INSECTA MUNDI

A Journal of World Insect Systematics

0098

A new fossil species of stag beetle from Dominican Republic amber, with Australasian connections (Coleoptera: Lucanidae)

Robert E. Woodruff
Florida State Collection of Arthropods
P.O. Box 147100
Gainesville, Florida 32614-7100

Date of Issue: September 25, 2009

CENTER FOR SYSTEMATIC ENTOMOLOGY, INC., Gainesville, FL

Robert E. Woodruff
A new fossil species of stag beetle from Dominican Republic amber,
with Australasian connections (Coleoptera: Lucanidae)
Insecta Mundi 0098: 1-10

Published in 2009 by
Center for Systematic Entomology, Inc.
P. O. Box 141874
Gainesville, FL 32614-1874 U. S. A.
http://www.centerforsystematicentomology.org/

Insecta Mundi is a journal primarily devoted to insect systematics, but articles can be published on any non-marine arthropod taxon. Manuscripts considered for publication include, but are not limited to, systematic or taxonomic studies, revisions, nomenclatural changes, faunal studies, book reviews, phylogenetic analyses, biological or behavioral studies, etc. **Insecta Mundi** is widely distributed, and referenced or abstracted by several sources including the Zoological Record, CAB Abstracts, etc.

As of 2007, **Insecta Mundi** is published irregularly throughout the year, not as quarterly issues. As manuscripts are completed they are published and given an individual number. Manuscripts must be peer reviewed prior to submission, after which they are again reviewed by the editorial board to insure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

Managing editor: Paul E. Skelley, e-mail: insectamundi@gmail.com
Production editor: Michael C. Thomas, e-mail: insectamundi@gmail.com
Editorial board: J. H. Frank, M. J. Paulsen
Subject editors: J. Eger, A. Rasmussen, F. Shockley, G. Steck, A. Van Pelt, J. Zaspel

Printed copies deposited in libraries of:
CSIRO, Canberra, ACT, Australia
Museu de Zoologia, São Paulo, Brazil
Agriculture and Agrifood Canada, Ottawa, Ontario, Canada
The Natural History Museum, London, England
Muzeum i Instytut Zoologii Pan, Warsaw, Poland
National Taiwan University, Taipei, Taiwan
California Academy of Sciences, San Francisco, CA, USA
Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA
Field Museum of Natural History, Chicago, IL, USA
National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Electronic copies in PDF format:
Printed CD mailed to all members at end of year.
Florida Center for Library Automation: http://purl.fcla.edu/fcla/insectamundi
University of Nebraska-Lincoln, Digital Commons: http://digitalcommons.unl.edu/insectamundi/

Author instructions available on the Insecta Mundi page at:
http://www.centerforsystematicentomology.org/insectamundi/

Printed Copy ISSN 0749-6737
On-Line ISSN 1942-1354
CD-ROM ISSN 1942-1362

INSECTA MUNDI 0098: 1-10 2009

A new fossil species of stag beetle from Dominican Republic amber, with Australasian connections (Coleoptera: Lucanidae)

Robert E. Woodruff
Florida State Collection of Arthropods
P.O. Box 147100
Gainesville, Florida 32614-7100

Abstract. The first New World amber member of the family Lucanidae is described from the Dominican Republic. Its age is presumed to be Miocene (20-30 million YBP). It is also the fourth known amber species, the second Miocene fossil species, the second fossil species in the subfamily Syndesinae, and the first species (fossil or extant) of Lucanidae from the entire Caribbean. It is especially interesting because it is a member of the Australasian genus *Syndesus* MacLeay. Other such disjunct Dominican amber insect fossils are also discussed.

Introduction

My first encounter with the specimen herein described was during a visit to the Dominican Republic in 1983 to assist the late Jacob Brodzinsky in identifying his extensive Dominican amber collection. He had set aside this fossil as an unknown beetle family. I immediately recognized it as a member of the family Lucanidae and requested a loan for later study. He added it to my registry of Dominican amber fossils as #5656.

Based on my initial identification, it was mentioned in a list by Poinar (1992: 285). Ratcliffe and Ocampo (2001) indicated that I was in the process of describing this fossil, but nothing further has been published. Subsequently I borrowed the specimen for description, but shortly thereafter the entire Brodzinsky collection was purchased by the Smithsonian Institution (Davis 1989), and I was asked to return my loan. The collection was originally housed in the Entomology Department of the U.S. National Museum, but later transferred to the Department of Paleobiology, where it now resides.

During a study trip to the Smithsonian in 1998, I was able to examine the specimen again and to compare it with extant members of the Lucanidae in the National Collection. Sometime between my first examination (Fig. 3) and the current study, the piece was broken and repaired (Fig. 8). Certain features were obscured by the fractures, making description more difficult. Not until the use of the Auto-Montage became a reality, which greatly assists in illustrating amber inclusions, was I encouraged to complete this description.

Fossil Lucanidae. The following summary is taken from a recent catalogue of fossil Scarabaeoidea (Krell 2007: 2-5), which listed 17 species of fossil stag beetles. These are distributed in 14 genera in 5 subfamilies. The oldest are known from the Jurassic of Mongolia (Nikolajev 1990), 1 of which was included in a separate family, the Paralucanidae (Nikolajev 2007). *Ceruchus fuchsii* Wickham (1911) and a single elytron of *Lucanus fossilis* Wickham (1913) are the only 2 previously known New World fossil species. Both are compression (flattened) specimens from the Florissant, Colorado shales and considered Oligocene in age. Wickham (1920, 1927, 1933) provided a catalogue and supplements to North American fossil Coleoptera. Horning (undated) provided a website bibliography of the Lucanidae of the world.

Geologically (from oldest to most recent) and geographically, the fossil Lucanidae are here summarized: Upper Jurassic (Mongolia, 2 spp.); Lower Cretaceous (Russia, 3 spp.); Upper Cretaceous (Kazakhstan, 1 sp.); Eocene (Germany, Czechoslovakia, 5 spp.); Oligocene (Germany, Russia, Colorado, 5 spp.); Miocene (France 1 sp.).

Only 3 species are listed as amber fossils, and all those were described from Baltic amber, listed as Eocene in age (Motschulsky 1856, Waga 1883, Zang 1905). *Ceruchus fuchsii* Wickham is the only other fossil member of the subfamily Syndesinae listed. Thus, of the family Lucanidae, *S. ambericus* n. sp. constitutes the fourth known amber species, the first New World amber species, the second Miocene fossil species, the second fossil species in the subfamily Syndesinae, and the first species (fossil or extant) from the entire Caribbean.

***Syndesus ambericus* Woodruff, new species**

Holotype. Amber fossil, Dominican Republic, probably Cordillera Septentrional. Deposited in the Brodzinsky-Lopez Peña Collection, USNM #502873, Acc. # 371429, Woodruff # 5656, housed in the Department of Paleobiology, National Museum of Natural History, Washington, D.C. Enclosed in the same piece is a fly of the family Scatopsidae.

General Description. Specimen contained in amber, cut in cabochon form of elongate oval, convex on one side (referred to as dorsal) and relatively flat on the reverse (ventral). Dimensions: 37.5mm long, 20.5mm wide, 7.1mm thick (all maximum measurements); beetle fossil 13mm long (from mandible tip to abdomen tip), ca. 4mm high, width unmeasurable. Amber dark orange (darkened since first examined). Fractures presently obscuring many features, but Fig. 3 shows the specimen as it appeared in 1984. Body cylindrical, convex, elongate, with coarse punctures on pronotum and elytra. Habitus remarkably similar (compare Fig. 3 and 5, lateral view) to the extant *S. cornutus* (Fabricius).

Head broad, eyes large, prominent, nearly round. Antennal club large, with 7 lamellae (Fig. 7); other antennomeres not visible. Head laterally with sharp projections in front of eyes (similar to Fig. 6). Maxillary palpi long, two-thirds mandible length, filiform, 3-segmented. Labial palpi 2-segmented, length half that of maxillary palpi. Mandibles prominent, symmetrical, horn-like, with 3 teeth (Fig. 4, 12), length two-thirds pronotal length.

Pronotum (Fig. 3, 10) convex, cylindrical, glabrous, coarsely punctate (most punctures deep and contiguous). Marginal line evident, appearing continuous laterally and posteriorly (no dorsal view). Medially with small projection, not carinate or sharply delineated, but clearly visible; concave below to head. Length two-thirds elytral length. Central furrow suggested in lateral view, but dorsal view obscured.

Elytra (Fig. 3, 8, 9) convex, cylindrical, glabrous; intervals (likely 10, difficult to count) prominently raised, intervening punctures coarse, deep, nearly contiguous. Fractures presently distorting and obscuring view. Pygidium not visible, but fine golden setae projecting at elytral margin. Margin appearing complete, terminating with smoothly rounded, gradual curve.

Legs similar to modern *S. cornutus*. Anterior tibiae dentate with 5 prominent teeth, becoming larger anteriorly, small teeth interspersed between each; spur broad, terminal.

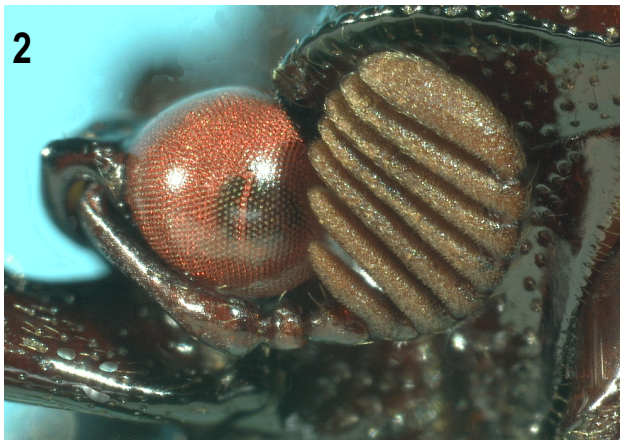
Sex. Based on the sexual dimorphism in the Syndesinae, and shape of the mandibles, the specimen appears to be a male.

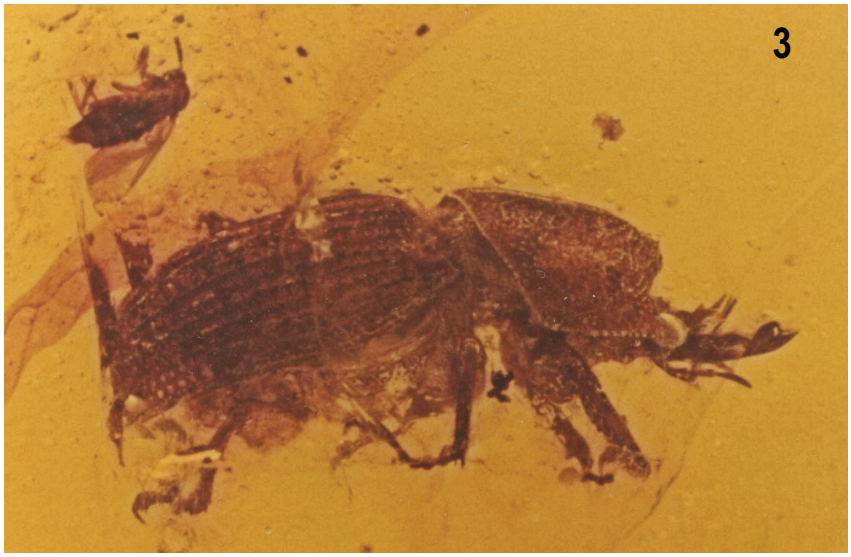
Comparisons. In most respects the fossil is so remarkably similar to the modern *S. cornutus* that there can be little doubt about the generic placement. Obvious specific differences are found in the mandibles, pronotal punctation, and pronotal projection (horn). The coarse, nearly contiguous pronotal punctures easily distiguish it from any known species.The mandibles of *S. cornutus* (Fig.1, 5, 6) are more elongate and with only 2 teeth (points), whereas *S. ambericus* (Fig. 4, 8, 12) mandibles are broader and have 3 teeth. The pronotal projection in *S. cornutus* (which is the origin of the specific name) is far more prominent and carinate (Fig.1, 5, 6) than in *S. ambericus* (Fig. 3). Few other character states are sufficiently visible in the fossil to distinguish it.

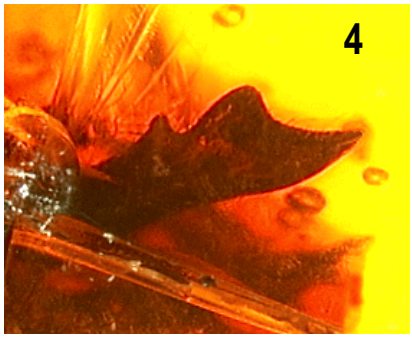
Etymology. The commercial amber fossil company formed by Jacob and Marianella Brodzinsky (Woodruff 2004b) was incorporated as "Amberica", combining "Amber" and "America". I have chosen to honor them for providing important fossils to the scientific community, by Latinizing their well-known company name.

Systematics. The family Lucanidae is not a large one by beetle standards. It has long been considered the ancestral stock within the Scarabaeoidea, and it contains many species with relict distributions. The latest checklist (Paulsen 2008), indicated 4 subfamilies, 109 genera, about 800 species, with 196 New World species in 32 genera, with only 24 Nearctic species in 8 genera. Paulsen (2005) stated that " The classification of the family at the tribal level is currently superfluous..." There are no current keys to species in many genera (including *Syndesus* MacLeay).

The genus *Syndesus* was created as the type of a new family by MacLeay (1819). In their treatment of the Lucanidae of the World, Didier and Séguy (1952, 1953) considered it as a subfamily (Syndesinae)







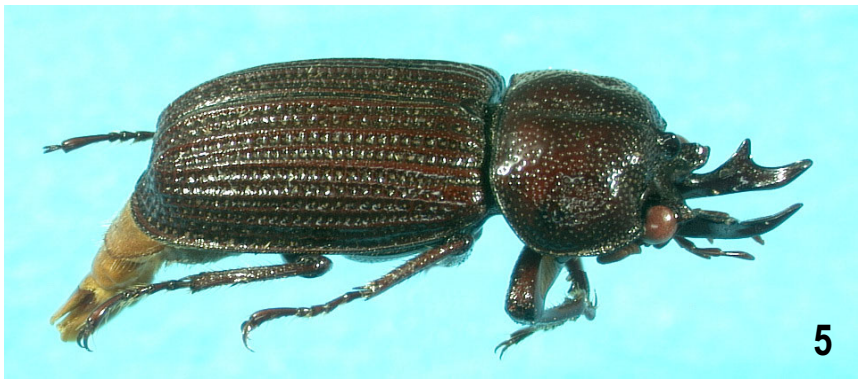


Figure 1-6. *Syndesus* spp. **1, 2, 5, 6:** *Syndesus cornutus* (Fab.). **1)** Left lateral view of head and pronotum (note prominent mandibles and palpi). **2)** Enlargement of eye and antenna (note 7 lamellae in club). **5)** Habitus, lateral. **6)** Habitus, dorsal. **3-4:** *Syndesus ambericus* Woodruff, n. sp. **3)** Amber fossil; habitus lateral in 1983. **4)** Enlargement of right mandible (note 3 "teeth").

with only 2 genera (*Syndesus* and *Psilodon* Perty). Within *Syndesus*, they recognized 5 species: 2 from Australia, 2 New Caledonia, and 1 erroneously from Africa (Benesh 1955: 73); in *Psilodon* (with *Hexaphyllum* Grey as a synonym) were 3 species from South America. In *Psilodon*, Martinez and Reyes-Castillo (1985) and Boucher (1993) added new species from Brazil and Bolivia, respectively.

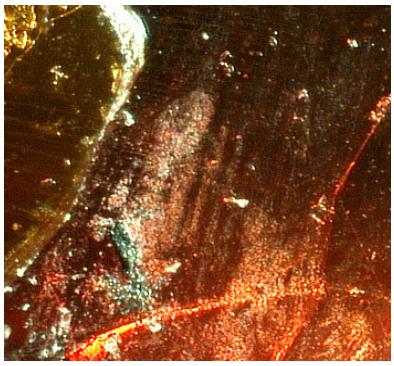
In his catalogue, Maes (1992) listed the subfamily Syndesinae to include *Syndesus* as the single genus (with *Psilodon* and *Hexaphyllum* as synonyms) of a separate tribe (Syndesini), along with Sinodendonini and Ceruchini. With this classification, the South American members (*Psilodon*) are combined with the Australasian ones, obscuring the disjunct distribution and morphological differences. Paulsen (2008) stated that "A meaningful classification of the Lucanidae at the tribal level cannot be created until all genera are properly diagnosed, and morphological and molecular phylogenetic analyses of the higher-level lucanid relationships are conducted." That process was begun by Paulsen and Hawks (2008) when they described the new tribe Platyceroidini based on "...preliminary molecular analysis...(unpublished)" and morphological differences with Platycerini.

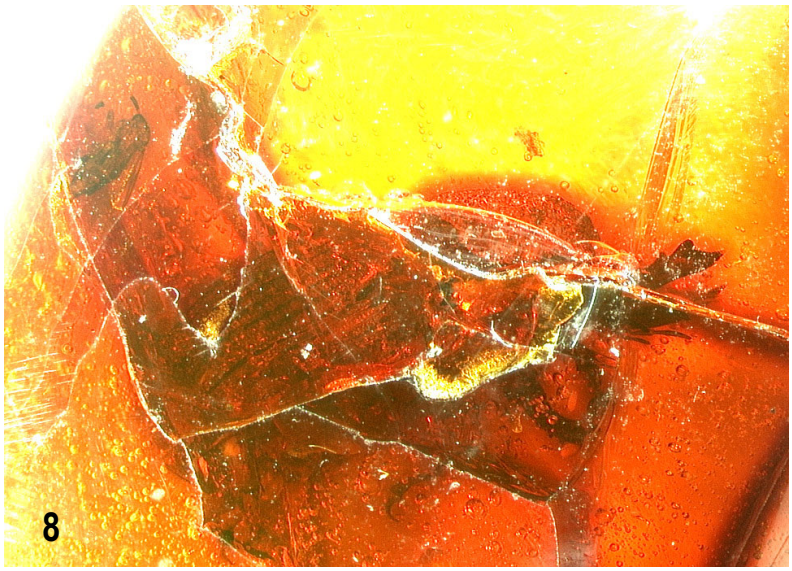
Ratcliffe (2002: 8) listed *Syndesus* and *Psilodon* as distinct. In his website checklist of 2005, Paulsen included the genus *Psilodon* as a synonym of *Syndesus*. However, in the most recent version (Paulsen 2008), the 2 genera are considered distinct. Several authors have weighed in on this classification (Holloway 1960, 1968; Howden and Lawrence 1974; Kikuta 1986; Krajcik 2001; Mizunuma and Nagai 1994; Smith 2006), but there seems to be little agreement. As recent as 1993, a new species (*P. gilberti* Boucher) was described from Bolivia (Nor Yungas at 1500 meters). Unlike all other South American species of *Psilodon*, it has 7 lamellae in the antennal club, showing its relationship to the Australasian *Syndesus*. In fact, pronotal and mandible characters, illustrated in Boucher's figures 6-7, show a remarkable similarity to *S. cornutus* from Australia. A thorough revision of both "genera" will be required to clarify their status. It is not my intent to evaluate classifications here, but to point out that the number of antennal lamellae (6 in *Psilodon*, 7 in *Syndesus*) would appear to be a sufficient morphological character (along with their distributions) to separate these 2 "genera". Although I have not examined all the species in either genus, Paulsen (2006) indicated that one species of *Syndesus* (*S. cancellatus* Montrouzier) has a 6-segmented club.

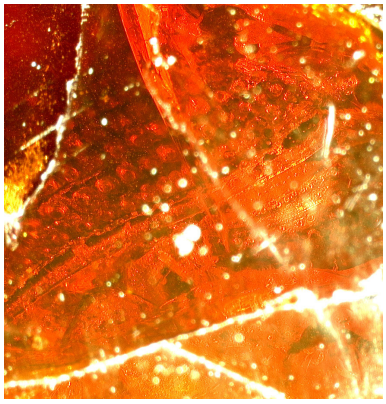
Provenance. There can be little doubt that this fossil is from the Dominican Republic. Brodzinsky never dealt in amber from elsewhere (Woodruff 2004b). Although he tried diligently to obtain specific locality data from the miners and suppliers, it was usually futile or unreliable. Because of color, inclusions, and vendor certainty, some pieces can be associated with specific mines. This specimen appears to have come from the Cordillera Septentrional (not the eastern, younger deposits). Brodzinsky said (personal communication) that it likely came from the famous Palo Quemado mine, located north of Santiago, near La Cumbre.

Age. There are no scientific techniques for dating amber itself. However, minimum ages can be obtained from associated microfossils in the sedimentary strata in which the amber is found. In the Dominican Republic, deposits were classified in the Altamira formation, once thought to be Eocene (Hueber and Langenheim 1986). Lambert et al. (1985) and Poinar and Canatella (1987) reported on a frog, which was dated by a controversial technique (MRI) as Eocene. However, most mines in the Cordillera Septentrional are now considered to be marine sediments of Miocene age (Grimaldi 1995; Iturralde-Vinent and McPhee 1996; Poinar 1992; Woodruff 1994). However, Dilcher et al. (1992) suggested that "...the amber clasts, from all physical characteristics, were already matured amber at the time of redeposition into marine basins. Therefore, the age of the amber is greater than Miocene and quite likely is as early as late Eocene".

The age of Hispaniola continues to be controversial. Donnelly (1988) indicated that the Greater Antilles started emerging 105 million years ago, with a rapid increase in size about 80 million years ago. Ross and Scortese (1988) indicated that the Caribbean tectonic activity began in the Apian (118 million years ago), and Hispaniola may have begun to break from Cuba during the Oligocene (35 million years ago). Their exact size and position during subsequent geological periods is unknown, but most geologists agree that the Caribbean plate has moved many times, and individual islands occupied very different positions from today.







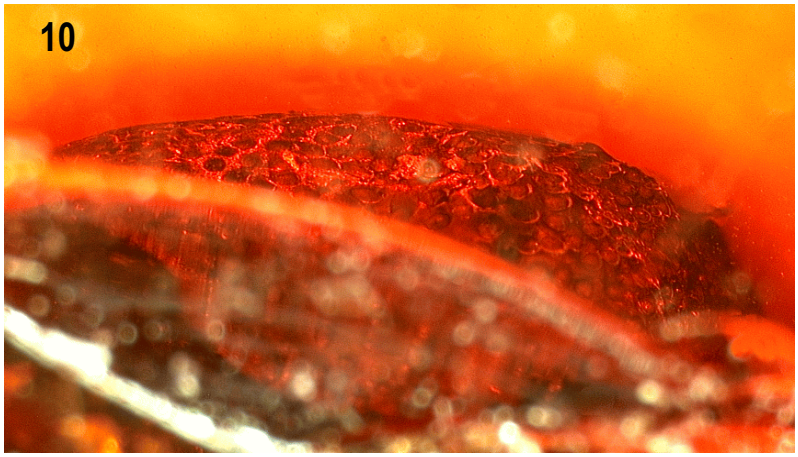


Figure 7-11. *Syndesus ambericus* Woodruff, n. sp. **7)** Antennal club (note 7 lamellae in club). **8)** Lateral view, habitus; note fractures in 2009. **9)** Enlargement of elytral punctures, right side. **10)** Enlargement of pronotum; note dense, coarse punctures. **11)** "Minute black scavenger fly" (Scatopsidae), located 5mm away from the *Syndesus ambericus* holotype. **12)** Right lateral view of head and pronotum; note mandibles and palpi.

As I indicated earlier (Woodruff *In* Woodruff and Sanderson 2004), Hispaniola is composed of 2 separate tectonic plates, the southern one subducting under the northern main island. On this southern plate there is concrete evidence that land existed in the late Cretaceous (De León 1989) of Hispaniola. Fossil trees are found in this deposit in the southern island that are replaced by the volcanic mineral pectolite (var. Larimar; Woodruff 1986; Woodruff and Fritsch 1989). All amber deposits are found in the "north island", but no amber has been discovered on this "south island" or on the Haitian side of the border.

Biogeographical significance. When such a disjunct presence of a species of Lucanidae is discovered as a fossil, and its relatives are geographically far removed, the initial question is "where did it originate?" West Indian biogeography has been a significant area of research in recent times, involving many geologists and biologists (Woods 1989). However, many questions remain unresolved. The occurrence of various animal and plant species on each island have been documented both by dispersal and vicariance. Many fossil species (and entire groups) are no longer present.

The amber insect fossils offer a unique clue to these origins, and continue to supply our oldest evidence of past Caribbean history. Sanderson and Farr (1960) were the first to call attention to the rich amber fauna in the Dominican Republic, and the first Caribbean insect fossil was described a short time later (Wille and Chandler 1964). A beautiful book, covering amber worldwide, was published by Grimaldi (1996). In the first catalogue of the Dominican Arthropod fossils ((Perez-Gelabert 1999), 508 species in 301 genera are recorded. In his latest magnificent catalogue of the Hispaniolan fauna (Perez-Gelabert 2008), he recorded 6,833 extant and (unbelievably) 1,404 fossil species.

Because I was aware that no member of the family Lucanidae was known from the Caribbean, I was surprised to see this amber fossil from the Dominican Republic. When I later discovered its relationship to the Australasian fauna, I was even more incredulous. However, recent studies of Dominican amber fossils provide a growing list of similar distributions and relationships. Because they establish a pattern of ancient extinctions and biogeographical evidence, special examples are summarized below.

1. *Leptomyrmex neotropicus* Baroni-Urbani (1980), and later (Baroni-Urbani and Saunders 1982). The first fossil insect with Australian connections to be described from Dominican amber was this unusual ant. The genus is presently confined to Australia, New Guinea, and New Caledonia, leading Wilson (1985) to doubt the original placement of this amber fossil in the genus *Leptomyrmex*, although it was later confirmed (Baroni-Urbani and Wilson 1987). Baroni-Urbani (1980) suggested that the disjunct distribution was the result of the genus having a "...former Tertiary cosmopolitanism or wide distribution...and a post Miocene contraction of the area."

2. *Valeseguya disjuncta* Grimaldi (1991). This woodgnat of the family Anisopodidae is a common amber fossil in the Dominican Republic. In fact, what was originally believed to be this species (subsequently identified as a species of Scatopsidae by D.A. Grimaldi 2009, *in litt*.) is present (Fig. 3, 11) in the amber piece with the Lucanid fossil described here. The type of the genus and the single other species is based on a unique extant male from Australia (Colless 1990). Such a gap in distribution is not easily understood, except by one-time faunas being connected and subsequent extinctions. Grimaldi (1991: 13) emphasized that "There is no doubt about the close relationship between the extinct (Dominican) and living (Australian) species."

3. *Mastotermes electrodominicus* (Krishna and Grimaldi 1991). This primitive, giant termite was described from Dominican amber, and it has 1 living relative; from Australia and New Guinea (another species has been described from Mexican amber). In Australia the living species thrives and is considered a serious pest species. This fossil was one of the first amber pieces to have DNA extracted (DeSalle et al. 1992). Although retaining many roach-like features, the DNA studies suggested that these fossils were true termites and not "missing links" with the roaches (Grimaldi 1996). In a recent paper (Inward et al. 2007), comprehensive molecular studies show that termites are eusocial cockroaches; they relegate the Order Isoptera to a family (Termitidae) within the Order Blattodea.

4. *Brachypsectra vivafosile* (Woodruff 2002 [2004a]). When this unusual beetle was discovered, the family Brachypsectridae contained only 3 known species, with relict distributions (India, Singapore, and South-

western United States. Two larvae had been found in Dominican amber, but no adults. For this reason, the extant adult specimens were therefore considered "living fossils" (i.e., *vivafosile*). An adult was found subsequently in Dominican amber and described as *Brachypsectra moronei* Branham (2006). Recently a modern larva of the family was discovered in Australia (Costa et al. 2006), but has not been named for lack of adults. It does establish additional evidence for the Australian-Dominican connection.

Extinction. Such distributions appear to be explained only by invoking theories of continental drift and plate tectonics. Grimaldi (1991) refers to this phenomenon as "geographical extinctions". For the genus *Syndesus* (and many of the insects mentioned above) to be present in the Miocene Caribbean and modern Australasia, their ancestors must have once existed on the same land mass of the southern continent Gondwanaland, after the first division of the supercontinent Pangaea. These insects are extremely ancient relics of a much broader distribution!

Curiously, this ancient stag beetle (and any other species of Lucanidae present in the Miocene) became extinct in the Caribbean, while other scarab beetles seemed to proliferate, speciate, and evolve into island endemics. Presently, the scarab genus *Phyllophaga* contains 48 Hispaniolan species, all of which are confined to that island (Woodruff and Sanderson 2004). Relationships to mainland faunas are obscure. Although the genus has hundreds of species in Central America, each Caribbean island appears to have mutually exclusive species.

Biology. Although there is no direct evidence for the behavior, biology, or habitats of this fossil, there is considerable general interest in postulating prehistoric environments (Poinar 1999). This species probably lived in similar forests to extant species of the genus *Syndesus*. Most species of Lucanidae live in decaying wood, and often in larger tree trunks. Most are presently rare, localized, and difficult to locate; some (e.g., European stag beetle) are currently on endangered species lists. Their relict distributions include most climatic zones, except the Arctic and Antarctic. Virtually none has ever been considered of economic concern, although Lawrence (1981) reported an incident of *Syndesus cornutus* damaging a bridge support in Canberra, Australia.

Monteith (*in litt.* 2009) provided the following details of the biology of *S. cornutus* in Australia and Tasmania: It is one of the "really common species" in eastern Australia from Tasmania in the South to tropical Queensland in the north. It is found mostly in rainforests, but also occurs in *Eucalyptus* forests, especially at higher and damper sites. It breeds in wood with red rot fungi, mostly in large logs where big colonies build up and may persist for many years in the same log. Adults are often found in the galleries with the larvae. Adults come to lights "fairly regularly".

Hueber and Langenhein (1986) pointed out that the tree which produced most Dominican amber was related to African ancestors, and it was later described as a new species by Poinar (1991). Dilcher et al. (1992) reported further on the leguminous trees from Dominican amber. The botanical inclusions are numerous, and many await taxonomic study. It appears that both insects and plants on the island of Hispaniola have some of their closest relatives currently living elsewhere!

Acknowledgments

I am indebted to the late Jake Brodzinsky for initially calling my attention to this specimen. I thank the following National Museum personnel for their assistance: Terry Erwin, David Furth, and Garry Hevel of the Entomology Department, and Jann Thompson and Conrad Labandeira of the Paleobiology Department for their courtesy in making the specimen available for study. Paul Skelley assisted with the Auto-Montage and the editorial process. Geoff Monteith provided valuable biological data on *S. cornutus* in Australia. I thank Frank Krell, David Grimaldi, and M. J. Paulsen for their careful peer reviews. This is Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Entomology Contribution No. 1158.

Literature Cited

Baroni-Urbani, C. 1980. The first fossil species of the Australian ant genus *Leptomyrmex* in amber from the Dominican Republic (Amber collection Stuttgart: Hymenoptera, Formicidae. IV: Ectatommini). Stuttgarter Beiträge zur Naturkunde. Serie B, 67: 1-10.

Baroni-Urbani, C., and J. B. Saunders. 1982. The fauna of the Dominican Republic amber: the present status of knowledge. Proceedings of the 9th Caribbean Geological Conference, Santo Domingo, Aug. 1980. 1: 213-223.

Baroni-Urbani, C., and E. O. Wilson. 1987. The fossil members of the ant tribe Leptomyrmecini (Hymenoptera: Formicidae). Psyche 94:1-8.

Benesh, B. 1955. Some further notes on the stagbeetles, with special reference to Figulinae (Coleoptera: Lucanidae). Transactions of the American Entomological Society 81(2): 59-76; 15 fig.

Boucher, S. 1993. Deux nouvelles espèces boliviennes des genres *Beneshius* Weinreich et *Psilodon* Perty (Coleoptera, Lucanidae). Bulletin Société Entomologique France 1992 (1993) 97(5): 419-424; 8 fig.

Branham, M. A. 2006. [Description of *Brachypsectra moronei* Branham.] *In*: Cleide Costa, S. A. Vanin, J. F. Lawrence, S. Ide, and M A. Branham. 2006. Review of the family Brachypsectridae (Coleoptera: Elateroidea). Annals of the Entomological Society of America 99(3): 409-432.

Colless, D. W. 1990. *Valeseguya rieki*, a new genus and species of Dipteran from Australia (Nematocera: Anisopodidae). Annales Société Entomologique France 26: 351-353.

Costa, C., S. A. Vanin, J. F. Lawrence, S. Ide, and M. A. Branham. 2006. Review of the family Brachypsectridae (Coleoptera: Elateroidea). Annals of the Entomological Society of America. 99(3):409-432.

Davis, D. R. 1989. An exceptional fossil amber collection acquired by Smithsonian Institution. Proceedings of the Entomological Society of Washington 91: 545-550.

DeLeón, R. O. 1989. Geología de la Sierra de Bahoruco, República Dominicana. Museo Nacional de Historia Natural. Editora Taller, Isabela la Católica; Santo Domingo. 112 p.; 1 geological map.

DeSalle, R., J. Gatesy, W. Wheeler, and D. Grimaldi. 1992. DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. Science 257: 1933-1936.

Didier, D. R., and E. Séguy. 1952. Catalogue illustré des Lucanides du globe. Atlas. Encyclopédie Entomologique, Serie A: 28. Paul Lechevalier [éditeur.], Paris. 112 plates, 903 fig.

Didier, D. R., and E. Séguy. 1953. Catalogue illustré des Lucanides du globe. Texte. Encyclopédie Entomologique Serie A: 27. Paul Lechevalier [éditeur.], Paris. 227 p.; 136 fig.

Dilcher, D. L., P. S. Herendeen, and F. Hueber. 1992. Fossil *Acacia* flowers with attached anther glands from Dominican Republic amber. p. 33-42. *In*:P. S. Herendeen and D. L. Dilcher. (editors). Advances in legume systematics: 4. The fossil record. The Royal Botanical Gardens; Kew, England. 326 p.

Donnelly, T. W. 1988. Geological constraints on Caribbean biogeography. p. 15-37. *In*: J. K. Liebherr (editor). Zoogeography of Caribbean insects. Cornell University Press; Ithaca, New York. 285 p.

Grimaldi, D. A. 1991. Mycetobiine woodgnats (Diptera: Anisopodidae) from the Oligo-Miocene amber of the Dominican Republic, and Old World affinities. American Museum Novitates 3014: 1-24; 47 fig., 3 tables.

Grimaldi, D. A. 1995. The age of Dominican amber. p. 203-217. *In*: K. B. Anderson and J. C. Crelling. Amber, resinite, and fossil resins. American Chemical Society Symposium Series 617. 297 p.

Grimaldi, D. A. 1996. Amber. Window to the past. H. N. Abrams, Inc. Publishers; New York, NY. 215 p.; copiously illustrated.

Holloway, B. A. 1960. Taxonomy and phylogeny in the Lucanidae (Insecta: Coleoptera). Records of the Dominion Museum 3: 321-365.

Holloway, B. A. 1968. The relationship of *Syndesus* MacLeay and *Sinodendron* Schneider (Coleoptera: Lucanidae). New Zealand Journal of Science 11: 264-269.

Horning, D. [undated; accessed 25 Apr., 2009]. Lucanidae of the world: Bibliography. http://www.bionica.info/Lucanidae/bib%20w.htm

Howden, H. A., and J. H. Lawrence. 1974. The New World Aesalinae, with notes on the North American lucanid subfamilies (Coleoptera, Lucanidae). Canadian Journal of Zoology 52: 1505-1510.

Hueber, F. M., and J. Langenheim. 1986. Dominican amber tree had African ancestors. Geotimes 31(1): 8-10; 11 fig., cover photo.

Inward, D., G. Beccaloni, and P. Eggleton. 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biology Letters (Royal Society) 3: 331-335; 2 fig., 2 tables.

Iturralde-Vinent, M.A., and R.D.E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science 273: 1850-1852.

Kikuta, T. 1986. On the higher taxa of the stag beetle family Lucanidae, p. 131-138. *In*: J. Aoki (editor). Papers on entomology presented to professor Takeshiko Nakane in commemoration of his retirement. Japanese Society of Coleopterology; Tokyo. 277 p.

Krajcik, M. 2001. Lucanidae of the World, Catalogue – Part 1, Checklist of the stag beetles of the world (Coleoptera: Lucanidae). M. Krajcik; Most, Czech Republic. 108 p.

Krell, F.-T. 2007. Catalogue of fossil Scarabaeoidea (Coleoptera: Polyphaga) of the Mesozoic and Tertiary. Denver Museum of Nature and Science Technical Report 2007-8: 1-79.

Krishna, K., and D. Grimaldi. 1991. A new fossil species from Dominican amber of the living Australian genus *Mastotermes* (Isoptera: Mastotermitidae). American Museum Novitates 3021: 1-10.

Lambert, J. B., J. S. Frye, and G. O. Poinar, Jr. 1985. Amber from the Dominican Republic: analysis of nuclear magnetic resonance spectroscopy. Archaeometry 27: 43–51.

Lawrence, J. F. 1981. The occurrence of *Syndesus cornutus* (F.) in structural timber (Coleoptera: Lucanidae). Journal of the Australian Entomological Society 20: 171-172; 1 fig.

MacLeay, W. S. 1819. Horae entomologicae: or essays on the annulose animals. Volume1(1). S. Bagster; London. 524 p., 3 pls.

Maes, J.-M. 1992. Lista de los Lucanidae (Coleoptera) del mundo. Revista Nicaragüense de Entomología 22: 1–121.

Martinez, A., and P. Reyes-Castillo. 1985. Un nuevo Lucanidae Neotropical (Coleoptera: Lamellicornia). Folia Entomologica Mexicana 63: 25-29.

Mizunuma, T., and S. Nagai. 1994. The Lucanid beetles of the World. Mushi-sha; Tokyo. 337 p.

Motschulsky, V. von. 1856. Études entomologiques. Cinquième année. Société de Litérature Finnoise; Helsingors. 88 p., 1 plate.

Nikolaev (Nikolajev), G. V. 1990. Grebenchatousye zhuki (Coleoptera, Lucanidae) iz paleogena Evrazii. Paleontologicheskii Zhurnal 1990(4): 120–123. [Translation: Nikolayev, G.B. [sic] 1991. Stag beetles (Coleoptera, Lucanidae) from the Paleogene of Eurasia. Paleontological Journal 1990(4): 119–122.]

Nikolaev (Nikolajev), G. V. 2007. Mezozoiskii Etap Evolyutsii Plastinchatousykh (Insecta: Coleoptera: Scarabaeoidea). Kazak Universiteti; Almaty. 222 p.

Paulsen, M. J. 2005. Annotated checklist of the New World Lucanidae (Coleoptera: Scarabaeoidea). Version 1.0. Uploaded 1 July, 2005. [non-paginated]. Accessed 2 October, 2008. http://www.museum.unl.edu/research/entomology/Guide/Scarabaeoidea/Lucanidae/Lucanidae-Catalog/LucanidaeC.htm

Paulsen, M. J. 2006. Genus *Psilodon* Perty. *In*: Generic guide to New World scarab beetles. Generated 19 Dec., 2006; accessed 9 Sept., 2009. http://www-museum.unl.edu/research/entomology/Guide/Scarabaeoidea/Lucanidae/SYN/PSI/Psilodon.html

Paulsen, M. J. 2008. Annotated checklist of the New World Lucanidae (Coleoptera: Scarabaeoidea). Version 2.0. Uploaded 24 November, 2008 [non-paginated]. Accessed 1 Apr., 2009. http://www.museum.unl.edu/research/entomology/Guide/Scarabaeoidea/Lucanidae/Lucanidae-Catalog/LucanidaeC.htm

Paulsen, M. J., and D. C. Hawks. 2008. Platyceroidini, a new tribe of North American stag beetles (Coleoptera: Lucanidae: Lucaninae). Insecta Mundi 0058: 1-2.

Perez-Gelabert, D. E. 1999. Catálogo sistemático y bibliografía de la biota fósil en ambar de la Republica Dominicana. Hispaniolana (Publicacíon Cientifíca Ocasional, Museo Nacional de Historia Natural de Santo Domingo, República Dominicana), Nueva Serie 1: 1-65.

Perez-Gelabert, D. E. 2008. Arthropods of Hispaniola (Dominican Republic and Haiti): a checklist and bibliography. Zootaxa 1831: 1-530.

Poinar, G. O. 1991. *Hymenaea protera* sp. n. (Leguminosae, Caesalpinoideae) from Dominican amber has African affinities. Experientia 47: 1075-1082.

Poinar, G. O. 1992. Life in Amber. Stanford University Press; Stanford, CA. xiii+350 p.; 8 pls., 147 fig.; 2 appendices.

Poinar, G. O., Jr., and R. 1999. The amber forest. A reconstruction of a vanished world. Princeton University Press, Princeton; New Jersey. 239 p.; 170 fig.; 2 appendices.

Poinar, G., Jr., and D. Cannatella. 1987. An Upper Eocene frog from the Dominican Republic and its implication for Caribbean biogeography. Science 237: 1215-1216.

Ratcliffe, B. C. 2002. Lucanidae. p. 6-9. *In*: R. H. Arnett, Jr., M. C. Thomas, P. E. Skelley, and J. H. Frank (editors). 2002. American beetles. Vol. 2. CRC Press; Boca Raton, Florida.: xiv+861 p.

Ratcliffe, B. C., and F. C. Ocampo. 2001. *Tyrannasorus rex* Ratcliffe and Ocampo, a new genus and species of Miocene hybosorid in amber from the Dominican Republic (Coleoptera: Scarabaeoidea: Hybosoridae). The Coleopterists Bulletin 55: 351-355.

Ross, M. I., and C. R. Scortese. 1988. A heirarchical tectonic model of the Gulf of Mexico and Caribbean region. Tectonophysics 155: 139-168.

Sanderson, M. W., and T. H. Farr. 1960. Amber with insect and plant inclusions from the Dominican Republic. Science 131: 1313.

Smith, A. B. T. 2006. A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. The Coleopterists Bulletin 60:144–204.

Waga, M. 1883. Note sur un Lucanide incrusté dans le Succin (*Paleognathus Leuthner succini* Waga.). Annales de la Société Entomologique de France (6) 3: 191–194, pl. 7.

Wickham, H. F. 1911. Fossil Coleoptera from Florissant, with descriptions of several new species. Bulletin of the American Museum of Natural History 30: 53–69.

Wickham, H. F. 1913. Fossil Coleoptera from Florissant in the United States National Museum. Proceedings of the United States National Museum 45: 283–303, plates 22–26. [Description of *Lucanus fossilis*, based on a single elytron].

Wickham, H. F. 1920. Catalogue of the North American Coleoptera described as fossils. p. 347–365. *In*: C. W. Leng (editor). Catalogue of the Coleoptera of America, North of Mexico. J. D. Sherman; Mount Vernon, New York. 470 p.

Wickham, H. F. 1927. Supplement to catalogue of the North American Coleoptera described as fossils. p. 53–56. *In*: C. W. Leng and A. J. Mutchler (editors). Supplement 1919 to 1924 (Inclusive) to catalogue of the Coleoptera of America, North of Mexico. J. D. Sherman; Mount Vernon, New York. 78 p.

Wickham, H. F. 1933. Second supplement to catalogue of North American Coleoptera described as fossils. p.103–105. *In*: C. W. Leng and A. J. Mutchler (editors). Second and Third Supplements 1925 to 1932 (Inclusive) to catalogue of the Coleoptera of America, North of Mexico. J. D. Sherman; Mount Vernon, New York. 112 p.

Wille, A., and L. C. Chandler. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera: Meloponini). Revista Biologia Tropical (San José, Costa Rica) 12: 187-195.

Wilson, E. O. 1985. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. Science 229: 265-267.

Woodruff, R. E. 1986. Larimar: beautiful, blue, and baffling. Lapidary Journal 39(10): 26-32; 8 photos.

Woodruff, R.E . 1994. Life or death in amber? Insecta Mundi 8(1-2): 137-142.

Woodruff, R. E. 2002 [2004a]. A new species of the beetle genus *Brachypsectra* from the Dominican Republic, with fossil connections (Coleoptera: Brachypsectridae). Insecta Mundi 16(4): 161-170; 19 fig.

Woodruff, R. E. 2002 [2004b]. Obituary. Jacob Brodzinsky (January 17, 1918-February 25, 2003). Insecta Mundi 16(4): 255-256.

Woodruff, R. E., and E. Fritsch. 1989. Blue pectolite from the Dominican Republic. Gems and Gemology (Gemological Institute of America) 25(4): 216-225; 13 fig., 1 table.

Woodruff, R. E., and M. W. Sanderson. 2004. Revision of the *Phyllophaga* of Hispaniola (Coleoptera: Scarabaeidae: Melolonthinae). Insecta Mundi 18(1-4): 1-154; 727 fig.

Woods, C. A. (editor). 1989. Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Inc.; Gainesville, Florida. 878p.

Zang, R. 1905. Über Coleoptera Lamellicornia aus dem baltischen Bernstein. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1905: 197–205; 1 pl.

Received August 17, 2009; Accepted September 11, 2009.