified using the key to *Xyleborus* in Wood (1982). However, it could easily key to *Theoborus* in that work (*op. cit.,* p. 69), if one does not have great familiarity with antennal club structure in this group, though it does not to key any species in that genus. *Euwallacea fornicatus* can be distinguished from native *Theoborus* species of Central America by a combination of size, shape, and details of the elytra (Wood, 1982).

Comments. The single Panama collection (Wood 1980) remained the only New World record until North American specimens were collected from the ornamental tree *Delonix regia* (Fabaceae) in Dade County, Florida in 2002, and in 2003 in Los Angeles County, California, from four different hosts (*Acer negundo, Alnus rubra, Platanus racemosa*, and *Robinia pseudoacacia*); since then, repeated collections in Dade and Broward counties suggest that *E. fornicatus* is solidly established in the southern tip of Florida (Haack, 2006; Thomas, 2005).

This Old World species is notorious as a pest of tea ("the shot-hole borer of tea"), in Sri Lanka and southern India, Borneo, and Java; elsewhere, it is a pest in plantations, recently reforested plots, and nurseries (Browne, 1961; CAB International, 2005a; Kalshoven, 1958). Most attacks are to twigs and small branches or stems. *Euwallacea fornicatus* seems to be much less abundant than the previously discussed species, with very few specimens yet known despite the intensive sampling of wood-boring insects at the collection sites. As with *X. crassiusculus*, we cannot say if the disjunct distribution (northeast Costa Rica–central Panama) reflects lack of sampling in the intervening region or separate populations resulting from multiple introductions.

Wood (2007) reports a series of specimens from Manaus, Brasil, but with no collection data.

Discussion

How recently established are these populations? There is a striking absence of specimens in large insect samples from the same or similar forests in Costa Rica, from the 1960s to 1990s. No specimens of these three species were found by Kirkendall among over 2000 scolytines from the Costa Rican Malaise trap network run between 1989 and 1995 by University by Costa Rica entomologist Paul Hanson (Hanson, 1992; Hanson & Gauld, 1995), among hundreds of scolytines collected from cacao between 1963–65 near Siquirres, Limón province, eastern Costa Rica by J. L. Saunders (collection at CATIE, Turrialba, Costa Rica), or among hundreds of scolytines collected by H. A. Hespenheide at La Selva Biological Station (Heredia province, C.R.) dating back to 1968 (Kirkendall, unpublished identifications).

These three species are from the haplodiploid clade which combines *Coccotrypes* and Xyleborini, after removing *Premnobius* from the latter (Jordal, 2002; Jordal *et al.*, 2000), and they regularly inbreed by brother-sister mating. Ambrosia beetles such as these three species tunnel in the sapwood of dead woody plants, and the sole food source of all stages is symbiotic fungus which they transport and cultivate. Given the simple, generic composition of dead xylem tissue, it is no wonder that ambrosia beetle species usually breed in a wide range of host plant taxa (Atkinson & Equihua, 1986; Beaver, 1979; Browne, 1961; Kirkendall, 1983; Noguera-Martinez & Atkinson, 1990; Wood & Bright, 1992).

These attributes—inbreeding and polyphagy—contribute to colonization success. Inbreeders presumably do not go through genetic bottlenecks when experiencing periods of small population size, do not face the mate location problems which confront beachhead populations, and can potentially start a new population from a single fertilized female (Jordal *et al.*, 2001; Kirkendall, 1993). And, breeding sites are potentially abundant, when new arrivals are able to utilize a broad range of woody plant species. Finally, beetles in tunnels deep in wood are readily transported from one continent to another, in timbers or in wood packing material and pallets, a fact which accounts for the high proportion of scolytines among established alien arthropods in North America (Haack, 2001; 2006).

It is striking that all three species prefer, or at least commonly breed in, small branches. In our experience in the southern Central American lowlands, small dead branches seem to be underutilized by saproxylophages. While fallen trees are usually quite densely colonized by scolytine and platypodine ambrosia beetles, the vast majority of isolated dead branches have no or very few ambrosia beetles colonizing them; nor are populations of other wood-utilizing insects such as other curculionoids, cerambycids, bostrichids and anobiids so abundant as to severely restrict the availability of breeding sites in fallen small branches.

Undisturbed, old-growth habitats are often thought to be impervious to invasion by introduced species, in part due to their high levels of species richness (Herbold & Moyle, 1986; Hooper *et al.*, 2005b; Huston, 1994; Simberloff, 1981; Stachowicz & Byrnes, 2006): indeed, the single most important factor influencing invasibility of an ecosystem is thought to be the degree to which it has been disturbed (Elton, 1958; but see also Hooper *et al.*, 2005a). Surprisingly, exotic scolytines such as those reported here seem well established in old-growth forests. Generally, highly successful exotic plants and animals are considered "tramp species" or "weedy", because they are characteristic of disturbed or early successional habitats (Connell, 1978; Huston, 1979), and alien species rarely if ever succeed in penetrating more established communities. However, in the primary forests in which we collected these three species, one readily collects such pantropical Oriental scolytine exotics as *Coccotrypes advena* Blandford, *C. carpophagus* (Hornung), *C. cyperi* (Beeson), and *Xylosandrus morigerus* (Blandford), as well as the African *Premnobius cavipennis* Eichhoff; all are inbreeders and host plant generalists, and the latter two are ambrosia beetles. Inbreeding Scolytinae, then, seem to make up an interesting exception to this "common wisdom" about alien species, apparently due to the success of their unusual mating system and their ecology. Although certain widespread scolytine bark and ambrosia beetles could be considered "weedy", the data presented in this paper indicate that scolytines may prove an interesting exception.

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NOTE ADDED IN PROOF

A specimen of *X. crassiusculus* has now been found which had been collected from a site ca 130 km SE of La Selva, 35 km S of the port of Limón: Prov. Limón, Reserva Biol. Hitoy Cerere, Est. Hitoy Cerere, Quebrada Borrera, 160 m, 10 April 2000; INBio coll. #56333. The locality is at ca N 9° 40’, W 83° 01’. This find strengthens the possibility of there being one continuous population of the species along the Caribbean coast of lower Central America.