

Pharaxonotha portophylla (Coleoptera: Erotylidae), new species and pollinator of *Zamia* (Zamiaceae) in Puerto Rico

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ABSTRACT.—*Pharaxonotha portophylla*, new species (Insecta: Coleoptera: Erotylidae: Pharaxonothinae), is described based on individuals collected on the cones of native populations of *Zamia amblyphyllidia* D. W. Stevenson and *Z. portoricensis* Urban (Cycadales: Zamiaceae) in the Puerto Rican Cambalache and Susúa Commonwealth Forests, respectively. The new species is a member of a complex centered around *P. floridana* (Casey), and may be distinguished from other *Pharaxonotha* species by the following traits: head lacking supraocular striae, with coarse punctation; pronotum slightly transverse, anterolateral edges weakly projected and angulate; protibia narrowly triangularly widened toward apex; elytra with an anterior marginal line, elytral punctures coarse, not impressed, elytral striae not grooved, and elytral intervals plane. *Pharaxonotha portophylla* is the second species in this genus reported for the Caribbean region, raising the number of known *Pharaxonotha* species to 13 worldwide. Samples of insect visitors on *Zamia* cones of either gender and at various stages of anthesis strongly suggest that *P. portophylla* is the primary and sole pollinator of these cycad species at the two locations. The abundance of adult individuals was much lower on the receptive megastrobili than on the pollen-releasing microstrobili which produced similar attracting odors. Larval development was restricted to the microstrobili, possibly indicating the presence of defensive metabolites in the megastrobili and a reproductive interaction with “pollination by deceit”.

KEYWORDS.—cycad pollination, insect systematics, Pharaxonothinae, pollinator reproduction

INTRODUCTION

Species in the predominantly pantropical genus *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae *sensu* Leschen 2003; see also Węgrzynowicz 2002, Robertson et al. 2004, Leschen & Buckley 2007) represent an old lineage of Erotylidae with longstanding reproductive associations with the Cycadales (see, e.g., Tang 1987, Vovides et al. 2003, Chaves & Genaro 2005; and references therein). As presently circumscribed the genus contains 12 species (Sen Gupta & Crowson 1971, Leschen 2003), of which two occur in Central America, Mexico, and the southeastern United States (Leschen & Skelley 2002), two additional species in Costa Rica (Pakaluk 1988), and one in Cuba (Chaves & Genaro 2005). The remaining species are predominantly (southeast) Asian. Together with weevils in the genera *Parallocorymus* Voss and *Rhopalotria* Chevrolat (Belidae: Oxycoryninae; see Marvaldi et al. 2006), *Pharaxonotha* are considered the primary pollina-

tors of many Central American and Caribbean cycads, and are therefore of interest to coevolutionary analyses and conservation management policies (e.g., Oberprieler 2004, Tang 2004).

The native Puerto Rican cycads are placed in the prominent New World genus *Zamia* Linnaeus (see Walters & Osborn 2004), and include the endemic *Z. portoricensis* Urban, as well as *Z. amblyphyllidia* D. W. Stevenson and *Z. pumila* Linnaeus which also inhabit other Caribbean islands (Eckenwalder 1980, Stevenson 1987, Liogier & Martorell 2000). In particular the population structure of *Z. amblyphyllidia* in northern Puerto Rico is well understood (Negrón-Ortíz & Breckon 1989, Negrón-Ortíz et al. 1996). In contrast, the only published reference on the pollinating agents of any Puerto Rican species of *Zamia* is a note by Breckon & Negrón-Ortíz (1983) who observed mycetophilid gnats visiting and reproducing in the cones of the same species. Here we describe a new species of *Pharaxonotha*, and present natural history infor-

mation indicating that this species is the primary pollinator of *Z. amblyphyllidia* and *Z. portoricensis* at two geographically separate Puerto Rican localities.

MATERIALS AND METHODS

Study Sites and Collecting Methods

Cones of *Z. amblyphyllidia* (Figure 1) and *Z. portoricensis* (Figure 2) were sampled for visiting insects at the Cambalache and Susúa Commonwealth Forest Reserves, respectively, during the period of January 12 to February 12, 2007. Cambalache is located centrally near Arecibo along the northern coast of Puerto Rico, and is classified as a subtropical moist forest habitat on limestone soils (see Negrón-Ortiz & Breckon 1989, Lugo et al. 2001). On the other hand, Susúa is located near Sabana Grande on the southwestern edge of the Central Cordillera, and is classified primarily as a dry slope forest habitat on serpentine soils (see Ewel & Whitmore 1973, Figueroa Colón 1996). While the species concepts for Puerto Rican *Zamia* are not conclusively resolved, we herein adopt the relatively narrow conceptions proposed by Stevenson (1987).

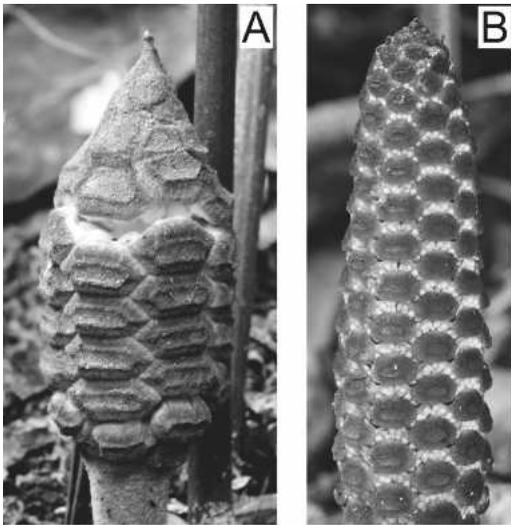


FIG. 1. *Zamia amblyphyllidia* at Cambalache. (A) receptive megastrobilus; (B) microstrobilus, approximately 12 hours prior to releasing pollen. Photos taken at 10:00 a.m.

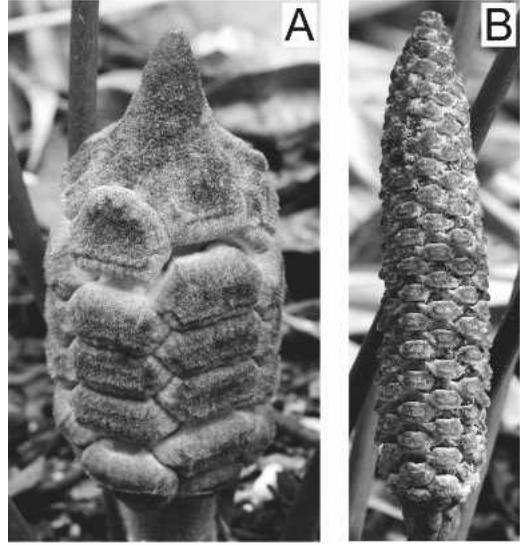


FIG. 2. *Zamia portoricensis* at Susúa. (A) receptive megastrobilus; (B) microstrobilus, approximately 20 hours past opening of anthers.

Insect visitors were taken from both female megastrobili (Figures 1A & 2A) and male microstrobili (Figures 1B & 2B), at various stages of development, by cutting off entire cones and placing them immediately in whirl-pak containers. Insects crawling out of receptive cones were subsequently transferred in separate vials with 95% ethanol. Older cones were returned to the laboratory and monitored for 1-3 weeks for emerging immature and adult insects. The samples were pooled into three major phases of development: (1) pre-anthesis, i.e. 1-5 days prior to the appearance of fissures between sporophylls and the production of odors; (2) anthesis, i.e. the stage of dehiscence, micropyle receptivity (♀) or pollen release (♂) and production of sweet, resinous odors, with a duration of approximately three days; and (3) post-anthesis, i.e. 5-30 days past cone receptivity (♀) or pollen release (♂), when odors are no longer perceptible. At this stage, the megastrobili are beginning to set fruit whereas the microstrobili are slowly decomposing.

Systematics

The description mostly follows the format of Franz (2003), with occasional refer-

ence to Chaves & Genaro (2005) to facilitate an understanding of similarities and differences with the species described in that publication. The new species of *Pharaxonotha* was identified through application of the phylogenetic species concept (emphasizing unique character combinations; see Wheeler & Platnick 2000). The morphological terms used are in accordance with Torre-Bueno (Nichols 1989) and particularly McHugh et al. (1997) for adult internal structures including male and female terminalia. Observations of external and internal morphology were made with a Leica MZ16 stereomicroscope (magnification: 7-115x) and an Olympus BX41 compound microscope (magnification: 20-400x), each equipped with an ocular graticule for measurements of lengths and length/width relations. The overall length was measured from the anterior margin of the head to the posterior margin of the elytra; measurements of the head width and dorsal interocular distances follow Pakaluk (1988) and Chaves & Genaro (2005). The numbers of measurements taken are given in parentheses for the preceding values. The habitus pictures of *Pharaxonotha* beetles were produced with a Microptics XLT imaging system. The line drawings were prepared with a drawing tube attached to the stereomicroscope (external structures) or compound microscope (internal structures). The initial sketches were scanned and redrawn using an illustration software program, emphasizing structures with systematic or diagnostic significance.

The identification labels for type specimens include the genus name and species epithet, a gender symbol (for holotype and allotype only), and the authors and year. They are colored red for the holotype, green for the allotype, and yellow for all paratypes. The insect collection codens are adopted from Arnett et al. (1993), and as used as follows:

AMNH – American Museum of Natural History, New York, NY
 BDVC – Barry D. Valentine collection, Sarasota, FL
 FSCA – Florida State Collection of Arthropods, Gainesville, FL

MAIC – Michael A. Ivie collection, Montana State University, Bozeman, MT
 MEBT – Museum of Entomology and Tropical Biodiversity of the Mayagüez Campus, University of Puerto Rico, Río Piedras, PR
 MUCR – Museo de Insectos, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica
 NMFC – Nico M. Franz collection, University of Puerto Rico, Mayagüez, PR
 NMNH – National Museum of Natural History, Washington, D.C.
 NZAC – New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand
 UGCA – Collection of Arthropods, University of Georgia, Athens, GA
 UPRM – Invertebrate Collection, University of Puerto Rico, Mayagüez, PR

SYSTEMATICS

Pharaxonotha portophylla Franz & Skelley, new species

Diagnosis. *Pharaxonotha portophylla* is readily identified as a member of *Pharaxonotha* using the diagnostic features in Leschen & Skelley (2002: 344), viz. pronotum with lateral margins subparallel, each side posteriorly with a short sulcus, and externally visible ventrite I lacking metasubcoxal lines, among others. This new species is a member of a complex centered around *P. floridana* (Casey), currently under study by PES. *Pharaxonotha portophylla* may be distinguished from other described and undescribed species by a combination of characters; i.e., body dorsally with short, indistinct setae; clypeus and frons flattened; head with coarse punctation, lacking supraocular striae, posteriorly with transverse line anterior of stridulatory files; pronotum slightly transverse; anterolateral edges of pronotum weakly projected, angulate, not evenly rounded; protibia narrowly triangularly widened toward apex; outer tooth of protibial apex separated from inner terminal row of spinules via small gap; elytra with anterior marginal line; elytral punctures coarse, not impressed; elytral striae not grooved, elytral intervals plane.

Description – male. Body in dorsal view elongate to oval (Figures 3A); small, length 2.75–3.38 mm, width 1.03–1.30 mm, greatest width near anterior 1/3 of elytra, length/width ratio 2.53–2.80 (N=10); in lateral view depressed (Figure 3B), dorsally and ventrally slightly convex; color reddish-brown,

head with darkest pigmentation, thorax (including pronotum and legs) and venter intermediate, and elytra with lightest pigmentation, light reddish-brown and weakly transparent; sculpture uniformly and fairly densely punctulate on head and pronotum, elsewhere more sparsely dis-

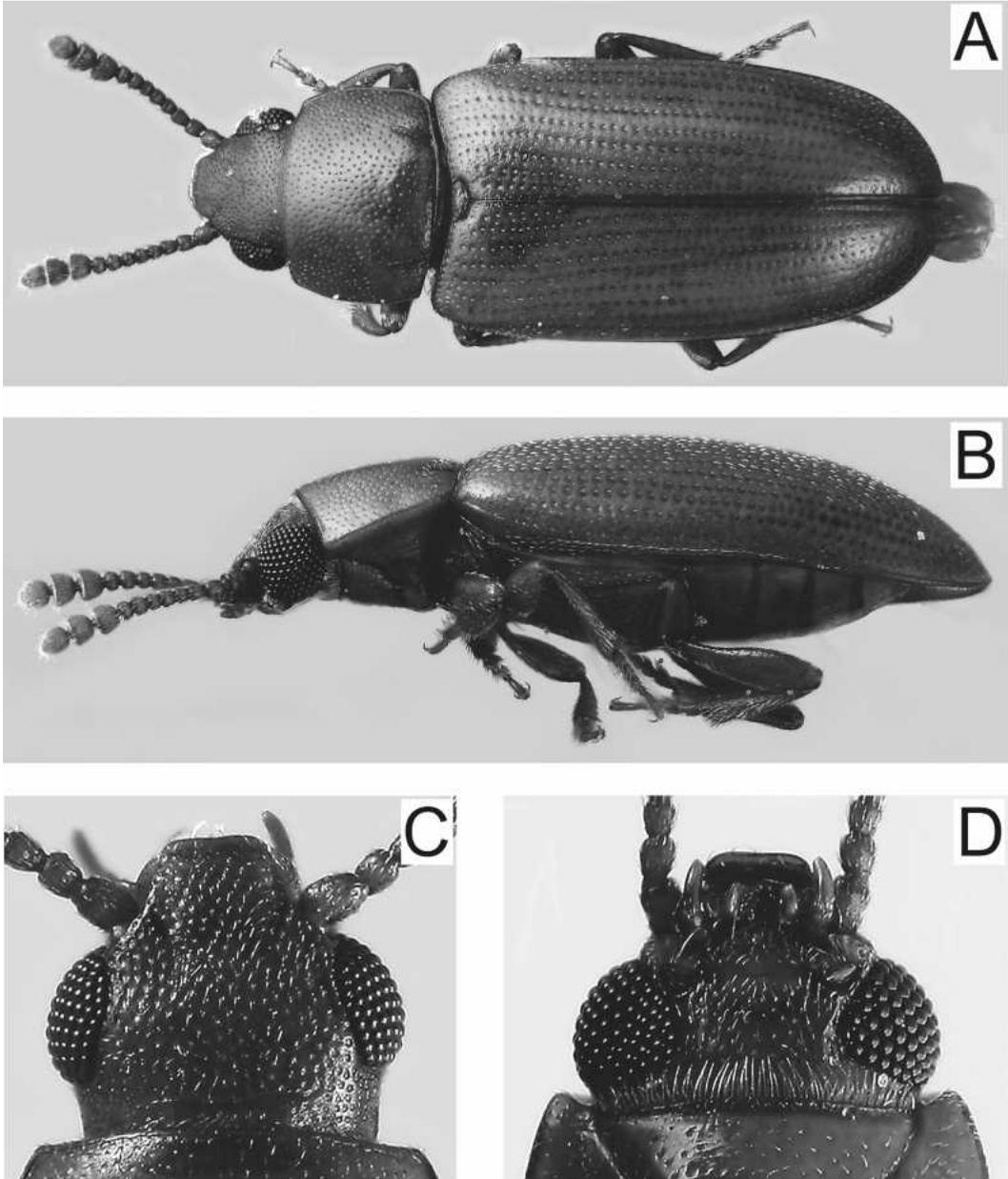


FIG. 3. Habitus of *P. portophylla*. (A) dorsal view; (B) lateral view; (C) head, dorsal view; (D) head, ventral view.

tributed; pubescence very fine and short, appressed, aurate, moderately densely arranged, longer on femora and tibiae.

Head – mouthparts. Clypeus plane, apically slightly rotundate, with row of fairly long setae. Mandible (Figure 4A) large, arcuate-triangular; apically with 2 small, narrowly superposed teeth, centrally variously sulcate, outer margin with row of setae. Maxilla (Figure 4B) with cardo apically expanded and setose; stipes narrowly triangular, apically acute, partially overlapping with palpiger; galea and lacinia with long, densely aligned setae; maxillary palp 4-segmented, each palpomere with row of sparsely arranged, subapically positioned setae; palpomere I very small, nearly 1/4 as long as II, transverse; II large, longer than III, elongate-clavate; III fairly large, nearly 1/2 as long as IV, equilateral; IV elongate-oval, apically densely papillate. Labium (Figure 4C) with mentum trapezoidal to triangular, apically distinctly narrowed, ventral surface with two larger subcentral setae, apical margin with 2 separate strong emarginations to accommodate ligula and labial palps, centrally with narrow projection; ligula with palpiger projecting beyond mentum, paraglossae elongate-lobulate,

apically with long, densely arranged setae; labial palps 3-segmented; palpomere I fairly small, elongate; II small, globular; III large, elongate-oval, apically papillate. Head in dorsal view conical (Figure 3C), apically gradually narrowed, plane to very slightly convex, width 0.64–0.74 mm; dorsal interocular distance 0.38–0.46 mm, head width/dorsal intraocular distance ratio 1.55–1.73 (N=10); ventral interocular distance 0.30–0.35 mm, head width/ventral interocular distance ratio 2.12–2.30 (N=10); dorsolateral margins bisinuate, occipital stridulatory carinae present, supraocular striae absent (cf. Chaves & Genaro 2005), punctation coarse, with short, dark, obliquely oriented subcuticular suture (apodeme) on each side above antennal insertion, apical margin truncate, posteriorly with transverse line anterior of stridulatory files; in lateral view slightly conical, with separate, angulate regions for eye (posterior) and antennal insertion (anterior), and with obtuse, lobulate to tuberculate, anteriorly directed projection at anteroventral edge; in ventral view slightly concave (Figure 3D), centrally with transverse linear impression, ventrolateral margins emarginate, apically truncate. Antennae 11-segmented,

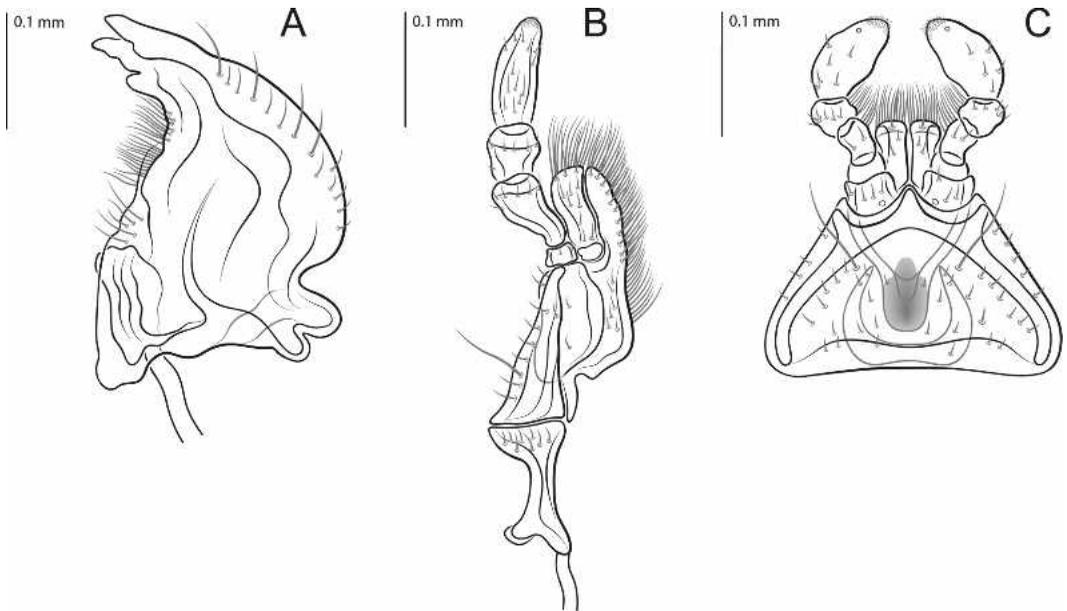


FIG. 4. Mouthparts, ventral view. (A) left mandible; (B) right maxilla; (C) labium.

inserted laterally near anterodorsal margin of eye, length similar to pronotum + 1/2 of head, antennomere I (scape) fairly large, elongate, antennomeres II + III, slightly smaller, equilateral to elongate, antennomeres IV-VIII small, progressing sequentially from equilateral to transverse; club 3-segmented, antennomeres fairly large, light reddish-brown, with dense setation, IX + X similar in length, clavate, XI slightly longer, globular, slightly depressed, with fine, dense pubescence. Eyes globular, protruded, with as many as 11 large black facets spanning from anterior to posterior margin, anterior margin slightly oblique, nearly straight.

Thorax. Pronotum in dorsal view slightly transverse, length/width ratio 0.75-0.80 (N=10), evenly convex, anterolateral edges weakly projected, angulate, not evenly rounded, posteriorly on each side with 1 narrow sulcus positioned at half distance between midline and lateral margin (cf. Leschen & Skelley 2002: 344); posterior margin slightly arcuate, centrally projected; lateral margins straight to slightly arcuate, subparallel, with slightly elevated carina; anterior margin nearly straight; in lateral view with pleural region concave and strongly directed inward underneath lateral margin, subglabrate. Epipleura glabrate; with mesepisternum triangular; mesepimeron narrowly pentagonal; metepisternum large, posteriorly slightly narrowed; metepimeron small, nearly entirely covered by elytra. Prosternum in ventral view nearly evenly convex; lateral margins anteriorly distinctly diverging along suture; anterior margin straight to slightly emarginate, with row of long, anteriorly directed setae; procoxal cavities separated by distance similar to breadth of antennal funicle, laterally closed yet posteriorly open. Mesosternum short, at the same level as metasternum (not inflected); mesocoxal cavities laterally closed. Metasternum long, laterally convex, centrally slightly impressed, with midline suture extending along posterior 3/5, at posterior end between narrowly separated metacoxal cavities with small, rotundate emargination. Metendosternite (Figure 5A) with lateral margins of stalk slightly diverging; lateral arms long and narrow, di-

rected lateroventrally; dorsal furcal arms directed dorsally at a nearly 90° to lateral arms, apically slightly narrowed; anterior tendons removed from median point by nearly 1/3 distance towards furcal arms.

Legs fairly short and slender, similar in length and shape; procoxae small, globular; mesocoxae globular; metacoxa transversely elongate-oval, without distinct posterior face; trochanters apically obliquely truncate; femora fairly stout, laterally compressed, ventrally with slightly concave, glabrate surface to receive tibiae; tibiae shorter than femora, protibia/profemur length ratio 0.78-0.86 (N=10); protibia slightly arcuate, compressed, margins weakly carinate, narrowly triangularly widened towards apex, apical margin obliquely truncate, with row of ca. 15 fairly short and narrow spinules, with 2 spinules at inner (mesal) angle slightly larger, and 1 small tooth at outer (lateral) edge, tooth separated from row of spinules via small gap; tarsi 5-segmented, similar in length to tibiae, tarsomeres I-IV ventrally with long, fine, densely arranged, anteriorly directed setae; tarsomere I large, longer than II, clavate; II and III fairly large, similar in length, clavate; IV small, nearly 1.2 as long as III, globular; V long and narrow, slightly shorter than II + III, apically slightly expanded; tarsal claws paired, simple.

Scutellum visible, transverse, posterior margin rotundate. Elytra in dorsal view elongate-oval, length/width ratio 1.72-1.90 (N=10), greatest width near anterior 1/3; anterior margins nearly straight, with narrow anterior marginal line (cf. Chaves & Genaro 2005), angulate at midline; humeri small (not protruded), convex; lateral margins slightly arcuate, subparallel along anterior 1/2, posteriorly slightly converging, more strongly converging along posterior 1/4; posterior margins subcontiguous; in lateral view slightly and evenly convex; 10 complete striae + 1 short scutellary striole (with 8-10 punctures) extending along anterior 1/4 near midline; striae I-IX narrower than intervals, not grooved, punctures coarse, not impressed, subcircular, centrally with 1 short seta, slightly irregularly spaced, size slightly increasing towards lateral margins; stria X nearly obso-

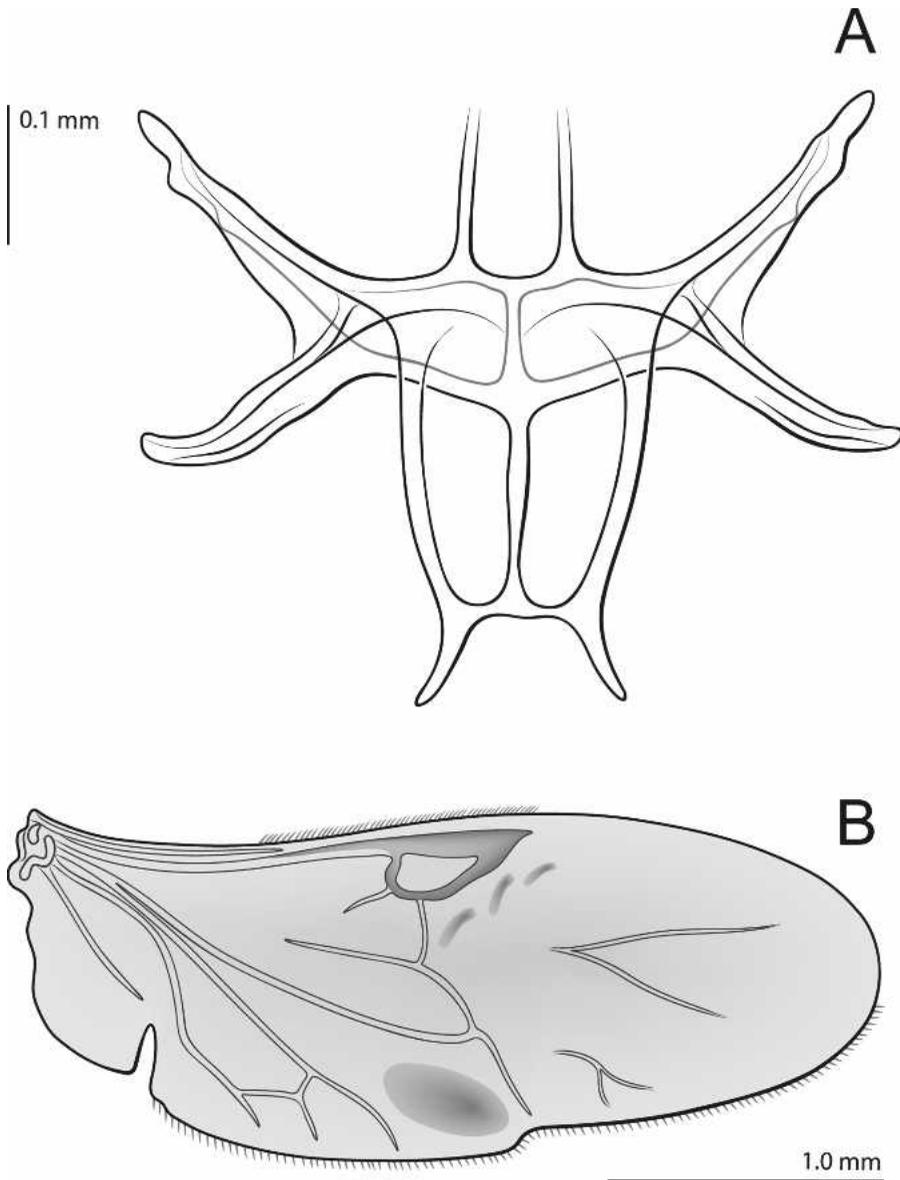


FIG. 5. Thorax. (A) metendosternite, posterior view; (B) right hind wing.

lete along anterior 1/3; elytral intervals plane. Wings (Figure 5B) slightly longer than body, wing/body ratio 1.05-1.13 (N=4), elongate to oval, length/width ratio 2.58-2.80 (N=4), greatest width near central region; anterior margin slightly sinuate, posteriorly slightly arcuate, with separate anal region along basal 1/6 and slight incurvation near apical 2/5; all major veins present (compare with McHugh et al. 1997,

Chaves & Genaro 2005), except for anal cell which is indistinct; radial, medial, and apical fields with maculations; macrosetae densely arranged along apical 1/2 of Sc, more sparsely arranged along posterior margin (absent in anal region); microsetae distributed densely throughout surface.

Abdomen. Venter in ventral view with 5 visible segments; anterior margin medially with distinct acute-triangular projection be-

tween metacoxal cavities, lateral edges slightly projected, lateral and posterior margins arcuate-rotundate, posteriorly converging; ventral segments separated by straight to laterally slightly arcuate line, at the same level (not inflected); ventral segment I longer than II, metasubcoxal lines absent (cf. Leschen & Skelley 2002); II to IV similar in length; V slightly longer than IV, posterior margin with row of short to fairly long, appressed, densely arranged setae. Pygidium in dorsal view transversely rectangular, lateral margins slightly arcuate, posterior margin nearly straight, with several rows of short to long, sparsely arranged, suberect setae; in lateral view slightly longer than ventral segment V, slightly convex, narrow, parallel to orientation of tergum.

Terminalia. Proctiger similar in length to tergum VIII, anterior margin evenly emarginate, anterior edges projected, lateral and posterior margins slightly arcuate, with short, densely arranged setae. Paraprocts posteriorly expanded, triangular, posterior margin straight-truncate, connected via membrane to small, rectangular, anteriorly acutely narrowed sternum IX; spiculum gastrale with two lateral, long and narrow, anteriorly converging and connected apodemes. Tegmen (Figure 6) with anterior region (2/5) ring-like, posterior region (3/5) sheath-like (slightly convex, enclosing median lobe), weakly sclerotized, triangular, centrally with large oval perforation to receive median lobe; lateral margins posteriorly gradually converging; posterior margin slightly arcuate, dorsally with 2 large, elongate, subparallel, apically setose parameres. Aedeagus (Figure 6) with median lobe in dorsal view elongate $l/w = 4.5-4.8$ ($N=3$), lateral margins subparallel to slight sinuate, apically narrowed, rotundate, symmetrical; apical $1/2$ more strongly sclerotized; in lateral view slightly deflexed, basal $3/5$ very narrow (laminar), apical $2/3$ broader, with distinct internal space, dorsal margin narrowed at apex, acute; internal sac membranous, with very long, variously wound flagellum; aedeagal apodemes, distinctly longer than median lobe, narrow and nearly straight; originat-

ing from lateral margins, thereafter adjacent to each other.

Description – female. Similar to male (see description above); with exception of the pygidium which is more strongly convex and very narrow, with the lateral margins posteriorly gradually converging and with 1 long, suberect setae near the posterior edge.

Terminalia (Figure 7A). Paraprocts (tergum IX) with oblique longitudinal separation, lateral regions more strongly sclerotized. Epiprocts (tergum X) and gonocoxites triangular, posteriorly gradually narrowed, apices of gonocoxites laterally with concave impression and various longer, suberect setae; gonostyli large, narrow, posteriorly diverging and very slightly broadened, with several shorter setae and 1 long seta. Vulvar tube membranous, posteriorly expanded. Spermatheca (Figure 7B) fairly narrow, breadth similar throughout; deflected by nearly 180° , C-shaped, basally and apically convex; duct strongly wound.

Variation. Relatively little external morphological variation is apparent in the examined specimens, apart from the differences in size, a slightly lighter and more heterogeneous pigmentation in general specimens, and variation in the shape, depth, and color of the elytral punctures.

Type material. Male holotype “Puerto Rico (USA), Bosque Estatal Susúa, Quebrada Peces, 800 ft., N $18^\circ 04.32'$, W $66^\circ 54.60'$ / ex cones *Zamia portoricensis*, leg. N. Franz, I-15-2007” (UPRM); female allotype, same label information as male holotype (UPRM); paratypes (unsexed), same label information as male holotype (AMNH, 5; FSCA, 10; MEBT, 8; NMNH, 8; UGCA, 5); “Puerto Rico (USA), Bosque Estatal Susúa, Quebrada Peces, 400 ft., N $18^\circ 03.75'$, W $66^\circ 54.43'$ / ex cones *Zamia portoricensis*, leg. N. Franz, I-12-2007” (MUCR, 8; NZAC, 8); “Puerto Rico (USA), Bosque Estatal Cambalache, trails near entrance, 120 ft., N $18^\circ 27.15'$, W $66^\circ 35.84'$ / ex cones *Zamia amblyphyllidia*, leg. N. Franz, II-12-2007” (FSCA, 3; NMFC, 5; UPRM, 5); “PUERTO RICO: Res. For. Cambalache, 20 km. e. Arecibo, 1-iii-'96, ex male cycad cone, coll. B&B Valentine” (BDVC, 2; FSCA, 4; MAIC, 3).

Etymology. The species epithet makes

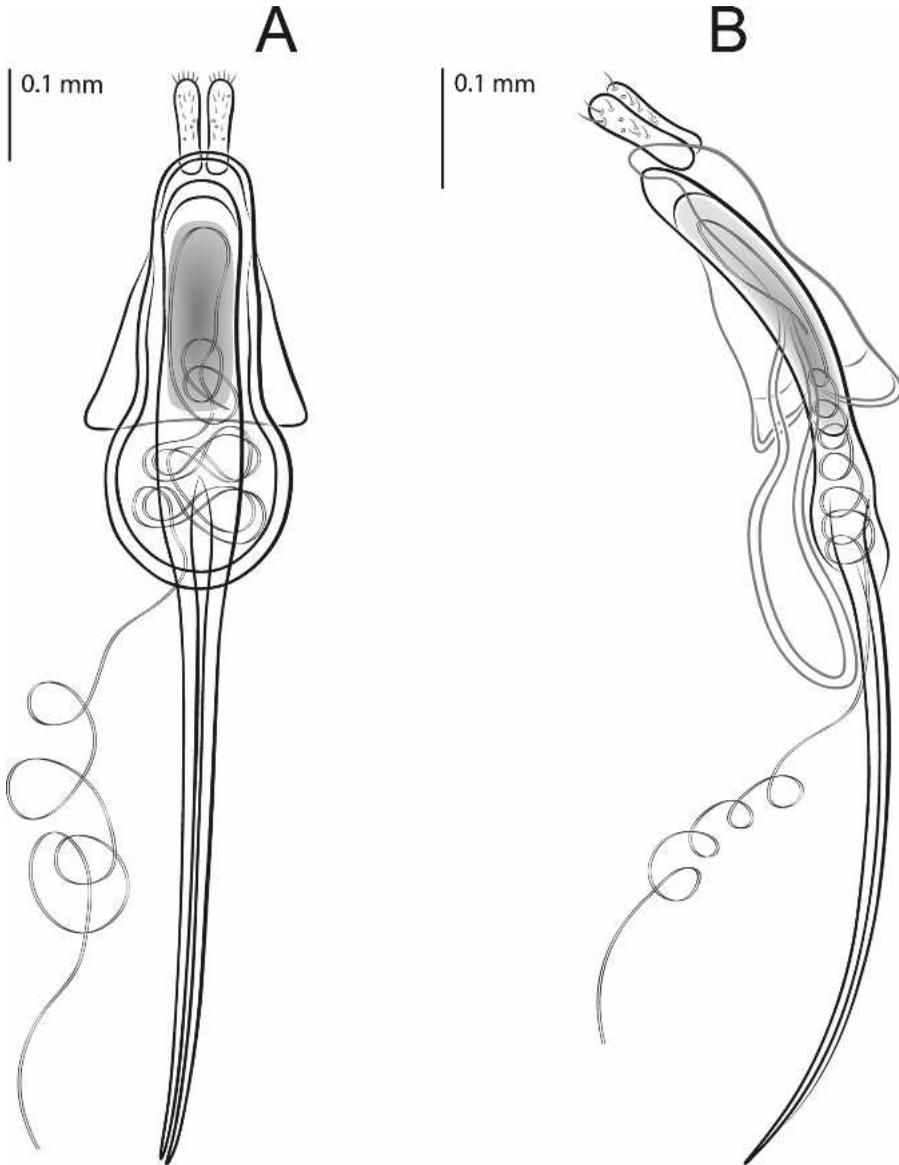


FIG. 6. Male terminalia; tegmen and aedeagus. (A) ventral view; (B) lateral view.

reference to the two putative host plant species *Z. portoricensis* ("porto-") and *Z. amblyphyllidia* ("-phylla") on which the examined specimens of *P. portophylla* were collected.

NATURAL HISTORY

Adults of *Pharaxonotha portophylla* were collected consistently on the microstrobili of *Z. amblyphyllidia* and *Z. portoricensis*,

with the greatest numbers of individuals present at the stage of anthesis (Table 1). Neither adults nor larvae were obtained at the earlier stage of pre-anthesis, suggesting that odor production is critical to this species' attraction to the cones. As many as 30 small to medium-sized larvae (Fig. 8A) were retrieved from a single pollen-releasing microstrobilus of *Z. portoricensis* at a late stage of anthesis. Presumably these immature individuals had emerged from

TABLE 1. Abundance of adults and larvae of *P. portophylla* on micro- and megastrobili of *Z. amblyphyllidia* and *Z. portoricensis* at the Susúa and Cambalache Commonwealth Forest Reserves, respectively, during three stages of development: pre-anthesis, anthesis, and post-anthesis (see also text). Mean values are provided \pm standard deviation, with the corresponding numbers of cones sampled shown in parentheses.

<i>Zamia amblyphyllidia</i> (Cambalache)				
	Microstrobili (δ)		Megastrobili (η)	
	Adults	Larvae	Adults	Larvae
Pre-anthesis	0.0 \pm 0.0 (N = 2)	0.0 \pm 0.0 (N = 2)	—	—
Anthesis	5.5 \pm 0.7 (N = 2)	2.0 \pm 2.8 (N = 2)	0.3 \pm 0.5 (N = 4)	0.0 \pm 0.0 (N = 4)
Post-anthesis	1.0 \pm 1.7 (N = 6)	3.2 \pm 3.3 (N = 6)	—	—
<i>Zamia portoricensis</i> (Susúa)				
	Microstrobili (δ)		Megastrobili (η)	
	Adults	Larvae	Adults	Larvae
Pre-anthesis	0.0 \pm 0.0 (N = 4)	0.0 \pm 0.0 (N = 4)	—	—
Anthesis	5.4 \pm 4.6 (N = 12)	4.0 \pm 8.3 (N = 12)	0.2 \pm 0.4 (N = 6)	0.0 \pm 0.0 (N = 6)
Post-anthesis	0.2 \pm 0.4 (N = 10)	12.2 \pm 15.3 (N = 10)	—	—

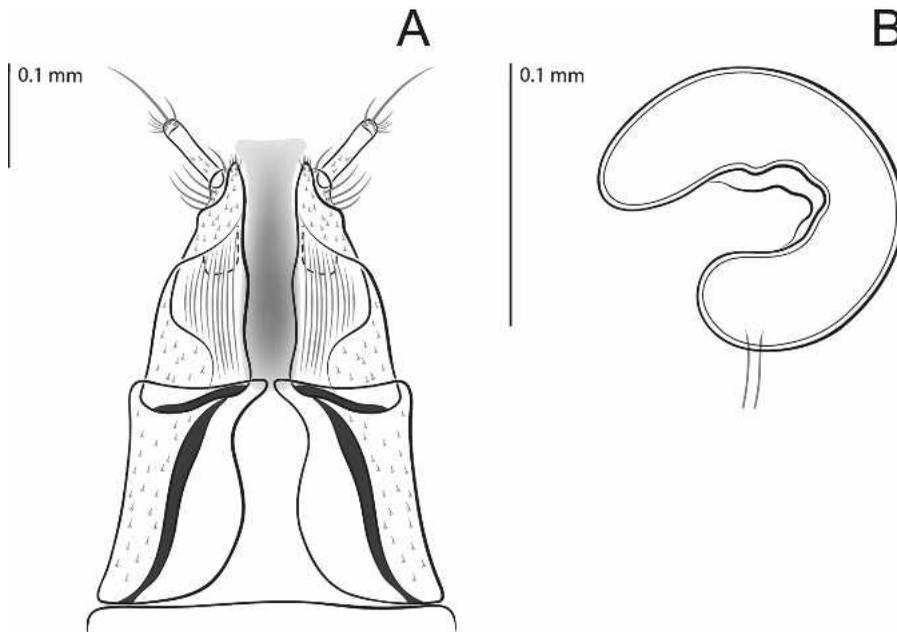


FIG. 7. Female terminalia. (A) oviposition structures (anterior to posterior): paraprocts, epiprocts, gonocoxites, and gonostyli, dorsal view; (B) spermatheca.

eggs laid by early-anthesis visitors, and underwent several molts in a period of 2-3 days. The number of adults sampled on post-anthesis microstrobili was low (range: 0-4 individuals); it remains unknown

whether these individuals had stayed on the cones since arriving at anthesis, or whether they recently emerged from the pupal stage. Conversely, the post-anthesis microstrobili yielded the highest abun-

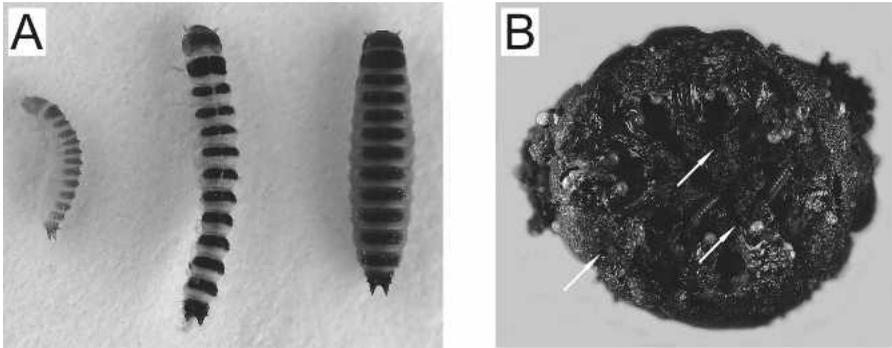


FIG. 8. Development of *P. portophylla* on *Z. portoricensis*. (A) habitus of early, intermediate, and advanced larval stages; (B) cross-section of microstrobilus at approximately three weeks past anthesis, with rotting microsporophylls showing traces of damage (white arrows) produced by feeding *P. portophylla* larvae.

dances of *P. portophylla* larvae, with a maximum of 45 individuals on a single *Z. portoricensis* cone.

Repeated sampling of receptive megastrobili produced only one adult specimen of *P. portophylla* on *Z. amblyphyllidia* cones (N = 4) and on *Z. portoricensis* cones (N = 6), respectively (Table 1). No larvae were observed on the megastrobili. Overall, samples of *Z. amblyphyllidia* cones yielded lower numbers of individuals than *Z. portoricensis* cones.

The reproductive behavior of *Pharaxonotha portophylla* beetles is difficult to observe directly on *Zamia* strobili, due to their relatively low density, low apparent levels of activity at any given time, and cryptic location between the bases of the sporophylls. The adults are rarely seen on the surface, exiting only after the cones are repeatedly perturbed or cut off. Nevertheless, examination and rearing of microstrobili indicates that beetles mate and oviposit frequently, and that the larvae develop while feeding on the parenchyma of the sporophylls (Fig. 8B).

Other insects visitors sampled on *Zamia* cones were predominantly caterpillars of unidentified species of snout moth (Lepidoptera: Pyralidae), with as many as 80 individuals on the post-anthesis microstrobili of *Z. amblyphyllidia* (average 22.6 ± 25.3 individuals on cones where present, N = 10), and up to 30 individuals on *Z. portophylla* (average 5.5 ± 7.5 individuals, N = 15). These lepidopteran species were not ob-

served on the megastrobili. Additional sporadic visitors of rotting *Zamia* microstrobili included myrmecine ants, drosophilid flies, bark beetles, and diplopods. These visitors were not considered to play a significant role in the plants' reproduction.

DISCUSSION

Systematics

Pharaxonotha portophylla is the second species assigned to this ancient lineage in the Caribbean region (see Chaves & Genaro 2005), thereby raising the number of known species in the genus to 13 worldwide (Leschen 2003). The new species furthermore represents a first record for Puerto Rico which has a depauperate erotylid fauna (Wolcott 1948). *Pharaxonotha portophylla* appears most similar to *P. floridana* by virtue of a shared coarse punctation on the head and anterolateral angulation of the pronotum. However, *P. portophylla* is readily distinguished from other congeneric species by a weakly transverse pronotum and shallowly impressed stria punctures; *P. floridana* has a more strongly transverse pronotum and distinctly impressed stria punctures. Both *P. floridana* and *P. portophylla* are restricted to *Zamia* host species in Florida and Puerto Rico, respectively (Tang 1987, Leschen & Skelley 2002). Geographically, *P. portophylla* is closest to the Cuban *P. esperanzae* Chaves & Genaro (2005), yet the latter species is unique among members of this complex in

having supraocular striae, lacking an anterior marginal line on the elytra, and in its association with the endemic Cuban cycad *Microcycas calocoma* (Miquel) A. de Candolle (Chaves & Genaro 2005).

At least ten new species of *Pharaxonotha* from the Caribbean archipelago, Mexico and Central and South America are present in research collections. Their systematic treatment is needed to establish a more complete picture of the relationships among the Neotropical species in the genus.

Natural History

The sampling of insect visitors on cones of *Z. amblyphyllidia* at Cambalache and on *Z. portoricensis* at Susúa strongly suggests that *P. portophylla* is the primary and sole pollinator of these cycad populations. Wind pollination, an early paradigm in cycad reproductive ecology (cf. Stevenson et al. 1998), has since been widely discarded in favor of insect pollination (e.g., Hall et al. 2004, Oberprieler 2004, Tang 2004). It is highly unlikely that anemophily can account for any apparent seed set in the observed *Zamia* plants (Negrón-Ortiz et al. 1996; NMF, personal observation). With regards to insect pollen vectors, *P. portophylla* was the only agent present on open cones of either gender, as well as the only species whose adults were visibly covered with pollen and located inside the microstrobili at the time of anthesis. The temporal and behavioral synchronization of *Pharaxonotha* beetles with their cycad hosts is well documented (e.g., Tang 1987, Norstog et al. 1992, Chaves & Genaro 2005). Other insect visitors of *Zamia* cones at the two sites lacked these attributes and therefore should not be regarded as pollinators.

The similar odors of male and female strobili yet differential rates of visitation and reproduction in the beetles may be indicative of "pollination by deceit" (Terry et al. 2004), where megastrobili contain secondary metabolites that counteract oviposition and larval growth (cf. Schneider et al. 2002). However, the chemical ecology of the *P. portophylla/Zamia* interaction in Puerto Rico remains entirely unexplored. A handful of one-minute probes of the central

axes of *Z. portoricensis* strobili (♂ and ♀) with a NiCr-Ni thermocouple element (Ahlborn) revealed no thermogenetic activity (NMF, personal observation).

Species of *Pharaxonotha* and members of the *Parallocorynus-Rhopalotria* weevil lineage (Marvaldi et al. 2006) have evidently played a critical role in the evolutionary radiation of cycads in the Neotropical region. This contribution reduces one of many significant gaps in our knowledge of a long-standing coevolutionary interaction that should receive more attention from systematists, chemical ecologists, and managers of natural resources.

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