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Xyloryctes Hope, 1837 (Coleoptera: Scarabaeidae:
Dynastinae: Oryctini) in the United States.
Qui es et ubi fuisti et quo vadis?

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Cover Illustration. A pair of *Xyloryctes jamaicensis* on a rotting log in Nebraska. Larvae seem to prefer the roots of white ash trees, and the range of this beetle overlaps remarkably with that of the ash tree.

Xyloryctes Hope, 1837 (Coleoptera: Scarabaeidae: Dynastinae: Oryctini) in the United States. *Qui es et ubi fuisti et quo vadis?*

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Abstract. Two species of *Xyloryctes* occur in the United States: *X. jamaicensis* (Drury) and *X. thestalus* Bates. Identification and distribution of these species has long been confused but is reviewed and clarified here. *Xyloryctes jamaicensis* occurs only in the eastern half of the U.S. and not in the southwestern U.S. as previously thought, while *X. thestalus* occurs in Guatemala and southern Mexico northwards to the southwestern United States. This hypothesis is corroborated by biogeographical and host plant data. Three new synonyms are listed for *X. thestalus*: *X. faunus* Casey 1915, *X. hebes* Casey 1915, and *X. thestalus borealis* Endrödi. The decline of *Fraxinus* spp., the food plant of *Xyloryctes* species, as a result of damage caused by the introduced emerald ash borer (*Agrilus planipennis* Fairmaire; Buprestidae) in the United States might portend a similar decline for *Xyloryctes* species in North America.

*The sparks of controversy very often illuminate
the way to truth. --- W. LeGros Clark*

Introduction

The genus *Xyloryctes* Hope, 1837 (Coleoptera: Scarabaeidae: Dynastinae: Oryctini) currently consists of 11 species (Endrödi 1976, 1985; Delgado and Najera-Rincon 1992; Bitar and Delgado 2009). Species of *Xyloryctes* are found from Panama to southeastern Canada, with most of the species occurring in Mexico and Guatemala. *Xyloryctes* species are recognized by the presence of a tridentate protibiae, a bilobed and strongly reflexed clypeal apex, mandibles completely hidden by the clypeus, males with a horn and females with a single tubercle on the frons, and usually an anteriorly declivous pronotum in the males and a convex pronotum in the females. Some of the species are difficult to separate from one another because of close similarity in external structure and the form of the male parameres. Endrödi (1976) provided the most recent synopsis of the entire genus; two new species have been described since that time.

Biological information and the larvae are known for *X. jamaicensis* (Drury) (Ritcher 1966; Stephan 1967; Ratcliffe 1981, 1991; Seastedt 1983; Ratcliffe and Paulsen 2008) and *X. thestalus* Bates (Morón 1976), but similar information is lacking for the Mesoamerican species. Some species are relatively uncommon, and most of them are usually found in forests above 1,000 meters in elevation; *X. thestalus* has been collected in Mexico as high as 3,000 meters (label data).

Xyloryctes jamaicensis occurs in the eastern half of the United States (Saylor 1946; Dillon and Dillon 1961; Ritcher 1966; Arnett 1968; Blackwelder and Arnett 1974; Ratcliffe 1991; Harpootlian 2001; Ratcliffe and Paulsen 2008), where it is occasionally locally abundant. The current wisdom is that it also found in New Mexico, Arizona, Utah, and eastern Mexico (Blackwelder 1944; Saylor 1946; Arnett 1968; Blackwelder and Arnett 1974; Endrödi 1976, 1985; Harpootlian 2001; Ratcliffe and Morón 1997), where it is sympatric with *X. thestalus*. The other U. S. species, *Xyloryctes thestalus*, occurs from Guatemala and southern Mexico northwards to Arizona, New Mexico, and Utah (Morón 1976; Endrödi 1976, 1985; Ratcliffe and Morón 1997). There has always been the problem of how to differentiate the two species in their supposed area of sympatry in the American Southwest. In nearly all collections in the United States, specimens from the Southwest are invariably identified as *X. jamaicensis*.

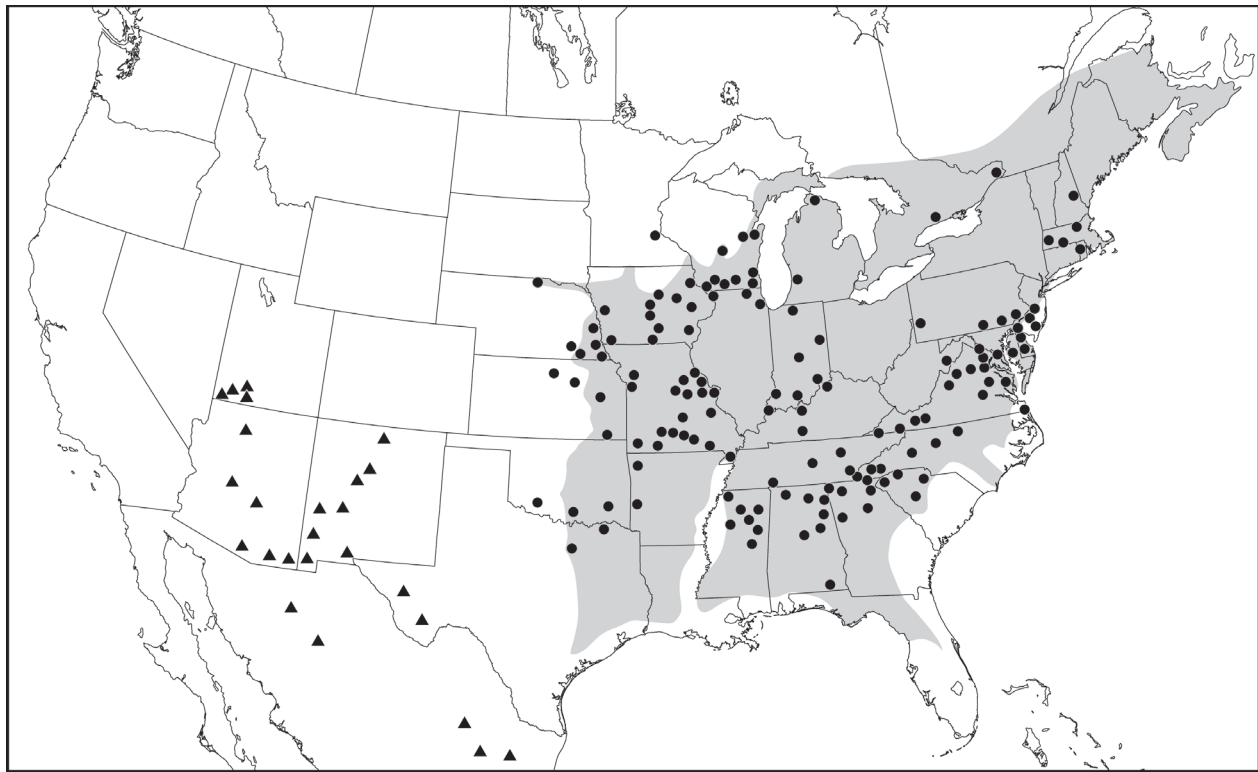


Figure 1. Distribution map for white ash, *Fraxinus americana* (shaded area; after Little 1971) and *Xyloryctes jamaicensis* (circles) and *X. thestalus* (triangles) in the United States.

Methods

In order to ascertain species limits (both morphological and geographic), I examined more than 2,000 specimens of *X. thestalus* and *X. jamaicensis* from the research collections of the U. S. National Museum (currently at the University of Nebraska), University of Nebraska, Texas A&M University, Louisiana State University, University of Arkansas, University of Mississippi, Mississippi State University, Purdue University, University of Missouri, University of Wisconsin, The Field Museum of Natural History, and databases from New Mexico, Oklahoma, Mississippi, Arkansas, and Alabama. In addition, I have received data and commentary from collectors in Alabama, Florida, Texas, Mississippi, Louisiana, Arizona, and Utah. I examined morphological characters, including the form of the pronotal prominence, sculpturing of the elytra and pygidium, form of the apex of the metatibia, and male parameres. Host plant distributions and biogeographical data were also examined. I use the phylogenetic species concept (Wheeler and Platnick 2000) in this work to delineate species: "A species is the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states."

Results

Based upon specimen records, I have concluded that *X. jamaicensis* occurs only in the eastern half of the United States (Fig. 1) and does not extend into the American Southwest as has been previously thought. The westernmost records I have found for *X. jamaicensis* are in eastern Nebraska south to eastern Oklahoma and eastern Texas (approximately Dallas). There exists a distinct gap in distribution of *Xyloryctes* species from eastern Texas across the low, dry plains to the mountains in New Mexico that extend diagonally from the southwestern part of the state to the northwest (Taos County) (where *X. thestalus* reaches its easternmost distribution). Not surprisingly, the western extent of the host plant of *X. jamaicensis*, *Fraxinus americana* L. (white ash) (Oleaceae) (Little 1971), mirrors almost exactly the distribution of *X. jamaicensis* (Fig. 1). There are no records of *X. jamaicensis* feeding on any other species of ash tree.



Figure 2. Map of Mexico showing northward dispersal corridors of the Sierra Madre Oriental into southern Texas and the Sierra Madre Occidental into Arizona, New Mexico, and southwestern Texas. Map source: Central Intelligence Agency.

Specimens of “*X. jamaicensis*” formerly recorded from Arizona, New Mexico, and southwestern Texas are, in fact, the northern elements of *X. thestalus*. Accordingly, *X. faunus* Casey and *X. hebes* Casey, described from Arizona and New Mexico, respectively, are transferred from their former synonymy with *X. jamaicensis* to new synonymy with *X. thestalus*. Specimens of *X. jamaicensis* (Fig. 3, 8) are characterized by a weakly arcuate pronotal prominence in the males, elytra with longitudinal rows of punctures in furrows (Fig. 3), apex of the metatibia with 7-8 small teeth, and a relatively short basolateral flange on the parameres (Fig. 8).

Xyloryctes thestalus has a distinctly protuberant pronotal process with an emarginate apex in the males, the elytra vary from smooth (Fig. 4, 6) to longitudinally furrowed with punctures (Fig. 5, 7), the apex of the metatibia also has 7-8 small teeth, and the parameres have a relatively long basolateral flange (Fig. 9). Specimens of *X. thestalus* occurring in southern to central Mexico are usually large with relatively smooth elytra. As one progresses northwards to northeastern Mexico and the southwestern United States, specimens of *X. thestalus* tend to become smaller and have distinctly punctate, furrowed elytra. Some Arizona specimens, however, are still large (35 mm) and occasionally with smooth elytra, while some Mexican specimens have punctate elytra and are small (28 mm). A subspecies designation for southern and northern populations of *X. thestalus* cannot be supported inasmuch as there is a clinal shift towards decreased body size and increased surface sculpturing from south to north. Accordingly, *X. thestalus borealis* Endrödi is reduced to synonymy. *Xyloryctes thestalus* also feeds on *Fraxinus* species in Arizona (William Warner, personal communication, April 2009).

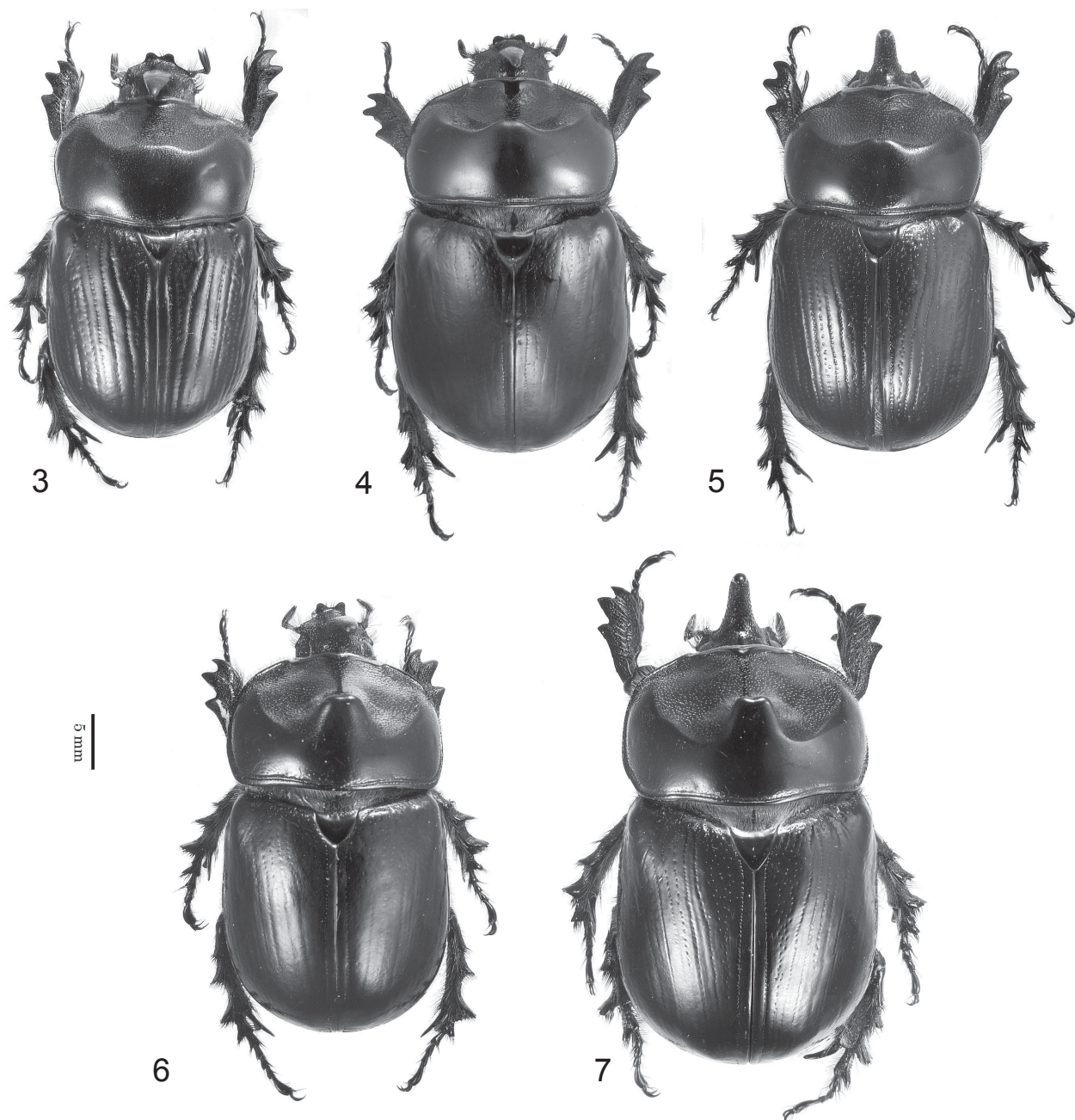


Figure 3-7. *Xyloryctes* spp. **3)** *Xyloryctes jamaicensis* (Drury). **4-7)** *Xyloryctes thestalus* Bates. **4)** Smooth elytra from USA. **5)** Striate elytra from USA. **6)** Smooth elytra from Mexico. **7)** Striate elytra from Mexico. Cephalic horn not at same angle in all specimens.

***Xyloryctes jamaicensis* (Drury, 1773)**
(Fig. 3, 8)

- Scarabaeus jamaicensis* Drury 1773: 54.
Scarabaeus satyrus Fabricius 1775: 12.
Scarabaeus americanus Palisot de Beauvois 1807: 75.
Xyloryctes lacustris Casey 1915: 255.
Xyloryctes tenuicornutus Casey 1915: 255.
Xyloryctes obsolescens Casey 1915: 256.

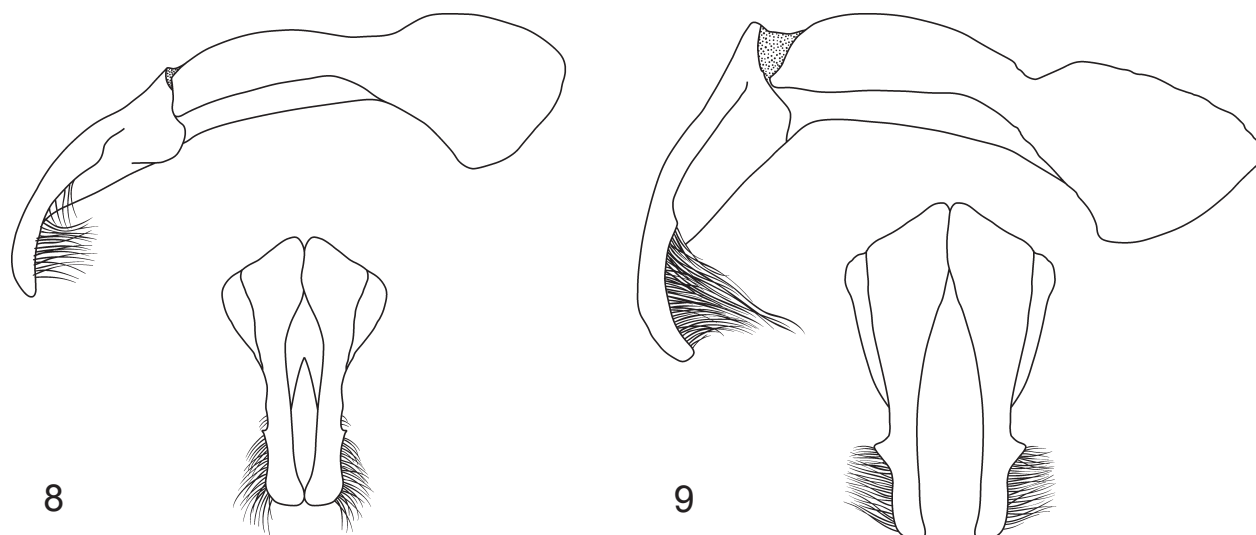


Figure 8-9. Parameres of *Xyloryctes* species, caudal and lateral views. **8)** *X. jamaicensis*. **9)** *X. thestalus*.

DIAGNOSIS. Length 21.0-38.0 mm; width 12.7-20.0 mm. Color castaneous to more commonly black. The pronotal lobe in males varies from barely to distinctly arcuate. The elytral disc normally has 6 punctate striae, the punctures are moderate to large and ocellate. The sides have 2-4 variably distinct (usually weak) rows of punctures similar to those on disc. The parameres are as in Fig. 8.

Xyloryctes jamaicensis is distinguished from northern specimens of *X. thestalus* most easily by their disparate distributions. Morphologically, males of *X. jamaicensis* have a shallow, arcuate pronotal prominence, whereas males of *X. thestalus* have a distinctly projecting prominence on the pronotum. This distinction is less noticeable in minor males of each species, although minor males of *X. thestalus* still have a projection, whereas minor males of *X. jamaicensis* do not. The parameres are similar, although those of *X. jamaicensis* usually have a shorter basolateral flange (in caudal view; Fig. 8) that usually extends less than halfway between the base of the paramere and the lateral tooth. The basolateral flange in *X. thestalus* usually extends well below the halfway point between the base of the paramere and the lateral tooth (Fig. 8), and in some cases almost reaches the lateral tooth. Females lacking geographical data probably cannot be reliably separated unless they are the large, smooth forms from central Mexico or are associated with males.

DISTRIBUTION. *Xyloryctes jamaicensis* ranges throughout the eastern United States (New Hampshire to northern Georgia) and west to eastern Nebraska, eastern Kansas, south to eastern Oklahoma and eastern Texas (Fig. 1). The distribution of white ash (Little 1971), its host, is nearly identical with that of *X. jamaicensis* (Fig. 1). There are no collecting records for Florida (Peck and Thomas 1998; Skelley, personal communication) and Louisiana (Carlton, personal communication) or the southern halves of Georgia, Alabama, and Mississippi (collection records).

BIOLOGY. Stephan (1967) observed that adults feed and oviposit on or near the roots of white ash trees, *F. americana*, usually in more sandy soil. He indicated that early instar larvae were always collected near the roots of white ash, and that larger larvae were found some distance from ash trees in the leaf litter, where they had dispersed to feed. Ratcliffe (1981) observed a large emergence of *X. jamaicensis* in August in southeastern Nebraska, where a farmer had reported that thousands of these beetles were congregating on a white ash tree and then burrowing into the grass at the base of the tree. This had happened in the previous two years, to a lesser extent, on the same tree. In August 1981, I observed literally thousands of these beetles flying to this one tree beginning at dusk. After landing, the beetles crawled down the trunk and proceeded to burrow into the ground, presumably to feed or oviposit on or near the roots of the ash tree. The tree appeared healthy with no trunk or foliage injuries. Within 30 meters of the tree were two other ash trees, but these were untouched by the beetles. There was also a

mercury vapor yard light about 50 meters away, but fewer than a dozen beetles were seen there. Normally, *X. jamaicensis* is attracted to light. These beetles were so abundant that 40 liters of them could easily have been gathered in a few minutes. They were reported to have been even more numerous the evening before, when the trunk of the tree was black with them. Skunks were observed foraging for beetles by digging in the soil during the 1980 occurrence. Presumably, other natural enemies fortuitously encountering such an emergence would also feed on these beetles. Label data on some pinned specimens also indicates adults being found on white ash trees. I have not seen any data to suggest any association between *X. jamaicensis* and green ash trees, *F. pennsylvanica* Marsh.

Larvae of *X. jamaicensis* (Drury) have been found beneath leaf litter in the soil feeding on roots, microrrhizae, or woody detritus (Stephan 1967; Seastedt 1983; Ratcliffe 1991; Ratcliffe and Paulsen 2008). The larval stage was described by Ritcher (1966).

***Xyloryctes thestalus* Bates, 1888**

(Fig. 4-7, 9)

Xyloryctes thestalus Bates 1888: 325.

Xyloryctes thestalus intermedius Sternberg 1908: 22 (synonym).

Xyloryctes faunus Casey 1915: 256 (**NEW SYNONYMY**).

Xyloryctes hebes Casey 1915: 257 (**NEW SYNONYMY**).

Xyloryctes thestalus borealis Endrödi 1975: 262 (**NEW SYNONYMY**).

DIAGNOSIS. Length 23.5-43.0 mm; width 12.8-22.4 mm. Color black. The pronotal process projects slightly upwards from the plane of the disc with subparallel sides (majors) or angularly arcuate sides (minors), and the apex is broadly truncate and weakly to distinctly emarginate. In southern populations (central Mexico), the elytra are relatively smooth and occasionally with weakly impressed rows of moderate to large punctures; in northern populations (southwestern U. S.), the elytral disc normally has 6 punctate striae, the punctures are moderate to large and ocellate; the intervals vary from weakly to strongly shagreened; the sides have 2-4 variably distinct (usually weak) rows of punctures similar to those on disc. The parameres are as in Fig. 9.

Males of *X. thestalus* (even most minor males) have a distinctly projecting prominence on the pronotum (Fig. 4-7), whereas males of *X. jamaicensis* have a shallowly arcuate pronotal prominence (Fig. 3). While the parameres are similar, the basolateral flange in *X. thestalus* usually extends well below the halfway point between the base of the paramere and the lateral tooth (Fig. 9), and in some cases almost reaches the lateral tooth. The parameres of *X. jamaicensis* usually have a shorter basolateral flange (in caudal view; Fig. 8) that usually extends less than halfway between the base of the paramere and the lateral tooth. I have seen exceptions to this, but these are rare. Specimens of *X. thestalus* from the southwestern U. S. can be distinguished from *X. jamaicensis* most easily by distribution. Females lacking geographical data probably cannot be told apart unless they are the large, smooth forms of *X. thestalus* from southern or central Mexico or associated with males.

The largest specimen of *X. thestalus* I have seen is a remarkably large 43 mm from central Mexico. Some central Mexican specimens have distinctly punctate, furrowed striae (more common in northern specimens), and these, along with *S. lobicollis*, are the only Mesoamerican species of *Xyloryctes* with this character. The smallest specimens I have seen are a short series from Las Vegas, New Mexico; this unusually small size (24 mm) has not been seen elsewhere.

DISTRIBUTION. *Xyloryctes thestalus* occurs from Guatemala and southern Mexico (in both the western and eastern cordilleras) northwards to the southwestern USA (Arizona, Utah, New Mexico, southwestern Texas) (Fig. 1).

BIOLOGY. Little is known of the biology of *X. thestalus*. Adults are commonly attracted to lights (personal observation) and to the Arizona ash, *Fraxinus velutina* Torr. (Oleaceae) (W. Warner, personal communication, April 2009). There are several species of *Fraxinus* in northeastern Mexico, and at least three species extend south into Guatemala and Honduras (R. Kaul, personal communication, May 2009). It would be interesting to know if the other Mesoamerican species of *Xyloryctes* also feed on *Fraxinus*.

species. Larvae have been found beneath leaf litter in the soil feeding on roots or microrrhizae (Morón 1976).

Biogeography

Howden (1966) observed that the scarabaeoid fauna of North America was well established before the Pleistocene, and that most of this fauna survived the four glaciations of the Pleistocene in refugia in Mexico or the southeastern United States. Lacking fossil evidence for *Xyloryctes* species, we are forced to rely upon data from present and paleodistributions of other plants and animals and ecological factors to formulate a model to best explain the current distribution of these beetles. Mares (1985) judiciously noted that biologists straying beyond the broadest interpretation of ancient patterns must recognize that they are moving from science to conjecture. Continents shift their positions, ocean currents and weather patterns change, mountains rise, and organisms evolve. The hard-science portion of paleobiogeography is based upon plant and animal fossils, geological evidence of plate tectonics and orogenesis, and paleoclimatology. Caution must be exercised in making deductions that propel us well beyond the limits of the data.

The north-south direction of dispersal corridors in the physiographically complex Mexican Transition Zone has been a major factor in the displacement of biotas during times of climatic change (Halffter 1976). Ancestral *Xyloryctes* species, mostly inhabitants of cooler, temperate mountain biotopes, dispersed northward, and they must have used as their principal expansion route from nuclear Central America the mountains of Oaxaca and Guerrero in Mexico. The Transverse Volcanic Belt and the Sierra Madre del Sur funneled the dispersal of some *Xyloryctes* species to the west toward the Sierra Madre Occidental and to the east toward the Sierra Madre Oriental. The Sierra Madre Occidental is the longest (1,400 km) and most continuous in the Mexican Transition Zone. It runs parallel to the Pacific coast from its juncture with the Transverse Volcanic Belt in Nayarit and Jalisco states to the U. S.-Mexican border. Similarly, the Sierra Madre Oriental became a dispersal route from the Transverse Volcanic Belt through the states of Hidalgo, San Luis Potosí, Tamaulipas, Nuevo León, and Coahuila to southwestern Texas. Dispersal of species ancestral to *X. thestalus* and *X. jamaicensis* into Arizona, Utah, New Mexico, Texas, and the eastern United States was probably enabled by these temperate corridors of the Sierra Madres (Fig. 2) prior to the formation of desert barriers during the Pleistocene glaciations. Paleoenvironmental reconstructions indicate that pine/oak forests and temperate vegetation dominated the Sierras and the Transverse Volcanic Belt in Mexico and were present also in Texas and New Mexico (Galloway 1970; Messing 1986; Harris 1988). Some ancestral *Xyloryctes* species probably occupied a contiguous range in northern Mexico and the eastern United States. Similar dispersal patterns (wherein the cordilleras are used as pathways) can be seen in several species of *Canthon* Hoffmannsegg, *Dichotomius* Hope, and *Onthophagus* Latreille (Scarabaeinae); *Diploaxis* Kirby and *Isonychus* Mannerheim (Melolonthinae); *Parabyrsopolis* Ohaus and *Chrysina* Kirby (Rutelinae); *Ancognatha* Erichson, *Cyclocephala* Dejean, *Tomarus* Erichson, *Strategus* Kirby, and *Phileurus* Latreille (Dynastinae); *Hologymnetis* Martínez (Cetoniinae); and *Trox* Fabricius (Trogidae) (see Howden 1966, Morón 2006a-b, and Ratcliffe and Deloya 1992) as well as numerous other invertebrates, vertebrates, and plants.

Research by Toledo (1982) illustrated that there were successive perturbations in plant and animal communities during the recurring Pleistocene glaciations and interglacials as these organisms responded to cool-dry, cool-wet, or warm-dry climatic cycles. One of these perturbations was the formation or expansion of deserts. According to the research of Axelrod (1950, 1958) and Findley (1969), extensive desert areas appeared in the Sonoran or Chihuahuan regions in the Pleistocene. The fossil evidence indicates that an extensive pine-oak savanna existed prior to desert formation in what is now northern Mexico, southern Arizona, and adjoining areas of the Texas panhandle when the climate was cooler and wetter (Rogers 1976). Tree lines became lower in elevation (perhaps by as much as 1,000 m during the Wisconsin glaciation 12,000-10,000 years BP; Martin and Mehringer 1965; Wells 1979; McDonald 1993), and temperate forest became established in semiarid regions of the southwestern United States. Expansion of *Xyloryctes* species northward through the Sierra Madre Occidental as far as Arizona, New Mexico, and Utah and the Sierra Madre Oriental to Texas and the eastern U. S. was facilitated by pre-Pleistocene suitable habitat and climate. With the formation of major deserts, *X. thestalus* became isolated on more humid and equable mountain islands surrounded by a sea of desert in the southwestern United States.

These deserts now form impassable barriers to further dispersal. These fragmented and isolated mountains are where we find *X. thestalus* today. Similarly, the ancestors of *X. jamaicensis* penetrated into the eastern United States when climate and habitat permitted during wetter pre-Pleistocene times. With the subsequent formation of arid regions in Texas and Oklahoma (occurring simultaneously with desert formation in northern Mexico and the southwestern U. S.), these eastern populations became isolated from those in Arizona and New Mexico. They survive in the eastern United States today because of more humid forest habitats where their host plant, white ash, also lives. Recent speciation of the *X. jamaicensis*/*X. thestalus* lineage is suggested by their close similarity in morphology (little divergence) and the known creation of arid barriers during the Pleistocene (relatively recent) that led to separation and isolation between the eastern (*X. jamaicensis*) and western (*X. thestalus*) populations.

Conservation Concerns

So far as known, species of *Xyloryctes* feed on the roots of ash trees (*Fraxinus* spp., Oleaceae). An invasive insect species that threatens all of North America's ash trees has now become established in the United States, and the loss of ash trees could severely and negatively impact populations of *Xyloryctes* species that use these trees for food. According to Anonymous (2009), the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), was discovered in southeastern Michigan in the summer of 2002. Adult beetles feed on ash foliage but cause little damage. The larvae, however, feed on the inner bark of ash trees, disrupting the tree's ability to transport water and nutrients. The natural range of *A. planipennis* is eastern Russia, northern China, Japan, and Korea. Before June 2002, it had never been found in North America. The emerald ash borer probably arrived in the United States from its native Asia in solid ash wood used for packing and crating heavy consumer products or stabilizing cargo in ships.

Since its introduction, the emerald ash borer has become established in Ontario, Canada and Ohio (2003), northern Indiana (2004), northern Illinois and Maryland (2006), western Pennsylvania and West Virginia (2007), and Wisconsin, Missouri and Virginia (2008) (Anonymous 2009). The emerald ash borer has killed tens of millions of ash trees in southeastern Michigan alone, with tens of millions more lost in Ohio, Illinois, Indiana, Pennsylvania, West Virginia, Missouri, Wisconsin, Virginia, Ontario, and Quebec. All species of North American ash appear to be susceptible. Its spread in the northeastern United States has been extremely rapid, and no one knows how far west and south it may ultimately extend. Similarly, no one knows how the loss of ash trees will affect populations of *X. jamaicensis* in eastern North America or possibly *X. thestalus* in the Southwest. If these rhinoceros beetles are indeed restricted to ash trees in their diet, then it is clear that these two species will be at risk of decline or extirpation in the United States if their food plant is eliminated. I believe an informative and valuable research project would be to monitor populations of *X. jamaicensis* relative to the decline of ash trees to ascertain any concomitant decline of the beetles. At this point, most of the concern by government agencies and municipalities is on the loss of the trees and not on the other organisms that might depend on those trees for their survival. And while we all value the beauty and shade of ash trees, we would all sleep better at night knowing there are rhinoceros beetles out there chewing on the roots of ash trees on warm summer nights. Wouldn't we?

So, to answer the Latin questions in the title of this paper, "who are you, where have you been, and where are you going?", it is now possible to say that there are two distinct species of *Xyloryctes* in the United States that are allopatric ("who are you?"), and that the ancestors of both species dispersed to their present locations and subsequently became isolated by climatic events that produced impassable barriers between a once contiguous population ("where have you been?"), and that the possibility exists for severe population reduction or extinction due to loss of the primary food plant ("where are you going?"). Thus, the saga of *Xyloryctes* in North America continues.

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