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Two new species of *Pharaxonotha* Reitter among the early-diverging lineages, with a key to the species of the genus (Coleoptera: Erotylidae: Pharaxonothinae)

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Abstract. Two species of the early-diverging lineages of *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae) are described: *Pharaxonotha taylori* Skelley and Tang, **new species**, and *Pharaxonotha thomasi* Skelley and Tang, **new species**. A new key to described species of *Pharaxonotha*, based on previously unused characters, is presented.

Key words. Cycad, *Zamia*, pollination, Central America.

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Introduction

In recent phylogenetic analyses of beetle diversity based on a large nuclear data set (McKenna et al. 2019) and on nuclear and mitochondrial legacy loci (Powell, pers. comm. 2020), the New World genus *Pharaxonotha* Reitter (Erotylidae: Pharaxonothinae) was shown to be sister to all remaining Erotylidae in a clade comprised of the Erotylidae+Phytophaga, which includes Cucujoidea, Chrysomeloidea and Curculionoidea. Since these three superfamilies of Coleoptera contain the majority of beetle pest taxa on human plant crops, a closer examination of this genus may provide some insight into the origin and evolution of these insect groups of agricultural concern. Except for the type species of *Pharaxonotha*, *P. kirschii* Reitter, which is a minor stored products pest, all other species of the genus that have been studied are inhabitants of cycad cones (Pakaluk 1988; Chaves and Genaro 2005; Franz and Skelley 2008; Skelley and Segalla 2019). Exclusion experiments on two of these species indicate that they are pollinators of cycads (Tang 1987; Valencia-Montoya et al. 2017), and it is probable that these ancient plant and beetle lineages have coevolved for many millions of years. Leschen and Buckley (2007) hypothesize that fungivory may be the ancestral state in the Erotylidae, however, adult and early instar larvae of *Pharaxonotha floridana* (Casey) inhabiting cycad cones appear to be pollen feeders, while late instar larvae feed on cone sporophyll and axis tissue (Norstog et al. 1992). Tang et al. (2018b, 2020) presented preliminary relationships of species within *Pharaxonotha*, based on analysis of the 16S rRNA gene, recognizing three distinct radiations: early-diverging lineages, a Caribbean radiation and a recent radiation. *Pharaxonotha* may inhabit cycad cones in the New World with other beetle genera, including *Ceratophila* Tang, Skelley and Perez-Farrera (Erotylidae: Pharaxonothinae) in the cycad host *Ceratozamia* Brongn., and primitive weevils of the subtribe Allocorynina (Belidae) in the host cycads *Dioon* Lindl. and *Zamia* L. (O'Brien and Tang 2015; Tang et al. 2018a, 2018b, 2020).

The purpose of this paper is to describe two species in the early-diverging lineages of *Pharaxonotha* identified in those analyses as D0063 from Panama and D0066 from Honduras, inhabiting the cycad genus *Zamia*. A

revised key to all species of *Pharaxonotha* is presented. Only previously described species of the Caribbean and recent radiations are represented in this review. Others in these and the early-diverging lineages will be described in future papers.

Materials and Methods

Pharaxonotha beetles are available in wild populations of the New World cycad genera, *Ceratozamia*, *Dioon*, *Microcycas* (Miq.) A.DC. and *Zamia* during the rapid elongation and pollen shedding phase of male cones (Tang 1987; Tang et al. 2018a, 2020; Chaves and Genero 2005; Franz and Skelley 2008). Typically, this is a brief window that lasts about one month (Griffith et al. 2012). Therefore, they are rarely collected, and most museum collections have no representatives. The specimens studied are from recent expeditions.

Materials studied. Data reported are for specimens cited herein, deposited in the following institutional collections:

ANIC	Australia, Australian Capital Territory, Canberra City, CSIRO, Australian National Insect Collection
FSCA	USA, Florida, Gainesville, Division of Plant Industry, Florida State Collection of Arthropods
MIUP	Panama, Universidad de Panamá, Museo de Invertebrados “GB Fairchild”
NHMUK	United Kingdom, London, The Natural History Museum
NZAC	New Zealand, Auckland, Landcare Research, New Zealand Arthropod Collection
STRI	Panama, Balboa, Smithsonian Tropical Research Institute
USNM	USA, Washington D.C., National Museum of Natural History

Data. The data reported for each species studied are verbatim. When necessary to alter label data for clarification or to fix errors, the altered data are placed in square brackets, i.e. [authors’ comments, additions or corrections]. The identification labels for type specimens include the generic names and specific epithet, a gender symbol (for holotype and allotype only), and the author(s) and year. The labels are colored—red for the holotype, blue for the allotype, and yellow for all paratypes. Geographic coordinates are omitted when it was deemed necessary to enhance the conservation work being carried out by our collaborators and others to protect the often-endangered host plants of these beetles; deleted coordinates are replaced with the remark “[GPS coord. omitted]”. These data remain on the labels of the specimens but are not included in the publication.

Morphology. Morphological comparisons were made with all known *Pharaxonotha* species and many undescribed species, and with *Pharaxonothinae* genera associated with cycads from around the world as cited throughout this work. Morphological terminology follows Lawrence et al. (2010). Beetles were collected from wild populations and preserved in 75–95% ethanol. Specimen dissection techniques followed that of Hanley and Ashe (2003). Photographs were taken with a Nikon DS-Fi2 camera attached to either a NIKON SMZ-1500 dissecting microscope or NIKON Eclipse 80i compound scope. All pictures are composites produced by taking a series of photographs of each specimen at different levels of focus and integrating them into one picture using the software program Helicon Focus®. Measurements were taken with a calibrated ocular micrometer in a Leica MS5 Stereomicroscope.

Taxonomic hypotheses. Species are the smallest aggregation of populations diagnosable by a unique combination of character states (a phylogenetic species concept as outlined by Wheeler and Platnick 2000). Character states are not limited to morphology or molecular clustering, they also include geographical distributions and host ranges.

Key to species. The key to *Pharaxonotha* species of Pakaluk (1988) requires detailed measurements or genitalic dissections of males. This makes it difficult to obtain confident results, especially when the presently known and mostly undescribed diversity is considered. The key of Santiago-Jiménez et al. (2019), which expanded Pakaluk’s key, is similarly problematic. Use of such characters is not necessary when simple external morphological characters are readily available. The following key takes a new approach to *Pharaxonotha* identification. It strives to use easily visible characters, relying on measurements and genitalia only when all other options fail.

An unfortunate event recently happened when two papers possibly describing the same species were in press in different journals at the same time. Tang et al. (2018a) and Santiago-Jiménez et al. (2019) described taxa

occurring on *Ceratozamia* in Veracruz, Mexico without knowledge of the other. The descriptions of *Pharaxonotha mexicana* Santiago-Jiménez, 2019, and *P. tenuis* Santiago-Jiménez, 2019, are thorough, but do not present needed morphological data to confidently recognize them from other undescribed species known from *Ceratozamia* in that region of Mexico. Also, it appears that one of Santiago-Jiménez's species may belong in *Ceratophila* (Tang et al. 2018a). A study of holotypes is needed to resolve the identity of these species. Thus, their tentative placement in the key below is based only on characters visible in the published habitus photographs of paratypes.

Morphological and molecular data suggest *Pharaxonotha* contains as many undescribed species as are presented in the key below. These are being studied and will be described in the future. This key emphasizes simple external characters to distinguish these species, making the key more user-friendly for researchers without expensive equipment or reference specimens to identify their materials.

Results

Key to species of *Pharaxonotha* Reitter

1. Head in lateral view robust, convex dorsally especially anteriorly; post-ocular ridge present (temple), tooth-like in dorsal view; male with small tooth at apex of last abdominal ventrite; USA (Texas, Louisiana) to Panama in nature, Europe and elsewhere in stored products, rarely associated with cycads ***P. kirschii* Reitter**
- Head in lateral view narrowed anteriorly, flattened dorsally; post-ocular ridge indistinct, usually lacking; male lacking modified last abdominal ventrite; widespread in the Neotropics, associated with cycad cones **2**
- 2(1). Head with supraocular line; elytra lacking marginal bead at base **3**
- Head lacking supraocular line; elytra with marginal bead at base **4**
- 3(2). Head with weak supraocular line; pronotal disc with distinct basal sulcus on each side; Cuba with *Microcycas calocoma* (Miq.) A.DC. ***P. esperanzae* Chaves and Genero**
- Head with strong supraocular line; pronotal disc lacking basal sulcus; Mexico (Veracruz) with *Ceratozamia tenuis* (Dyer) D.W.Stev. and Vovides ***P. mexicana* Santiago-Jiménez et al.**
- 4(2). On *Ceratozamia tenuis* in Mexico (Veracruz) ***P. tenuis* Santiago-Jiménez**
- On *Zamia* from Bolivia (Santa Cruz) to Mexico, USA (Florida) and the Caribbean **5**
- 5(4). All tibiae strongly triangularly dilated toward apex, tibiae appearing shortened; protibia with lateral apical tooth small and no gap in the apical row of spinules; Honduras (Cortés) with *Zamia onan-reyesii* C.Nelson and Sandoval ***P. thomasi* Skelley and Tang, n. sp.**
- Not all tibiae strongly dilated toward apex, usually not appearing shortened; protibia usually with strong lateral apical tooth and a gap in apical row of spinules near tooth; widespread **6**
- 6(5). Anterior pronotal angles projecting forward slightly, angle distinct; USA (Florida) and West Indies to Puerto Rico **7**
- Anterior pronotal angles not projecting forward, angle indistinct, broadly rounded; Mexico to Bolivia **8**
- 7(6). Elytral striae punctures coarse, impressed; striae weakly grooved, intervals convex; USA (Florida) with *Zamia integrifolia* L.f. ***P. floridana* (Casey)**
- Elytral striae punctures fine to coarse, not impressed; striae evident only by rows of punctures, intervals flat; Puerto Rico with *Zamia erosa* O.F.Cook and G.N.Collins and *Z. portoricensis* Urb. ***P. portophylla* Franz and Skelley**
- 8(6). Pronotal hind angle and elytral humerus rounded, lacking angulation or small denticle; body small, length < 2.1 mm; Panama (Panamá) with *Zamia cunaria* Dressler and D.W.Stev. and *Z. ipetiensis* D.W.Stev. ***P. taylori* Skelley and Tang, n. sp.**

- Pronotal hind angle and elytral humerus with angulation or small denticle; body larger, length > 2.1 mm; Bolivia to Central America **9**
- 9(8). Antennomere XI distinctly larger than IX; Bolivia (Santa Cruz) and Brazil (Mato Grosso) with *Zamia boliviana* (Brongn.) A.DC. ***P. cerradensis* Skelley and Segalla**
- Antennomere XI equal to or smaller than IX; Costa Rica **10**
- 10(9). Body length 2.1–2.4 mm; scutellary striole with 7–9 punctures; elytral disc with fine interval punctures less than ¼ diameter of stria punctures; northeastern Costa Rica (Heredia) east of Continental Divide with *Zamia neurophyllidia* D.W.Stev. ***P. clarkorum* Pakaluk**
- Body length 2.8–3.6 mm; scutellary striole with 9–11 punctures; elytral disc with coarser interval punctures more than ½ diameter of stria punctures; southern Costa Rica (Puntarenas) west of Continental Divide with *Zamia fairchildiana* L.D.Gómez and *Z. pseudomonticola* L.D.Gómez ex D.W.Stev. and Sabato ***P. confusa* Pakaluk**

***Pharaxonotha taylori* Skelley and Tang, new species**

Figure 1A–J

Diagnosis. *Pharaxonotha taylori* is the smallest known member of the genus, length 1.67–2.08 mm. Other distinguishing characters include the pale brown body coloration; pronotum with basal lateral sulcus of disc indistinct to absent; pronotal hind angles and humerus of elytra rounded, lacking small denticle; narrowed protibia with straight apical margin bearing complete row of short stout spinules; male terminalia not distinctly dorsoventrally flattened; and known distribution in Panama on *Zamia cunaria* and *Z. ipetiensis*.

Description. Type series length 1.67–1.91 mm, width 0.60–0.72 mm. Body (Fig. 1A–C) in dorsal view elongate, somewhat cylindrical, greatest width at middle of elytra; in lateral view weakly convex dorsally. General body color entirely pale yellow-brown; dorsal surface punctate, weakly alutaceous, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesoventrite and abdomen with short sparse procumbent setae.

Head. Not broad (Fig. 1D–E), width = 0.75–0.80× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 3–4× width of puncture; head width 0.40–0.49 mm; dorsal interocular distance 0.26–0.27 mm, head width/dorsal interocular distance ratio 1.55–1.91, ventral interocular distance 0.14–0.19 mm, head width/ventral interocular distance ratio 2.63–2.86. Eye with large black facets, about 2× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.2× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly larger than III; IV circular; IV–VIII small, equal in length, VII–VIII becoming slightly wider with flattened apex; club fairly large, IX and X similar in length; XI not enlarged, slightly longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] distinct from eye to eye. Mentum and submentum coarsely punctured, distance between nearest punctures approximately 2–3× own diameter, each puncture with a short seta; submentum with weak medial depression visible on some. Gular area smooth, without punctation or setae, border with submentum marked by change in punctuation and with a shallow transverse depression.

Thorax. With pronotum transversely quadrate in dorsal view, length/width ratio 0.73–0.77; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; surface mostly convex, slightly flattened medially; anterior angles broadly rounded, not projecting forward; posterior angles rounded, lacking small denticle at angle; lateral margin evenly shallowly arcuate medially, more strongly anteriorly and posteriorly; posterior margin slightly projecting medially, projection beginning approximately by pair of small, dark pores in margin located ¼ width from posterior angles, each pore marks base place where an indistinct sulcus may extend anteriorly onto disc at most ½ length of pronotum, sulcus usually lacking. Prosternum in ventral view convex, with few scattered punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately ⅓ length of eye; prosternal process convex apically, expanded and truncate at apex. Hypomer on laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse, posterior margin weakly roundly pentagonal. Elytra in dorsal view elongate, convex; length/width 1.66–1.78, greatest width near midlength; with distinct marginal line basally; 10

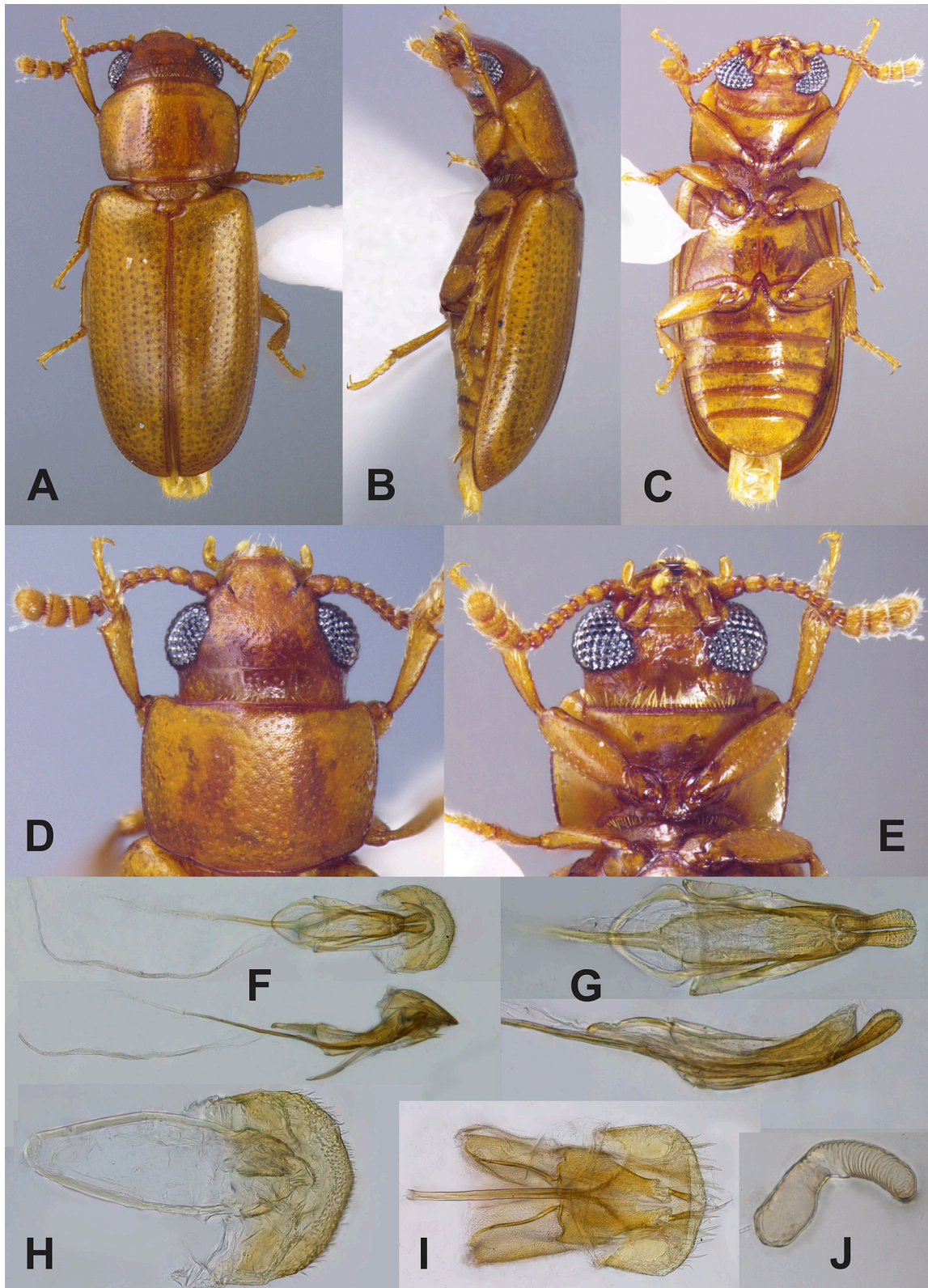


Figure 1. *Pharaxonotha taylori*, paratype. **A)** Dorsal habitus. **B)** Lateral habitus. **C)** Ventral habitus. **D)** Dorsal head and pronotum. **E)** Ventral head and pronotum. **F)** Male terminalia, dorsal and lateral. **G)** Penis and tegmen, dorsal and lateral. **H)** Male abdominal segments VIII–IX. **I)** Female genitalia. **J)** Spermatheca.

complete striae of moderate puncture size; scutellary striole extending $\frac{1}{4}$ elytral length, with 10–15 punctures; punctures of elytral striae slightly larger than pronotal punctures, striae not impressed; intervals of striae with fine, shallow punctures, $\frac{1}{2}$ size of striae punctures; all punctures of elytral bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with fine indistinct punctuation. Metaventricle glossy, with weak lateral punctuation separated by 4–5× own diameter; medial surface indistinctly punctured; entire surface convex, metathoracic discrimen extending approximately $\frac{3}{4}$ metaventricle length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora weakly robust, moderately compressed laterally; tibiae shorter than femora, weakly widening to truncate apices; protibia with apical lateral tooth weak, with complete apical fringe of short spinules on straight ventral apical margin; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

Abdomen. Ventricle apical margin bearing short, sparse setae; all ventrites finely, sparsely punctate across surface, distance to nearest puncture approximately 4–5× diameter of puncture, punctures bearing mostly reclining setae; ventrite V with setae length nearly uniformly approximately 2× diameter of puncture; I–IV each with 2 or more median pairs of longer, semi-erect sensory hairs (difficult to see in poor lighting, often abraded). Male genitalia ($n = 6$) not distinctly dorsoventrally flattened, tegmen parallel-sided in dorsal view, parameres in dorsal view with asymmetrical apices; elongate cylindrical median lobe, and long coiled flagellum (Fig. 1F–H).

Female. Similar to male, no sexual dimorphism observed. Genital tube elongate, length past abdominal segment VIII = 4× width ($n = 6$); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width (Fig. 1I). Spermatheca C-shaped, length > 4× width, base slightly swollen and smooth, apex annulated (Fig. 1J).

Range. Known from eastern Panama in male cones of *Zamia cunaria* and *Z. ipetiensis*.

Material examined. Holotype (by designation) male of *Pharaxonotha taylori* with the following labels: 1) [rectangular; white; printed in black ink] “PANAMA: Panamá Province, Llano Carti, 300–400 m asl, Nov-18-2000 or Sept-8,23-2004, A. Taylor, Vial #15, *Zamia cunaria*, wet, lowland tropical forest”. 2) [rectangular; red; printed in black ink] “HOLOTYPE ♂ *Pharaxonotha taylori* Skelley & Tang 2020”. Deposited in the FSCA.

Allotype female and adult paratypes ($n = 61$): same data as holotype (allotype, 6 FSCA; 4 MIUP; 4 NHMUK); **PANAMA: Panamá Province**, Llano Carti, 300 m asl, Sept-2-2003, A. Taylor, #25, *Zamia ipetiensis* in population, of *Z. cunaria*, wet, lowland tropical forest” (4 ANIC; 3 FSCA; 4 USNM); same locality, 300–400 m asl, Sept-2-2003, A. Taylor, #5, *Zamia ipetiensis* in population, of *Z. cunaria*, wet, lowland tropical forest (1 FSCA; 4 NZAC; 4 STRI); same locality, ♂ bait cone *Zamia ipetiensis* (*Z. cunaria* habitat), 26-VIII-2011, A. Taylor (21 FSCA); same province, Ipeti-Emberá, 200 m asl, Nov-18-2000 or August 12-2001, A. Taylor, Vial #21, *Zamia ipetiensis*, wet, lowland tropical forest” (6 FSCA). In Tang et al. (2020), these are presented on their tree as “D0063 *Z. cunaria* > PANAMA”

Additional specimens studied but not included in type series: **COLOMBIA: Chaco**, near Quibdó, III-2009, M. Colonje, *Zamia pyrophylla* ♂ cones (4 FSCA). In Tang et al. (2020), this population is presented on their tree as “D0021 *Z. pyrophylla* > COLOMBIA”.

Etymology. Named to honor Dr. Alberto S. Taylor Blake for his many years of work on *Zamia* diversity, taxonomy, conservation and pollination biology in Panama, for providing many of the specimens studied here and having recently celebrated his 88th birthday.

Remarks. The two recognized hosts of *P. taylori*, *Zamia cunaria* and *Z. ipetiensis*, occur within the same province of Panamá. Morphologically, these *Zamia* are separated by small differences in leaflet and cone characters (Steven-son 1993) and a phylogenetic analysis of the genus *Zamia*, based on 10 genes and encompassing the majority of recognized species in the genus (Calonje et al. 2019), indicate these two host species are closely related, although not identical. A preliminary cross-pollination experiment (Taylor and Calonje 2015) using hand-pollination techniques suggests that some genetic reproductive barriers may exist between the two host species, however, the fact that *Pharaxonotha* beetles in *Z. cunaria* habitat are readily attracted to *Z. ipetiensis* bait cones (Terry et al. 2012), reveals no reproductive barriers by the hosts to the beetles that inhabit their cones. Based on the information available we treat the beetles from these two host *Zamia* as a single species. Beetles collected on cones of *Z. pyrophylla*, a host that is restricted to Colombia, are morphologically similar, but tend toward a larger size range (body length = 1.98–2.07 mm, $n = 4$; vs. 1.67–2.08 mm) and exhibit some genetic difference with those from the *Z. cunaria* habitat (Tang et al. 2018b, 2020). Although morphological and genetic analyses indicate that *Z.*

pyrophylla belongs within the same host species group as *Z. cunaria* and *Z. ipetiensis* (Calonje et al. 2010, 2019), its habitat is separated by some 400 km from the latter two species. Here, we treat these Colombian beetles as a potentially separate species from *P. taylori* and exclude them from the type series.

***Pharaxonotha thomasi* Skelley and Tang, new species**

Figure 2A–I

Diagnosis. *Pharaxonotha thomasi* is one of the most recognizable species of the genus. It is the only species where all tibiae are strongly triangularly dilated apically; protibia with a complete row of short stout spinules on a straight ventral apical margin; body distinctly flattened; and with a known distribution in Honduras on *Zamia onan-reyesii*.

Description. Length 2.44–2.96 mm, width 0.96–1.19 mm. Body (Fig. 2A–C) in dorsal view elongate, distinctly flattened, greatest width at middle of elytra; in lateral view flattened dorsally. General body color entirely red-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctuation on pronotum and elytra, ventrally shining and appearing glabrous except mesoventrite and abdomen mostly covered with short procumbent setae.

Head. Not broad, width = $0.68\text{--}0.74\times$ pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures $2\text{--}3\times$ width of puncture; head width 0.56–0.65 mm; dorsal interocular distance 0.33–0.37 mm, head width/dorsal interocular distance ratio 1.63–1.80, ventral interocular distance 0.21–0.26 mm, head width/ventral interocular distance ratio 2.55–2.89. Eye with large black facets, about $2\times$ diameter of head punctures. Antennal length slightly shorter than pronotal width, $1.2\times$ head width; antennomere I (scape) fairly large, slightly elongate; antennomere II equal in size to III; IV small, circular; V–VII same length as IV, gradually becoming wider with VIII distinctly transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, $1.4\times$ longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] distinct from eye to eye. Mentum and submentum somewhat coarsely punctured, $2\text{--}3\times$ diameter of facet, distance between nearest punctures approximately $1\times$ own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation.

Thorax. With pronotum transversely rectangular in dorsal view, length/width ratio 0.67–0.73; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral margin parallel-sided in medial half, shallowly arcuate inward anteriorly and posteriorly; posterior margin slightly projecting medially, projection beginning approximately by pair of small, dark pores in margin located $\frac{1}{4}$ width from posterior angles, each pore marks base of a distinct sulcus extending anteriorly onto disc $\frac{1}{4}$ length of pronotum. Prosternum in ventral view convex, with few scattered punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately $\frac{1}{3}$ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomer on laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse, posterior margin weakly roundly pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.44–1.62, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending $\frac{1}{4}$ elytral length, with 10–15 punctures; punctures of elytral striae $1.5\times$ larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, shallow punctures, $\frac{1}{4}$ size of striae punctures; all punctures of elytral bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctuation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventr ite glossy, with strong lateral punctuation separated by $1\text{--}2\times$ own diameter; medial surface finely distinctly punctured, separated by $3\text{--}4\times$ own diameter; surface medially flattened, metathoracic discrimen extending approximately $\frac{3}{4}$ metaventr ite length. Legs broadened, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, compressed laterally; tibiae shorter than femora, triangularly dilated

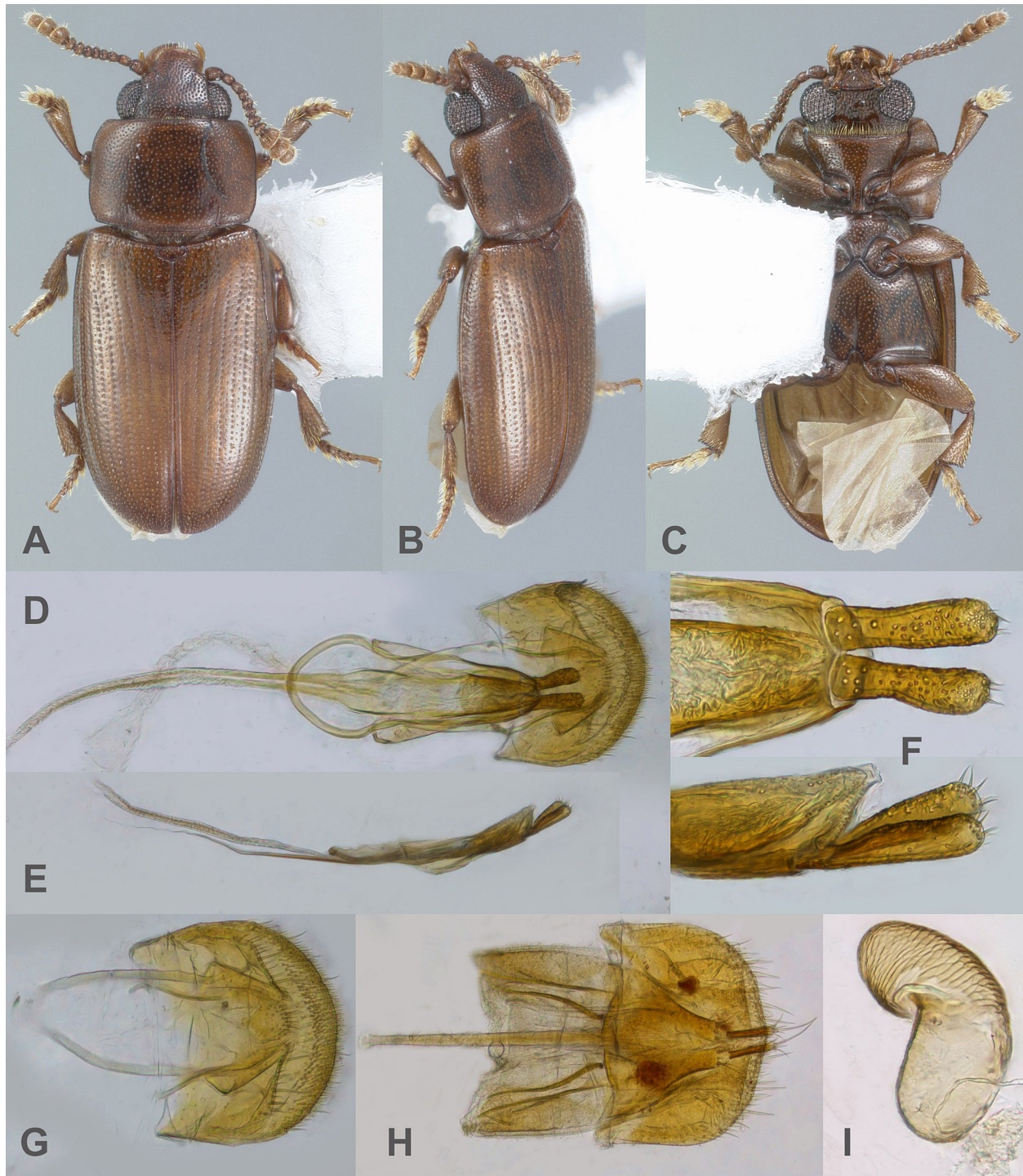


Figure 2. *Pharaxonotha thomasi*, paratype. **A)** Dorsal habitus. **B)** Lateral habitus. **C)** Ventral habitus. **D).** Male terminalia, dorsal. **E)** Male terminalia, lateral. **F)** Apex of penis and tegmen, dorsal and lateral. **G)** Male abdominal segments VIII–IX. **H)** Female genitalia. **I)** Spermatheca.

to obliquely truncate apices, obliquely truncate apical margin width $\frac{1}{3}$ tibial length; protibia with apical lateral tooth small, with complete apical fringe of very short stout spinules on straight ventral apical margin; meso- and metatibia with apical fringe of short stout spinules on anterior margin, finer setae on posterior margins.

Abdomen. Ventrite apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation evenly distributed across surface, distance to nearest puncture approximately $2\times$ diameter of puncture, punctures bearing mostly reclining setae; ventrite V with setae length nearly uniformly approximately $2\times$ diameter of puncture; I–IV each with 2 or more median pairs of longer, semi-erect sensory hairs (difficult to see in poor lighting, often abraded). Male genitalia ($n = 2$) similar to all others in the genus, with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum (Fig. 2D–G).

Female. Similar to male, sexual dimorphism weakly evident with male protarsomere I more broadly dilated. Genital tube shortened, length past abdominal segment VIII = $1.5\times$ width ($n = 2$); gonostylus set apically on gonocoxite, gonostylus length = $4\text{--}5\times$ width (Fig. 2H). Spermatheca shaped like a pill capsule, length approximately $3\times$ width, basal half smooth, apical half with reticulation, folding at center (Fig. 2I).

Range. Known from Honduras, the type locality, on male cones of *Zamia onan-reyesii*.

Material examined. Holotype (by designation) male of *Pharaxonotha thomasi* with the following labels: 1) [rectangular; white; printed in black ink] “HONDURAS: San Pedro Sula, Filo del Cerrito, Laguna Tembladeros, 30-VII-2003, [GPS coord. omitted], col. Jody Haynes, on male cone of *Zamia* sp.” 2) [rectangular; red; printed in black ink] “HOLOTYPE ♂ *Pharaxonotha thomasi* Skelley & Tang 2020”. Deposited in the FSCA.

Female allotype and adult paratypes ($n = 41$): same data as holotype (4 ANIC; allotype, 25 FSCA; 4 NHMUK; 4 NZAC; 4 USNM). In Tang et al. (2020), this species is presented on their tree as “D0066 *Z. onan-reyesii* > HONDURAS”.

Etymology. In the early 1990s, Andrew Vovides sent specimens from a *Ceratozamia* cone to Michael C. Thomas for identification, who recognized them as multiple undescribed taxa. While Mike was an expert on cucujoid beetles, he had not published on this group of beetles. James Pakaluk, who had recently described species in the group (Pakaluk 1988), agreed to describe them. However, Pakaluk left entomological work in the late 1990s and the task of describing the new taxa fell back to Thomas. In the early 2000s, Węgrzynowicz (2002) and Leschen (2003) independently merged several higher taxa into the family Erotylidae, including *Pharaxonotha*. At that time, author PES agreed to help Mike Thomas with the descriptions. With this new enthusiasm additional materials began arriving from cycad researchers, most representing obviously undescribed taxa or presenting taxonomic problems that needed more detailed study before being described. Mike eventually turned the entire project over to PES, who was quickly overwhelmed with the diversity and complexity, but was able to help others describe individual species (Chaves and Genaro 2005; Franz and Skelley 2008). Around 2010, Willie Tang, Guang Xu, and others began work on relationships of cycad pollinating beetles using molecular methods. A team formed and progress on “*Pharaxonotha*” finally started (Skelley 2013; Xu et al. 2015; Skelley et al. 2017; Tang et al. 2018a, 2018b, 2020; Skelley and Segalla 2019).

After his initial 1990s work, Mike Thomas encouraged and helped others working on this complex genus, until he died in October 2019. It is an honor that we recognize Mike’s enthusiasm and encouragement of others to study beetles by naming this species after him. If not for his initial push, a lot of this work would not have happened.

Remarks. The host for *P. thomasi* is *Zamia onan-reyesii* (Nelson and Sandoval 2008, Schutzman et al. 2008), an arborescent species of the Mesoamerica clade of *Zamia* as identified via genetic analysis by Calonje et al. (2019).

Discussion

While genetic analysis indicates *P. taylori* and *P. thomasi* are among the early-diverging lineages of *Pharaxonotha* (Tang et al. 2018b, 2020), genetic analysis indicates the hosts are part of recent radiations of the *Zamia* clade (Calonje et al. 2019). This suggests that *Pharaxonotha* and *Zamia* do not exhibit close parallel evolution and that radiations in *Pharaxonotha* have been to some extent independent from the evolution of the host cycads. Alternatively, there may have been a number of host-shifts in *Pharaxonotha* from possibly older, extinct lineages of cycads onto more recently evolved species or onto other genera of cycads (Tang et al. 2018b, 2020). Unlike other species of *Pharaxonotha* in Florida, Mesoamerica and Central America which co-inhabit cones with

Allocorynina weevils (Tang 1987; Norstog et al. 1992; O'Brien and Tang 2015; Tang et al. 2018a, 2018b, 2020) in other species of cycads in the genera *Ceratozamia*, *Dioon* and *Zamia*, *P. taylori* and *P. thomasi* appear to be the sole cone inhabitants and pollinator of their hosts.

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