

The bark and ambrosia beetles (Curculionidae, Scolytinae) of Cocos Island, Costa Rica and the role of mating systems in island zoogeography

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Cocos Island is a small oceanic island midway between Costa Rica and the Galápagos Archipelago; about 2 Myr in age, it is the only tropical oceanic island in the eastern Pacific with tropical wet forest. We identified several hundred bark beetle specimens collected during recent expeditions by INBio, the National Biodiversity Institute of Costa Rica, and re-examined all specimens from earlier collections. We report 19 species in ten genera, seven or eight of which are endemic, making scolytines the largest group of beetles known from the island. We describe as new *Pycnarthrum pseudoinsulare*, *Xyleborinus cocoensis*, and *Xyleborus sparsegranulosus*, resurrect *Xyleborus bispinatus* as separate from *X. ferrugineus*, and report six other species as new to Cocos Island. Three-quarters of the scolytines reproduce by brother–sister mating, and we argue that inbreeders are superior island colonists because they are less affected than are outbreeders by problems of mate location and inbreeding depression. The fauna and flora of Cocos Island arrived by dispersal and human transport. We examine natural colonization patterns for the fauna, using the distributions of the relatives of island endemics: most colonization came from the Americas, but the closest relatives to some endemics are found on Caribbean or Galápagos islands. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 89, 729–743.

ADDITIONAL KEYWORDS: Baker's rule – colonization – inbreeding – island biogeography.

INTRODUCTION

Since the voyage of the Beagle, investigations of island biotas have led to key insights into major evolutionary processes behind the origin of organismal diversity. Research on the Hawaiian, Canary, and Galápagos Islands in particular has provided a wealth of information on modes of speciation, relationships between ecology and speciation, and the time scales over which speciation processes occur (Juan *et al.*, 2000; Gillespie & Roderick, 2002). Islands that are isolated over extended geological time scales ultimately foster divergent phenotypes or ecotypes, often sufficiently different from their continental relatives to be named

as evolutionarily separate entities. However, detailed analyses of island diversity and endemism are critically dependent upon thorough sampling and sound taxonomic analyses of focal taxa. Small islands are therefore excellent model systems, because these can be sampled more thoroughly for hyperdiverse taxa such as arthropods, resulting in more complete taxonomic lists.

Cocos Island (Isla del Coco) is a small island (46.6 km²) belonging to Costa Rica, located midway between that country and the Galápagos Archipelago, about 500 km west of Costa Rica and 630 km north-east of the Galápagos. The island was formed by recent (2 Mya) volcanic activity; its highest peak, Cerro Iglesias, is 575 m (Castillo *et al.*, 1988). Because of its small size, young age and isolation, this tropical island is particularly suited to the study of colonization and establishment of populations; among evolu-

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tionary biologists, it is perhaps best known for studies of ecological release or niche expansion, in which single species experiencing little or no interspecific competition evolve an extraordinary degree of ecological and behavioural plasticity [as in a theridiosomatid spider (Eberhard, 1989) and the endemic 'Darwin's finch' (Werner & Sherry, 1987)]. Of particular importance is the fact that Cocos Island, with its 7-m rainfall annually, is the only tropical oceanic island in the eastern Pacific that has tropical wet (as opposed to dry) forest, a habitat which is similar in form and structure (though not in species composition) to those of most of the closest potential mainland source areas in Central and northern South America (Hogue & Miller, 1981).

As is typical for such a small isolated island, the flora and fauna are depauperate relative to their continental source communities, and taxonomically imbalanced ('disharmonious'), with the island lacking many abundant mainland taxa (Fournier, 1966; Hogue & Miller, 1981; Brown, 1990). Among terrestrial vertebrates, for example, there are only four resident bird species, two reptiles, one freshwater fish, and no amphibians or native mammals (World Conservation Monitoring Centre, 1997). Fewer than 400 insect, arachnid, and myriapod species have been recorded from the island (Hogue & Miller, 1981; Bright, 1982; Cwikla & Freytag, 1982; Johnson, 1982; Adams, 1983; Nickle, 1983; Bellamy, 1986; Brown, 1990; Brown, Donahue & Miller, 1991; Woodley, 1991; Davis, 1994; Jordal, 1998a; Brown & Miller, 1999; Anderson & Lanteri, 2000). Wood-boring, leaf-mining, and epiphyte-dwelling species are among the more species-rich insect groups on the island, supporting a key role for rafting on plant material in the colonization process (Hogue & Miller, 1981).

Comparative studies of island faunas have demonstrated a close relationship between mating behaviour and the bark beetle (Curculionidae, Scolytinae) communities of islands: species with regular brother-sister inbreeding are overrepresented on small islands compared with neighbouring mainland forests; tropical islands have a higher proportion of inbreeders than do temperate islands; outbreeding species are more likely than are inbreeders to speciate on small islands (Kirkendall, 1993; Jordal, Beaver & Kirkendall, 2001). Faunistic details for particular islands and archipelagos are needed in order to explore such patterns further and to understand more fully the historical and ecological conditions necessary for successful colonization (Bright & Peck, 1998).

In this context, we here update the faunal composition of scolytine beetles for Cocos Island, roughly doubling the number of species known from the island. (Scolytines we refer to collectively as 'bark beetles', but this term is also used in a more restrictive, eco-

logical sense to refer to those scolytines breeding in inner bark.) Four papers have dealt with the bark beetle fauna of Cocos Island (Schedl, 1974; Bright, 1982; Wood, 1982; Wood, 1986a), bringing the number of species previously known from the island to 10.

We describe three species new to science, report another seven species as new to the island, and correct previous misidentifications, resulting in a compilation of 19 species of Scolytinae – making bark beetles the largest group of beetles, tied with ants as the largest family or subfamily of arthropods currently known from Cocos Island (Solomon & Mikheyev, 2005). We conclude with a brief discussion on general zoogeographical trends that can be deduced from patterns of endemism for the terrestrial fauna of Cocos Island.

MATERIAL AND METHODS

Cocos Island collections examined and type material are deposited in the National Institute for Biodiversity, Costa Rica (INBio) unless noted otherwise. Other collections examined included those from the Museum of Comparative Zoology, Harvard University (MCZ); Natural History Museum, London (NHM); California Academy of Science (CAS); Natural History Museum of Los Angeles County (LACM); Stephen L. Wood, Brigham Young University, property of the US National Museum (SLWC); private collection of Lawrence R. Kirkendall, University of Bergen, Norway (LRKC). Material of the *X. ferrugineus* complex was borrowed from the Zoological Museum of the University of Copenhagen (ZMUC), the Royal Museum for Central Africa (RMCA, in Belgium), Institute Royal des Sciences Naturelles de Belgique (IRSNB), and the Karl Schedl collection in the Natural History Museum of Vienna (NHMW).

Species determinations of problematic taxa were made by direct comparison with type material wherever possible. Identification of scolytines often requires meticulous observation of surface sculpture details (e.g. Wood, 1982) which are difficult or impossible to see with normal light sources (such as fibre optic lights); we used one or two small fluorescent lamps with 7-W bulbs as sources of flat light for this purpose.

Terminology follows Wood (Wood, 1986b) and measurements were in accordance with methods described by Jordal (1998a). Note that all measurements were based on perpendicular views of the dorsal aspect of a specimen. Species are listed alphabetically by genus, with the order of genera following the classification by Wood (1982). Full synonymies and other taxonomic information for previously described species can be found in Wood & Bright (1992) and are not repeated here. Complete label data are given only for type material of new species; label data were translated

from Spanish for the INBio collections, including most place names.

Unless otherwise stated, information on overall species distribution and host plant usage were obtained from Wood & Bright (1992), and ecological data (such as type of breeding material used) from Wood (1982). Classification as inbreeding or outbreeding follows Kirkendall (1993; see also Hamilton, 1967). Thus, all Xyleborini, *Coccotrypes* and *Hypothenemus*, as well as the small *Araptus* complex discussed below, were classified as inbreeding by sibling mating because: (1) in all cases where males are known, they are morphologically adapted to extreme inbreeding, having reduced eyes and nonfunctional flight wings, (2) usually only one or a few males occur per brood, and (3) females reproduce alone (males are found with breeding females in most outbreeding species, Kirkendall, 1983).

ANNOTATED LIST OF SPECIES

(1) *PHLOEOTRIBUS PACIFICUS* BRIGHT

New records: Wafer Bay (close to sea level), January 1994 (2), February 1994 (3), and March 1994 (10), Malaise traps, Yolanda Camacho (INBio).

Comments: The type material was taken at a black-light trap at Wafer Bay in March 1978, and at light at Chatham Bay in April 1979. According to Bright (1982), the species is most similar to *P. biguttatus* Blandford; the latter is known from Panama, Columbia and Venezuela, the host for which is given as *Brosimum*. All species in this genus are outbreeding and breed in inner bark.

(2) *PYCARTHURUM BROSIMI* WOOD

Comments: This record is based on eight specimens (SLWC) collected from *Brosimum* by G.C. Stevens in April 1980 (Wood, 1982), and the identification of these specimens was verified by L.R.K., by comparison with type material in SLWC. This species has previously been collected only in Venezuela and Columbia. All species in this genus are outbreeding and breed in inner bark.

(3) *PYCARTHURUM PSEUDOINSULARE* SP. NOV.

(FIG. 1)

Type material: Holotype female(?): COSTA RICA, Puntarenas, Isla del Coco, Wafer Bay, 25 March 1978, C. Hogue & S. Miller (Steele exp.) (LACM).

Etymology: The name is based on the similarity to *P. insulare* Blair, endemic to the Galápagos Islands.

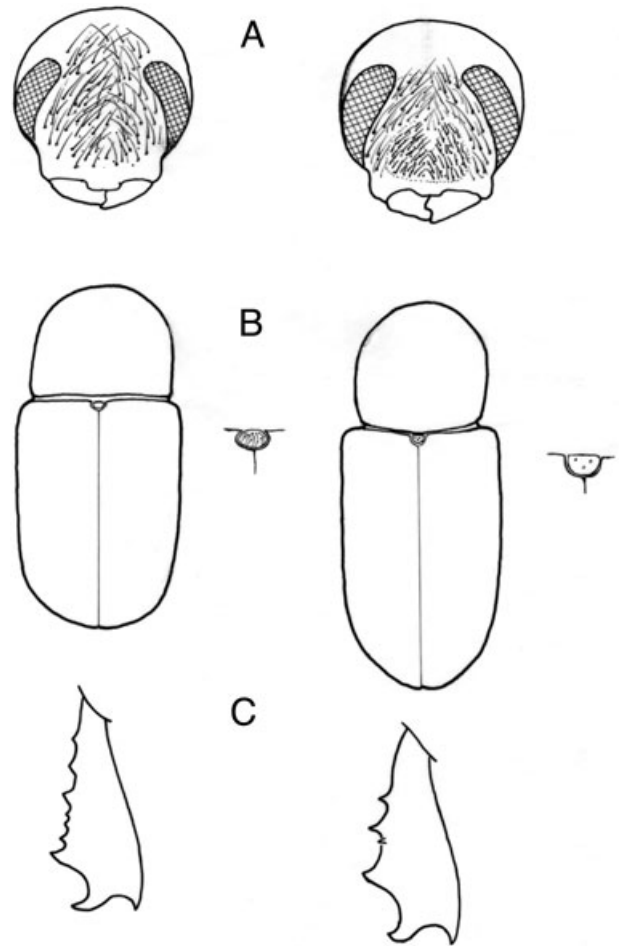


Figure 1. Comparison of *Pycnarthrum pseudoinsulare* sp. nov. (left side) and *Pycnarthrum insulare* Blair (right side). A, frons. B, dorsum (on the right is the scutellum, enlarged). C, posterior face of left protibia.

Description of female (male unknown): Length 2.0 mm, 2.1 times longer than wide; colour yellowish brown.

Frons (Fig. 1A) weakly convex above, flattened below; surface granulate, reticulate, subshining; granules associated with base of long hairlike setae which are evenly distributed from epistoma to well above upper level of eyes. Eyes separated above by more than twice their width. Antennal club 1.8 times longer than wide, with two weakly procurved, oblique sutures; funicle six-segmented.

Pronotum 0.93 times as long as wide; sides subparallel to anterior third, then rather broadly rounded in front (Fig. 1B); surface reticulate, subshining, punctures shallow, separated by a distance equal to their diameter; vestiture consisting of bristles and hairlike setae.

Elytra 1.45 times longer than wide, 1.8 times longer than pronotum, sides straight and parallel on basal

two-thirds, broadly rounded behind (Fig. 1B); scutellum (Fig. 1B) with tiny hairlike setae, base of elytra extending to and partly embracing anterior part of scutellum; striae 1 weakly impressed, other not impressed, punctures separated by a distance equal to their diameter; interstriae three times as wide as striae, punctures minute, obscure. Declivity steep, broadly flattened, striae 1 more deeply impressed than on disc. Vestiture consisting of scalelike interstitial setae in three irregular rows, bristles in median rows stouter and twice as long as those in lateral rows; tiny hairlike setae arising from striae punctures.

Procoxae separated by 0.4 times the width of one procoxa; protibiae armed by a lateral row of irregularly sized unsocketed teeth, distal teeth one and two larger than the others (Fig. 1C). Lateral, apical edge of metatibiae truncately arched, with four small, socketed lateral teeth on distal fifth.

Sex judged to be female by comparison with males and females of *P. insulare*.

Comments: The holotype was compared with two syntypes of *P. insulare* (CAS) and eight other males and three other females of the latter species (MCZ). The new species is distinguished from the otherwise similar *P. insulare* by the different female frons, scutellum, protibiae and general outline (Fig. 1). *P. pseudoinsulare* is stouter (2.1 vs. 2.3 times longer than wide), has more widely spaced eyes, has a hairy scutellum that is embraced anteriorly by the elytral bases, and has protibiae which lack an additional tooth inside the lateral margin (between lateral teeth 2 and 3). In addition, the pronotal punctures are distinctly smaller in *P. pseudoinsulare*.

The specimen identified by D.E. Bright as *P. insulare* (Bright, 1982) is our designated holotype of *P. pseudoinsulare*. The species described by Blair is consequently removed from the list of species on Cocos Island.

(4) *SCOLYTODES PACIFICUS* JORDAL

Comments: Previous records were included with the description of the species (Jordal, 1998a). This outbreeding species colonizes petioles of fallen *Cecropia pittieri* leaves. It is most closely related to *S. impressus* Wood, known from Cartago in central Costa Rica (Wood, 1982) and from the Osa Peninsula on the Pacific coast where it was taken from *Xylopia* sp. (Annonaceae) (Jordal, 1998b).

(5) *COCCOTRYPES CYPERI* (BEESON)

New record: Isla del Coco, April 1980, G.C. Stevens (2) (SLWC).

Comments: Recorded for the first time on Cocos Island. In Costa Rica, this species is common at lower elevations, and collected from trunks, branches, petioles, and seeds of a wide variety of woody plants (Wood, Stevens & Lezama, 1991). According to Wood (1982; p. 736), this inbreeding species was introduced recently to the western hemisphere (where it is widespread) from the Indo-Malayan area. The earliest American record is from San José, Costa Rica (6 May 1915).

(6) *AMBROSIODMUS PAUCUS* WOOD

Comments: This species was described from a single female specimen collected in April 1980 from 'Isla del Coco' by G.C. Stevens (SLWC) (Wood, 1986a). No subsequent collections exist. It is related closely to *A. devexulus* (Wood), a Caribbean species, and there are several other similar species from Mexico and Central America. *Ambrosiodmus* is predominantly Asian and was separated only recently from *Xyleborus* (see Wood, 1986b); none of the neotropical species are collected frequently in Central America. As for all Xyleborini, *Ambrosiodmus* species are inbreeding ambrosia beetles.

(7) *XYLEBORINUS COCOENSIS* SP. NOV. (FIGS 2, 3)

Material: Holotype female: COSTA RICA, Puntarenas, Isla del Coco, Cerro Iglesias, 600 m, October 1994, Intersección, #3352, J.F. Quesada (INBio). Paratype females: same data as holotype (13); Bahia Chatan, October 1994, yellow pan traps, #3350, J.F. Quesada (83); Bahia Wafer, February 1994, Y. Camacho, Malaise, #2601 (2); 26–28 February 1980, T.K. Werner & T.W. Sherry, Malaise trap (1) (INBio); 17–21 March 1980, T.K. Werner & T.W. Sherry, Malaise trap (5) (INBio).

Other material: 'treefall, top C. Iglesias', 28 February 1980, T.W. Sherry & T.K. Warner, *Xyleborinus intersextosus* (Bldf.), D.E. Bright 1980 (this individual was used for the SEM photos in Fig. 2).

Etymology: The name is derived from the type locality, Isla del Coco.

Description of female (male unknown): Length 1.78–1.94 mm, 2.5–2.7 times longer than wide; mature colour dark brown, holotype yellow.

Frons broadly convex; surface rugosely reticulate, a few coarse, shallow punctures; vestiture consisting of a few hairlike setae. Funicle five-segmented, antennal club obliquely truncate.

Pronotum (Fig. 2A) 1.1–1.2 times longer than wide; sides straight and subparallel, rather broadly rounded in front; summit at middle; anterior slope coarsely asperate; posterior half reticulate, punctures fine,

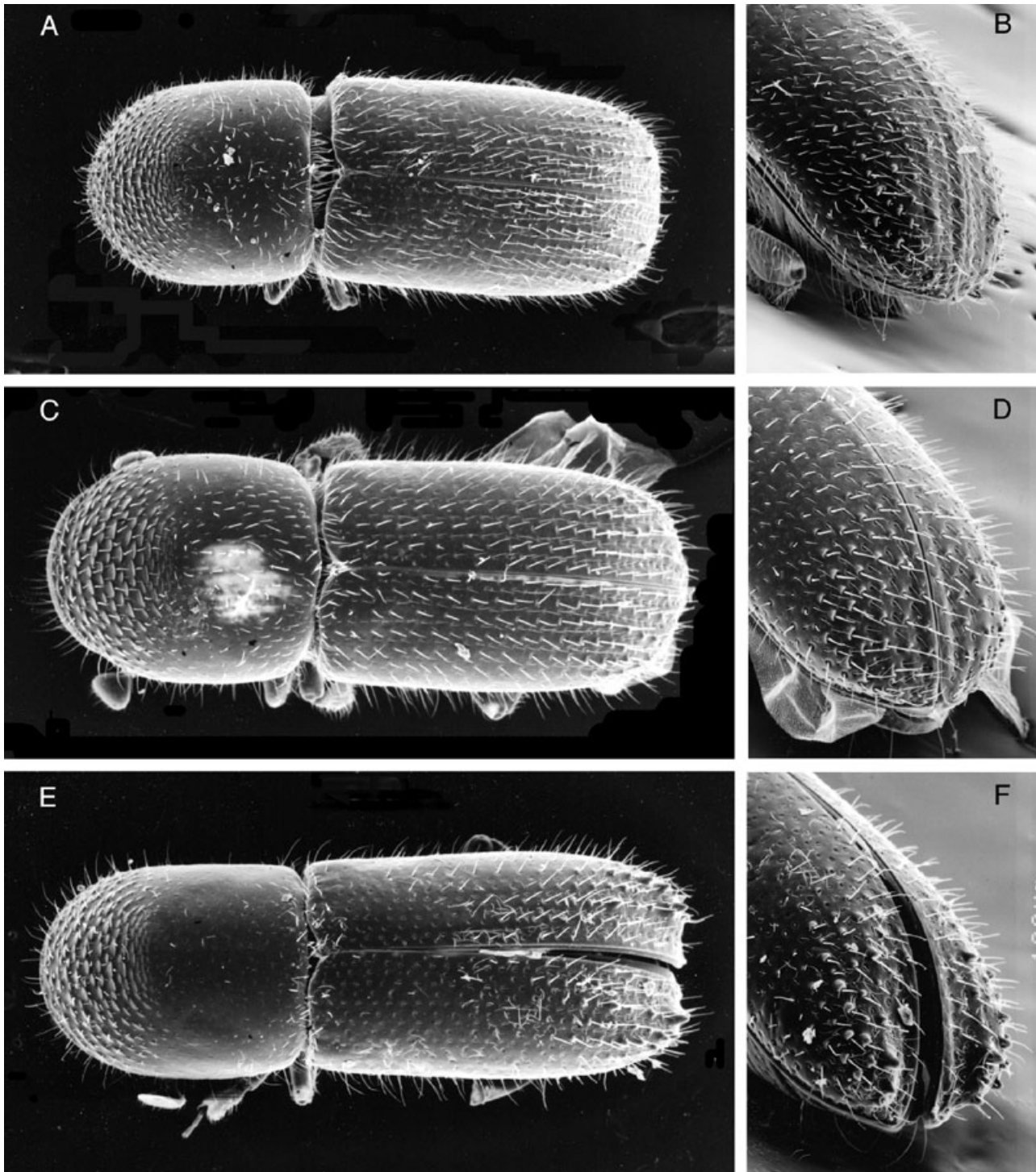


Figure 2. SEM photographs of three *Xyleborinus* species showing whole body and declivity. A, B, *X. cocoensis* sp. nov. C, D, *X. intersetosus*. E, F, *X. gracilis*. (The lighter area on the pronotum in 'C' is an artifact.)

closely separated. Vestiture consisting of hairlike setae, confined mostly to marginal areas.

Elytra (Fig. 2A) 1.5–1.6 times longer than wide, 1.4 times longer than pronotum; sides straight and paral-

lel on basal two-thirds, then weakly tapered to the broadly rounded apex; disc confined to slightly more than basal half; scutellum conical and does not fit into the sutural notch; striae not impressed, punctures

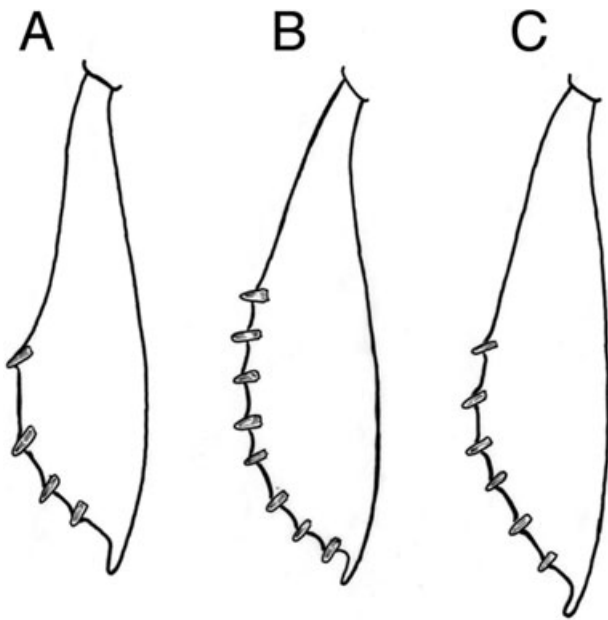


Figure 3. Posterior face of left protibia for three xyleborine species: A, *Xyleborinus intersetosus*; B, *X. cocoensis* sp. nov.; C, *X. gracilis*.

minute, separated within a row by two to four times their diameter; interstriae smooth, shining, five times wider than striae, punctures slightly smaller than those of striae. Declivity (Fig. 2B) moderately steep, broadly convex; striae 1 and 2 slightly impressed; interstriae 1 with tubercles absent or obscurely indicated, interstriae 2 smooth and with no tubercles, interstriae 3 with one minute tubercle near base and a larger one close to apex which is as large as the largest on the posterolateral margin. Vestiture consisting of rows of small hairlike strial setae, and rows of slightly confused interstitial bristles, each bristle twice as long as the distance between bristles within a row.

Procoxae contiguous; protibiae (Fig. 3B) broad, with eight lateral, socketed teeth on distal half.

Comments: Specimens were compared with the holotype of *X. intersetosus* Blandford (NHM) and with numerous specimens of that species from Cocos Island and the Costa Rican mainland deposited in the INBio and LRK collections. The new species is readily distinguished from the closely allied *X. intersetosus* by the numerous teeth on the protibiae (Fig. 3B), the latter having only four socketed teeth on distal third (Fig. 3A). Furthermore, *X. intersetosus* is smaller (max. 1.6 mm vs. max. 1.9 mm), and has rows of subequal tubercles on interstriae 1, 2 and 3 on the declivity, none of which are as large as are those on ventrolateral angles of the declivity. Interstitial bris-

gles of *X. intersetosus* are more widely spaced (by their length vs. by half their length), stouter, and in more complete rows. The declivital apex is more acutely rounded in *X. intersetosus* (Fig. 2C).

(8) *XYLEBORINUS GRACILIS* (EICHHOFF) (FIGS 2, 3)

New records: Chatham Bay, 5–9 February 1993, hand sampling, F. Quesada (2); Wafer Bay, Malaise trap, February 1994, Y. Camacho (1); Chatham Bay, October 1994, yellow pan trap, J.F. Quesada (4); Cerro Iglesias, 600 m, flight intercept trap, October 1994, J.F. Quesada (4).

Comments: First record for Cocos Island. The seven specimens collected from Cocos Island deviate slightly from mainland Costa Rican material in that the major denticle on the third interstriae on the declivity is not as dramatically produced. On the mainland, this ambrosia beetle has been taken from a variety of branches, lianas and tree saplings.

(9) *XYLEBORINUS INTERSETOSUS* (BLANDFORD)
(FIGS 2, 3)

New Records: Wafer Bay, Malaise trap, March 1994, Y. Camacho (4).

Comments: The single specimen of *X. intersetosus* previously reported from Cocos Island (Bright, 1982) belongs to the new species described above. Hence, the four specimens reported here constitute the first true record of this polyphagous ambrosia beetle from this island.

10. *XYLEBORUS AFFINIS* EICHHOFF

New Records: Wafer Bay, Malaise trap, Feb (4), March (5), April (31), May (11), June (8) 1994 (total 59), Y. Camacho; Chatham Bay, 5–9 February 1993, J.F. Quesada, Malaise trap (75), by hand (10); Chatham Bay, yellow pan trap, October 1994, J.F. Quesada (11); Cerro Iglesias, 600 m, flight intercept trap, October 1994, J.F. Quesada (3); El Guarumal, trail Wafer-Chatham, 30 m, 29 December 1997, at light, E. Ulate and C. Flores (3); Iglesias waterfall at Bahia Iglesias, hand sampling, 21 December 1997, E. Ulate and C. Flores (1); El Gallinero coast, trail to Cerro Iglesias, 260 m, Malaise trap 28 December 1997–28 February 1998, E. Ulate and C. Flores (1).

Comments: Previous records are from blacklight, white light, and hand sampling. No host records have been recorded from the island, but this cosmopolitan inbreeding ambrosia beetle is extremely polyphagous.

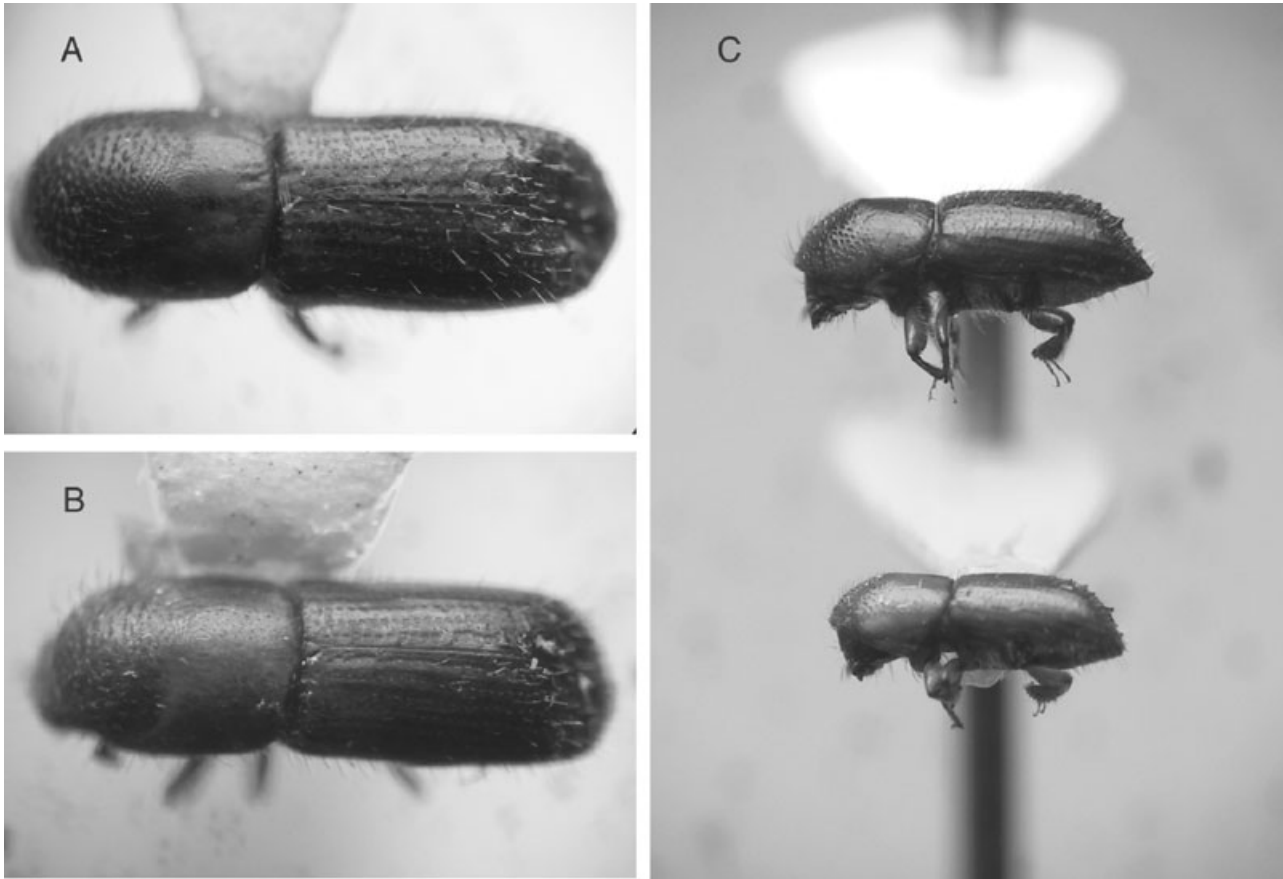


Figure 4. Comparisons of elytral interstriae and of lateral profiles for *Xyleborus bispinatus* and *X. ferrugineus* (digital photos). A, dorsal view of elytra of *X. bispinatus*. B, dorsal view of elytra of *X. ferrugineus*. C, lateral view of *X. bispinatus* (above) and *X. ferrugineus* (below).

11. *XYLEBORUS BISPINATUS* EICHHOFF
(REINSTATED SPECIES) (FIG. 4)

New Records: Wafer Bay, Malaise trap, June 1994, Y. Camacho (3); Chatham Bay, October 1994, J.F. Quesada (9); Chatham Bay, yellow pan trap, October 1994, J.F. Quesada (6); Cerro Iglesias, 600 m altitude, flight intercept trap, October 1994, J.F. Quesada (9).

Comments: We believe that neotropical specimens currently being identified by bark beetle specialists as *X. ferrugineus* actually comprise two species, *Xyleborus ferrugineus* s.s. and a second, larger species. These two forms are broadly sympatric in Central and northern South America, and were clearly distinguished by Blandford (1905) for Central America. The smaller taxon with the pair of large denticles in the middle of the declivity (Fig. 4B, C) is *X. ferrugineus* (Fabricius) (lectotype examined by Kirkendall). The larger species agrees with the Brazilian syntypes of *X. bispinatus* Eichhoff, which is currently a synonym of *X. ferrugineus* (Schedl, 1960b); *X. bispinatus* is the

senior-most of several synonyms which we believe apply to this second species. [The taxonomy of North American '*ferrugineus*' is also unclear, and the subject of current research; two forms are found, one of which is *X. impressus* Eichhoff (Rabaglia, 2005), the other of which seems to be consistently different from *X. ferrugineus* and *X. bispinatus* and which should probably be treated as *X. fuscatus* Eichhoff (L.R. Kirkendall, unpubl.).]

Xyleborus bispinatus is larger on average than is sympatric *X. ferrugineus* (seen clearly when series of the two are compared directly) and usually slightly darker; it has the major pair of denticles on the declivity closer to the base of the declivity (Fig. 4A, C). It has regularly spaced hairlike setae in the discal interstriae (the interspaces between the rows of punctures) of the elytra (Fig. 4A); these setae are few or absent in *X. ferrugineus*, especially near the base of the elytra (Fig. 4B). *X. ferrugineus* has a weak, broad impunctate vertical median carina on the frons. The frons of *X. bispinatus* is usually flattened medially (with at

most a very short broad carina just above the epistoma); in the place of the carina is an impunctate median area in the shape of an inverted triangle, the upper portion of which occasionally appears slightly impressed.

Specimens of *X. bispinatus* have been examined from countries as far north as Belize and as far south as Ecuador, Bolivia and Brazil, but an exhaustive search of museum collections has not yet been carried out, so its exact distribution is not yet known.

Lectotype designation: We hereby designate one of Eichhoff's seven Brazilian syntypes as the lectotype for *X. bispinatus*. The original, round locality label reads 'S. Cathr./Deyr.', which we interpret as being collected by Henri Deyrolle from the province of Santa Catarina in southern Brazil (see collection data for species 99 in Schedl, 1960a). The handwritten round label has been mounted on a printed purple museum label reading 'Coll. R. I. Sc. N. B./Brazil', to which is also glued an original 'Coll. Chapuis' label. Also on the pin is a 'Type' label, and a mounted, handwritten label in Eichhoff's hand, '*Xyleborus bispinatus m*' ('meus', mine). Four other specimens have similar mounted round labels but with the locality given as 'Bresil'. All seven specimens have printed 'Type' labels. All have labels saying they were determined by Eichhoff; four (including the lectotype) have determination labels written by Eichhoff. We designate the other six specimens as paralectotypes, and have labelled the seven in accordance with this treatment.

12. *XYLEBORUS FERRUGINEUS* (F.)

New Records: Chatham Bay, Río Genio, Malaise trap, 5–9 February 1993, J.F. Quesada (17); Wafer Bay, Malaise trap, June 1994, Y. Camacho (3); Cerro Iglesias, 600 m altitude, flight intercept trap, October 1994, J.F. Quesada (1); Casa Wafer, 15–31 December 1997, hand collecting, Ulate and Flores (1); El Guarumal, Wafer-Chatham trail, 30 m, at light, 29 December 1997, Ulate and Flores (10).

Comments: See comments under *X. bispinatus*. Previously recorded Cocos Island specimens of *X. ferrugineus* were taken from rotting wood and at blacklight. One host has been recorded, *Ochroma pyramidalis* (balsa) (Schedl, 1974), but these ambrosia beetles are quite polyphagous.

13. *XYLEBORUS PARALLELOCOLLIS* EGGERS (FIG. 5)

New Records: Chatham Bay, 5–9 February 1993, by hand, J.F. Quesada (1); Chatham Bay, October 1994, J.F. Quesada, yellow pan trap (2), unspecified (1).

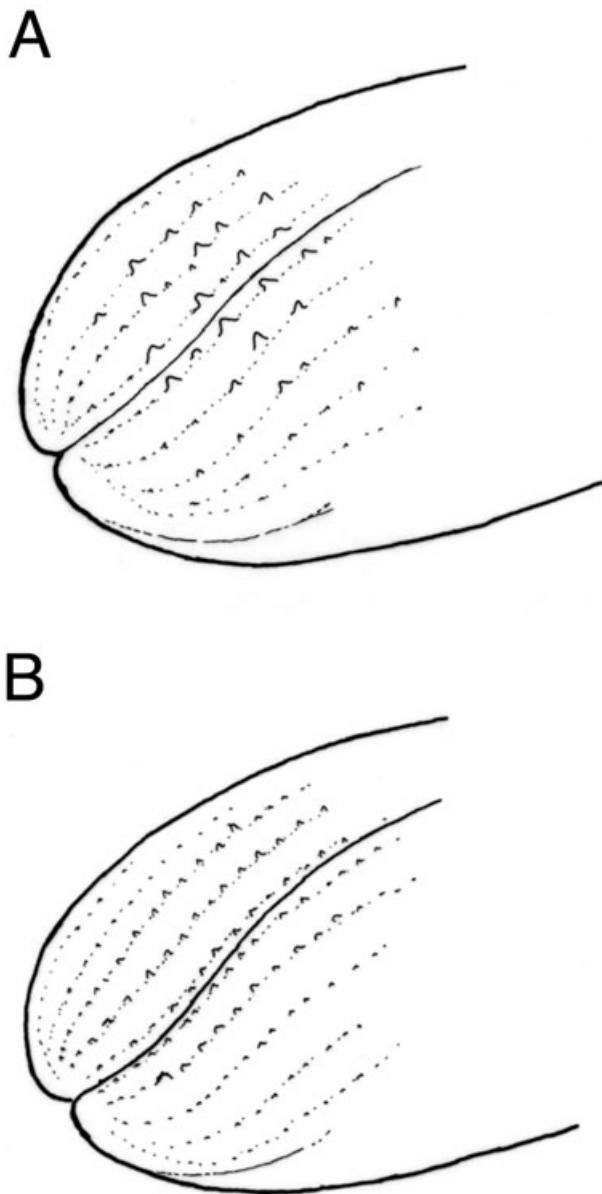


Figure 5. Outline of declivity. A, *Xyleborus sparsegranulosus* sp. nov. B, *X. parallelocollis*.

Comments: These specimens are identical to the specimen collected in a blacklight trap by the Steele expedition (determined by D.E. Bright as *X. parallelocollis* Eggers). L.R.K. studied the holotype of *X. parallelocollis*, and material which was compared directly with the holotype was compared in turn with numerous specimens in SLWC, UCR and INBio collections which were collected from both the Pacific and Atlantic sides of Costa Rica and from Venezuela, and with a series of specimens from Ecuador (LRKC). These specimens are clearly conspecific. Published records of *X. parallelocollis* are from Costa Rica, Colombia and

French Guiana (Wood & Bright, 1992). (See also comments under species 15, below.)

14. *XYLEBORUS PERFORANS* WOLLASTON

New Records: Chatham Bay, February 1993, Malaise trap (18) and by hand (4), J.F. Quesada; Chatham Bay, October 1994, yellow pan trap, J.F. Quesada (7); Wafer Bay, Malaise trap, Feb (2), March (6), April (2), and June (2) 1994, Y. Camacho; Cerro Iglesias, 600 m, flight intercept trap, Oct. 1994, J.F. Quesada (5); Iglesias waterfall, Iglesias Bay, by the trail, 21 December 1997, Ulate and Flores (26); El Guarumal, Wafer-Chatham trail, 30 m, at light, Ulate and Flores (12); El Gallinero coast, trail to Cerro Iglesias, 260 m, Malaise trap 28 December 1997–28 February 1998, E. Ulate and C. Flores (1).

Comments: The earlier collection (two individuals) by Sherry and Werner (*X. volvulus* (F.) according to Bright, 1982) was at light. No host records are known, but the species is quite polyphagous.

Occasionally the east Asian *X. perforans* Wollaston has been considered a synonym of the neotropical *X. volvulus* (e.g. Bright, 1982), but the two remain as doubtfully separate taxa which are very difficult to distinguish by morphological characters (Wood & Bright, 1992). Mitochondrial DNA sequences of cytochrome oxidase I from two Cocos Island specimens were identical; to our surprise, this Cocos haplotype was very similar to haplotypes from three Papua New Guinean populations of *X. perforans* but very divergent from sequences from Costa Rican populations of *X. volvulus* (unpubl. data). For the present, we must consider the Cocos Island population, then, to be *X. perforans* rather than *X. volvulus* (in agreement with morphology: Schedl, 1974; contra Bright, 1982) and we consequently remove *X. volvulus* from the island list. (It is very likely, of course, that future molecular taxonomic research will reveal the presence of *X. volvulus* on the island as well, given the abundance of that species throughout the neotropics.)

15. *XYLEBORUS SPARSEGRANULOSUS* SP. NOV.

(FIG. 5)

Material: Holotype female: COSTA RICA, Puntarenas, Isla del Coco, Bahia Chatan, intersección, October 1994, #3352, J.F. Quesada [INBio]. Paratypes: same data as holotype, 8 females [INBio]; Bahia Chatan, 1–100 m, October 1994, #3350, J.F. Quesada [INBio] (1 female); Bahia Wafer, 1 m, October 1994, #3314, J.F. Quesada [INBio] (1 female).

Etymology: The new species has relatively few declivital granules compared with *X. parallelocollis* and related species.

Description of female (male unknown): Length 3.1–3.2 mm, 2.5–2.6 times longer than wide, colour brown.

Frons broadly convex, with a broad, median, weakly elevated carina; surface reticulate, with rather coarse shallowly impressed punctures. Vestiture consisting of a few hairlike setae, mostly close to epistoma. Antennal club obliquely truncated; funicle five-segmented.

Pronotum 1.15 times longer than wide, subquadrate; summit at middle; asperate on anterior slope, posterior disc smooth, tiny asperities extending laterally behind summit, punctures minute, sparse and obscure; vestiture consisting of a few hairlike setae in asperate area.

Elytra 1.6 times longer than wide, 1.45 times longer than pronotum; lateral margins subparallel to posterior third, narrowly rounded behind; striae not impressed, punctures small, distinctly impressed, separated by their diameter; interstriae twice as wide as striae, smooth, with confused minute punctures separated by a distance equal to their diameter. Declivity (Fig. 5A) broadly flattened, transversely impressed on lower third, striae impressed, punctures shallow, separated by less than their diameter; on average, three to four large granules on interstriae 1–3 above transverse impression, the largest granule more than three times as large as the smallest, the larger granules separated within a row by three to four times their diameter. Vestiture consisting of a few scattered interstitial bristles on disc, and much shorter interstitial bristles on declivity, each declivital bristle equal in length to one third the distance between rows, and minute interspersed interstitial and striae hairlike setae.

Procoxae contiguous, protibiae with eight lateral socketed teeth on distal half; metatibiae with nine to 11 lateral socketed teeth on distal two thirds, lateral edge evenly arched to apex.

Comments: Although species delimitation of inbreeding beetles (such as those of *Xyleborus*) can be difficult from a limited sample, *X. sparsegranulosus* is distinct from all similar species. It is readily identifiable by the pattern of declivital granules (Fig. 5). In addition, it is distinguished from *X. parallelocollis* and *X. semipunctatus* by its larger size, and from sympatric *X. parallelocollis* also by the more rounded anterior margin of the pronotum. It can be distinguished from *X. discretus* and *X. semipunctatus* by the more gradually sloping declivity, and from *X. concentus* by the obtuse (vs. acute) apex of the declivity. Examination of many *X. parallelocollis* from Costa Rica, Ecuador and Venezuela, as well as holotypes of *X. semipunctatus*, *X. concentus*, and *X. usticus* (a junior synonym of *discretus* Eggers) led us to conclude that the Cocos Island population deserves specific status.

16. *HYPOTHENEMUS ERUDITUS* WESTWOOD

New Records: Wafer Bay, Malaise trap, February 1994 (1), Wafer Bay, Malaise trap, March 1994 (1), Wafer Bay, Malaise trap, May 1994 (1), Cerro Iglesias, 600 m, flight intercept trap, Oct. 1994, J.F. Quesada (1); Wafer Bay, 17–22 April 1975, by hand, C.L. Hogue (2).

Comments: Recorded for the first time on Cocos Island. The genus had not been collected previously from the island but was to be expected there, since many species of *Hypothenemus* are good colonists and are easily spread by human activity (see e.g. Wood, 1982). For example, ten of 24 scolytines on the Galápagos Islands are species of *Hypothenemus*.

This tiny (1.0–1.3 mm) species is argueably the most abundant and widespread scolytine; it has been collected from the Americas, all of Africa, southern Europe, the warmer parts of Asia and Australia, and many tropical and subtropical islands around the world. It is ecologically flexible, having been collected from several hundred plant species and from a wide variety of plant tissues. On mainland Costa Rica, the species has been collected by Malaise traps at elevations ranging from sea level to 3000 m altitude (L.R. Kirkendall, unpubl. data). Not infrequently, *H. eruditus* is the only species, or one of only a few species, of bark beetle collected on isolated small islands (e.g. Bright & Peck, 1998) and in dry, hot microclimates such as sun-exposed bark or petioles (e.g. Jordal & Kirkendall, 1998).

All *Hypothenemus* are inbreeders. The taxonomy of *H. eruditus* is very uncertain, as is the case for many inbreeding scolytines, and 70 synonyms of this taxon are listed in Wood and Bright's (1992) catalogue. There is considerable morphological variability among specimens assigned to this species, particularly in characters such as the sculpture of the frons, body colour, and vestiture.

17. *HYPOTHENEMUS SERIATUS* (EICHHOFF)

New Records: Wafer Bay, March 1994, Malaise trap (1).

Comments: Recorded for the first time in Cocos Island. This and previously determined Cocos Island specimens (Bright, 1982) were compared with the lectotype of *H. seriatus* and with specimens of *H. seriatus* from Costa Rica, and with type and nontype material of *H. obscurus* and *H. crudiae*, two species with which *H. seriatus* is confused frequently. This widespread, polyphagous species breeds in twigs and branches, seeds, seedpods, and other plant material (Wood, 1982). Its primary distribution is from eastern North America south through Mexico and Central America

to Brazil, but it is also found on tropical and subtropical islands throughout the world, including the Galápagos (Bright & Peck, 1998).

18. *ARAPTUS* SP.

New Records: Wafer Bay, 24 March 1978, blacklight trap, C. Hogue and S. Miller, Steele expedition (1); Bahia Chatan, 5–9 February 1993, F. Quesada (2); Cerro Iglesias, 600 m altitude, flight intercept trap, October 1994, J.F. Quesada (3); banks of the Río Genio, 10 m altitude, 17–19 December 1997, flight intercept trap, Ulate and Flores (5: 2 are incomplete, 3 were extracted for DNA and then mounted); Los Llanos, 24 December 1997, beating sheet ('sombrereta'), Ulate and Flores (1).

Comments: The specimen previously determined as '*Pityophthorus* sp.' (Bright, 1982), collected from the Steele expedition blacklight trap in March 1978, is an *Araptus*, and is clearly a member of the distinctive *A. costaricensis* complex of inbreeding bark beetles. *A. costaricensis*, *A. laevigatus* (Eggers), and at least five undescribed species occur in Costa Rica and Panama. The Cocos Island species can be distinguished from other species of the complex by characteristics of the frons and by body size and shape. Species of this *Araptus* complex are apparently all inbreeding by sibmating, and five are known to breed primarily in unusual plant material, such as fallen woody pods and fallen woody leafstalks. (The taxonomy and ecology of this complex will be published separately by L.R.K.).

19. *CORTHYLUS* SP.

New record: Hill between Chatham and Cape Atrevida, flight intercept trap, 600 m altitude, October 1994, J.F. Quesada (1).

Comments: The single, damaged male of this *Corthylus* species could not be identified from the literature because keys to this genus rely heavily on characters of the female frons. Neither could it be identified by comparison with the material at hand or in the collection of the University of Costa Rica. We compared it with paratypes or authenticated male specimens of a variety of Costa Rican species of similar form and size, including *C. collaris* Blandford, *C. comatus* Blandford, *C. retusus* Wood, *C. splendens* Wood, *C. spinifer* Schwarz, and *C. villus* Bright, as well as with males of several unidentified, probably new species from Costa Rica (in the INBio collections). The male specimen has no unusual features. It is 2.2 mm long, black, with an antenna similar to that of *C. comatus*, and with a coarsely faceted eye; the declivital interstriae 1 are raised and flattened (but interstriae 3 are not raised). All *Corthylus* are outbreeding ambrosia beetles.

BEHAVIOURAL ECOLOGY OF COCOS ISLAND SCOLYTINAE

Although botanists have long recognized the potential significance of selfing for successful colonization of islands ('Baker's Rule': Baker, 1955; Brown & Burdon, 1987; McMullen, 1987; Anderson *et al.*, 2001; Rambuda & Johnson, 2004), it seems that zoologists have largely ignored the possible importance of inbreeding in this context. Bark beetles are not the only terrestrial arthropods with clades in which both outbreeding and incestuous species are found – regular close inbreeding occurs in, for example, certain mites, thrips, aphids, solitary bees and wasps, ants and social spiders (Thornhill, 1993; Wrensch & Ebbert, 1993). However, they are apparently the only group in which an association between zoogeography and close inbreeding has been documented (Kirkendall, 1993; Jordal *et al.*, 2001). The proportion of the scolytine fauna that inbreeds by repeated sib-mating increases with decreasing latitude, and is highest on tropical islands. In agreement with these patterns, species which regularly inbreed by brother–sister matings represent nearly three quarters (74%, Table 1) of the known scolytine fauna of Cocos Island. This is about average for small tropical islands, compared with 40–50% for mainland (e.g. Costa Rican lowland forests) and large island tropical faunas (Bright & Peck, 1998; Kirkendall, 1993; Jordal *et al.*, 2001: fig. 7.1).

The over-representation of inbreeders on islands such as Cocos suggests that they have a higher success rate than do outbreeders for establishing viable populations after colonization. Females of inbreeding species mate with a brother before dispersal from the natal breeding material; mate finding in recently established, sparse inbreeding populations is not the problem that it would be for outbreeders. Furthermore, presumably inbreeding colonists do not suffer the sudden decrease in absolute fitness due to inbreeding depression that is expected to afflict small initial populations of outbreeders.

Eleven of the 19 species reported here are ambrosia beetles (Table 1), a typical proportion for small tropical islands (Kirkendall, 1993, fig. 7.2D). Unlike most phloem-feeding bark beetles, ambrosia beetles are host plant generalists; they feed on mats of fungal hyphae growing in their tunnels instead of on host tissues directly, and these fungal symbionts are host generalists. The ability to utilize a broad range of plant taxa should increase their likelihood of colonization success relative to that of host specialists.

COCOS ISLAND ZOOGEOGRAPHY

Only seven or eight (depending on the *Corthylus* species) of the 19 species reported here are endemic to Cocos Island (Table 1), compared with the estimate of 52% endemic for the total arthropod community

Table 1. Systematic placement (Wood, 1982), distribution and mating systems of Scolytinae found on Cocos Island; the Xyleborini and *Corthylus* are ambrosia beetles

Tribe	Species	Distribution	Mating system
Phloeotribini	<i>Phloeotribus pacificus</i> Bright	Endemic	Outbreeding
Ctenophorini	<i>Pycnarthrum brosimi</i> Wood	Costa Rica-Colombia	Outbreeding
	<i>Pycnarthrum pseudoinsulare</i> sp. nov.	Endemic	Outbreeding
	<i>Scolytodes pacificus</i> Jordal	Endemic	Outbreeding
Dryocoetini	<i>Coccotrypes cyperi</i> (Beeson)	Pantropical	Inbreeding
Xyleborini	<i>Ambrosiodmus paucus</i> Wood	Endemic	Inbreeding
	<i>Xyleborinus cocoensis</i> sp. nov.	Endemic	Inbreeding
	<i>Xyleborinus gracilis</i> (Eichhoff)	Tropical America	Inbreeding
	<i>Xyleborinus intersetosus</i> (Blandford)	Tropical America	Inbreeding
	<i>Xyleborus affinis</i> Eichhoff	Pantropical	Inbreeding
	<i>Xyleborus bispinatus</i> Eichhoff	Tropical America	Inbreeding
	<i>Xyleborus ferrugineus</i> (F.)	Pantropical	Inbreeding
	<i>Xyleborus parallelocolis</i> Eggers	Tropical America	Inbreeding
	<i>Xyleborus perforans</i> Wollaston	Pantropical	Inbreeding
	<i>Xyleborus sparsegranulosus</i> sp. nov.	Endemic	Inbreeding
Cryphalini	<i>Hypothenemus eruditus</i> Westwood	Pantropical	Inbreeding
	<i>Hypothenemus seriatus</i> (Eichhoff)	Pantropical	Inbreeding
Corthylini	<i>Araptus</i> sp.	Endemic	Inbreeding
	<i>Corthylus</i> sp.	?	Outbreeding

(Hogue & Miller, 1981). However, three (possibly four) of the five outbreeding species are endemic, which is more in line with the general pattern for arthropods. The contrast with inbreeding species (only four of 14 endemic) is in accordance with a pattern seen for other tropical islands (Jordal *et al.*, 2001) including the intensively collected Galápagos archipelago (Bright & Peck, 1998). These data, then, add support to our previous conclusions that, even when correcting for ecological differences between inbreeders and outbreeders, (1) inbreeders are clearly superior colonists, and (2) successful colonization of small islands by outbreeders is more likely to result in species-level morphological divergence than is that by inbreeders, resulting in higher levels of endemism in the former (Jordal *et al.*, 2001).

There are three patterns of colonization for the putative sister relationships we could find for insects, a scorpion, and a bird endemic to Cocos Island (Table 2). Primary colonization routes have been from the Pacific side of Central and northern South America (13 cases), the Caribbean (five), and the Galápagos (two). Five of the seven endemic scolytine species are related to species found primarily in Central or northern South America, which suggests that the main route of overseas dispersal for these beetles was westwards from the Americas, as surmised for the Galápagos insect fauna as a whole (Peck, 1994). Species not endemic to Cocos Island, but with narrow geographical distributions, further support this trend, as demonstrated by *P. brosimi* and *X. parallelocollis*. The fact that the neotropical *Xyleborinus intersetosus* and *Xyleborus parallelocollis* appear to be sister species to Cocos Island endemics strongly suggests that there have been repeated successful colonizations from the American mainland by these inbreeding lineages, and that the island was initially colonized without the aid of human transport. Anthropogenic spread, however, is the only plausible explanation for the immigration of *X. perforans* and the tineid moth *Erechthias flavistriata* (Davis, 1994) from the West Pacific, since these species are otherwise not known from the Americas. Several lepidopteran groups and one ambrosia beetle seem to have a Caribbean islands–Cocos Island vicariant distribution (Table 2), which could be explained by dispersal by an extinct or uncollected Central or South American ancestor rather than dispersal directly from any of the Caribbean islands.

Lepyrotica acantha is found on both the Galápagos and Cocos Island, a distribution pattern shared with *Pycnarthrum insulare*/*P. pseudoinolare* and with Darwin's finches (Sato *et al.*, 2001). Only phylogeographical studies can reveal the details of the colonization direction, but at least for Darwin's finches, Sato and co-workers argue that Cocos Island was colonized from the Galápagos. Cocos Island originated *c.* 500 km

south-west of its current position and hence was initially much closer to the Galápagos Islands than it is today (Castillo *et al.*, 1988).

CONCLUDING REMARKS

The scolytine fauna of Cocos Island is notable for its species richness relative to other arthropod groups, when compared with mainland faunas. La Selva Biological Station on the Caribbean side of Costa Rica is the site of a long-term, intensive survey of selected arthropod groups (e.g. Colwell & Longino, 2005). In this typical mainland wet tropical forest, compared with bark beetles there are twice as many species of ants, two thirds as many buprestids, one and a half times as many cerambycids and probably an order of magnitude more weevils (other than scolytines) (L.R. Kirkendall and J.T. Longino, unpubl. data; H.A. Hespenheide, pers. comm.; F. Hovore, pers. comm.). On Cocos Island, bark beetles and ants are equal in terms of numbers of species, while bark beetles outnumber buprestids by 19 : 1, cerambycids by about 2 : 1, and other weevils by about 2 : 1 (Hogue & Miller, 1981; E. Ulate, INBio, unpubl. data). Are these unusual proportions simply an example of the stochasticity of long-distance colonization?

We argue that scolytines should be extraordinarily successful colonizers because of a combination of factors. First, as discussed above, many scolytines benefit (in this context) from being inbreeders. Second, scolytines are an appropriate size for long-distance aerial transport (e.g. Hespenheide, 1977). Third, biologists have long known that insects and spiders living in temporary habitats (such as dead woody tissues) are good colonizers because of their adaptations to a lifestyle dependent upon long-distance dispersal (e.g. Peck, 1994). Fourth, unlike most other wood-boring beetles, both adults and immatures tunnel in dead wood, and adults are capable of tightly blocking tunnel entrances with frass or their own bodies (which could protect tunnel inhabitants from flooding), increasing the likelihood of surviving a long oceanic voyage in dead floating vegetation.

Understanding the evolution of the Cocos Island fauna depends on taxonomic research. Unfortunately, despite the large number of insect specimens collected and prepared by INBio personnel in the past decade, the comprehensive summary of Hogue & Miller (1981) has not yet been updated; in fact, our paper is the first review of Cocos Island representatives of any arthropod family or subfamily which includes the INBio collections, and apparently only the second publication of newly discovered insect species from those collections (the other being Anderson & Lanteri, 2000). We hope that our paper will inspire others to follow suit: we feel that Cocos Island is especially valuable for studies of

Table 2. Summary of well-documented sister relationships in a bird, a scorpion and various insects endemic to Cocos Island, including the scolytine species described in this paper; the distribution of putative closest relatives are given along with reference to primary sources

Order	Endemic taxon	Sister taxon/taxa	Distribution (sister taxon/taxa)	Reference
Neuroptera	<i>Chrysoperla externa cocosensis</i>	<i>C. e. externa</i>	Central America, SE US, Antilles	Adams (1983)
Orthoptera	<i>Parascopioricus binoditergus</i>	<i>P. cordillericus</i>	Columbia	Nickle (1983)
Orthoptera	<i>Cocconotus bellicosus</i>	Not given	Columbia	Nickle (1983)
Lepidoptera	<i>Oxydia hoguei</i>	<i>O. lalanneorum</i>	Guadeloupe	Brown <i>et al.</i> (1991)
Lepidoptera	<i>Coelostathma insularis</i>	<i>C. binotata</i>	Mexico	Brown & Miller (1999)
Lepidoptera	<i>Protodarcia cocosensis</i>	<i>Protodarcia</i> spp. (4)	Caribbean islands	Davis (1994)
Lepidoptera	<i>Lepyrotica acantha</i> *	<i>Lepyrotica</i> spp. (6)	Caribbean islands	Davis (1994)
Lepidoptera	<i>Tortyra hoguella</i>	<i>Tortyra</i> spp.	Mexico to South America	Heppner (1980)
Diptera	<i>Paracanace hoguei</i>	<i>P. aicea</i> and <i>P. leban</i>	Greater Antilles	Mathis & Wirth (1978)
Diptera	<i>Merosargus insularis</i>	<i>M. penai</i>	Ecuador	Woodley (1991)
Diptera	<i>Limonia hoguei</i>	<i>L. willistoniana</i>	Lesser Antilles & Costa Rica	Byers (1981)
Diptera	<i>Helius brunneus</i>	<i>H. micracanthus</i>	Brazil	Byers (1981)
Diptera	<i>Orimaga flavescens</i>	<i>O. omisineris</i>	Bolivia	Byers (1981)
Coleoptera	<i>Halecia cocosae</i>	<i>H. auropunctata</i>	Nicaragua to Peru	Bellamy (1986)
Coleoptera	<i>Phloeotribus pacificus</i>	<i>P. biguttatus</i>	Panama-Columbia/Venezuela	Bright (1982)
Coleoptera	<i>Scolytodes pacificus</i>	<i>S. impressus</i>	Costa Rica	Jordal (1998a)
Coleoptera	<i>Pycnarthrum pseudoinsulare</i> sp. nov.	<i>P. insulare</i>	Galápagos	This paper
Coleoptera	<i>Ambrosiodmus paucus</i>	<i>X. devertexus</i>	Caribbean islands	Wood (1986a)
Coleoptera	<i>Xyleborinus cocosensis</i> sp. nov.	<i>X. intersetosus</i>	Tropical America	This paper
Coleoptera	<i>Xyleborus sparsegranulosus</i> sp. nov.	<i>X. parallelocolis</i>	Tropical America	This paper
Coleoptera	<i>Araptus</i> sp.	<i>A. costaricensis</i> complex (c. 6 spp.)	Costa Rica-Panama	This paper
Scorpiones	<i>Opisthacanthus valerioi</i>	<i>Opisthacanthus</i> spp. (4)	Northern S. America, Peru	Lourenço (1980)
Passerine birds	<i>Pheuticus ludovicianus</i>	<i>P. aureoventris</i>	Galápagos	Sato <i>et al.</i> (2001)

SE, south-eastern.

neotropical biogeography, given that it is the only eastern Pacific oceanic island with wet tropical forest.

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