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# Review of *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting cones of the cycad *Zamia* L. (Cycadales) in Panama, with descriptions of five new species

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# Review of *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting cones of the cycad *Zamia* L. (Cycadales) in Panama, with descriptions of five new species

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**Abstract.** The beetle genus *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae) is found in the cones of cycad genera in the New World, including species of *Ceratozamia* Brongn., *Dioon* Lindl., *Microcycas* (Miq.) A.DC and *Zamia* L. Its presence and diversity are analyzed for the 17 species of *Zamia* known to occur in Panama. Nine species are recognized, and five new species are described: *Pharaxonotha clarkorum* Pakaluk, *P. confusa* Pakaluk, *P. fortunensis* Tang, Skelley and Taylor **new species**, *P. holzmani* Tang, Skelley and Taylor **new species**, *P. kirschii* Reitter, *P. manicatae* Tang, Skelley and Taylor **new species**, *P. panamensis* Tang, Skelley and Taylor **new species**, *P. pseudoparasitica* Tang, Skelley and Taylor **new species**, and *P. taylori* Skelley and Tang. A key to species of *Pharaxonotha* in Panama is presented.

**Key words.** Gymnosperm, beetle, co-evolution, pollination, Central America.

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## Introduction

The New World beetle genus *Pharaxonotha* Reitter (Erotylidae: Pharaxonothinae) is closely associated with cycads (Cycadales), an ancient lineage of gymnosperms (Norstog and Nichols 1997). Except for the type species, *P. kirschii* Reitter, an inhabitant of leaf litter that feeds on a diverse assemblage of food plants, all other species of *Pharaxonotha* that have been described are inhabitants of cycad cones (Pakaluk 1988; Chaves and Genaro 2005; Franz and Skelley 2008; Xu et al. 2015; Skelley et al. 2017, 2022; Skelley and Segalla 2019; Skelley and Tang 2020; Tang and Gomez Dominguez 2022), where adults and early instar larvae appear to feed on pollen, while late instar larvae feed on parenchyma tissue in the cone sporophyll and axis (Norstog et al. 1992). Exclusion

experiments on the cycad genus *Zamia* L. indicate that they are pollinators (Tang 1987; Valencia-Montoya et al. 2017; Segalla et al. 2021). In recent phylogenetic analyses of beetle diversity based on a large nuclear data set (McKenna et al. 2019) and on nuclear and mitochondrial loci (Powell 2021), this genus was shown to be an early diverging lineage that is sister to all remaining Erotylidae as well as to a clade that includes all other Cucujoidea, Chrysomeloidea and Curculionoidea.

The country of Panama, for its small size, possesses an unusually high diversity of cycads, with 17 described species of *Zamia* (Stevenson 1993; Taylor et al. 2008, Taylor and Holzman 2012). Tentative behavioral and molecular analyses of the beetles that inhabit the cones of Panamanian cycads have been published (Terry et al. 2012; Tang et al. 2018b, 2020) with two described species of *Pharaxonotha* attributed with certainty to the country (Skelley and Tang 2020; Skelley et al. 2022). Based on an analysis of the 16S rRNA gene, three distinct radiations are recognized for *Pharaxonotha*: early-diverging lineages, Caribbean radiations, and recent radiations (Tang et al. 2018, 2020). Three early diverging lineages as well as two recent radiations of *Pharaxonotha* appear to inhabit cycad cones in Panama.

In this paper we identify the diversity of *Pharaxonotha* inhabiting *Zamia* cones in Panama, determine which may be shared with neighboring countries in Central and South America, which are likely unique to the country, and describe five new species. In some Panamanian *Zamia*, *Pharaxonotha* may occur with weevils of the genus *Notorhopalotria* (Curculionoidea, Belidae: Allocorynina) (O'Brien and Tang 2015). These are also likely to be pollinators (Norstog and Fawcett 1986; Tang 1987), and their co-occurrence with *Pharaxonotha* in Panamanian *Zamia* species is indicated.

# Materials and Methods

*Pharaxonotha* beetles are available in wild populations of the New World cycad genera, *Ceratozamia* Brongn., *Dioon* Lindl., *Microcycas* (Miq.) A.DC. and *Zamia* L. during the rapid elongation and pollen shedding phase of male cones (Tang 1987; Tang et al. 2018a, 2020; Tang and Gomez Dominguez 2022; Chaves and Genero 2005; Franz and Skelley 2008; Skelley and Segalla 2019; Skelley et al. 2022). 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 here 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 |
| **IEXA** | Mexico, Veracruz, Xalapa, Instituto de Ecología |
| **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 |
| **RHTC** | USA, Alabama, Enterprise, Robert H. Turnbow collection |
| **SEMC** | USA, Kansas, University of Kansas, Snow Entomological Museum |
| **STRI** | Panama, Balboa, Smithsonian Tropical Research Institute |
| **TAMU** | USA, Texas, College Station, Texas A&M University |
| **USNM** | USA, Washington D.C., National Museum of Natural History |

**Data.** The holotype 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 and nearby location names have been omitted for some accessions to enhance the conservation work being carried out by our collaborators and others to protect the endangered host plants of these beetles; deleted coordinates are replaced with the remark "[GPS coord. omitted]" and locality names are replaced with the remark "[locality name omitted]" or "[island name 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 and measurements were taken with a calibrated 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®.

Abbreviations used throughout the keys and text include:

**DI** Dorsal interocular distance
**EL** Elytra length
**EW** Elytra width
**EL/EW** Ratio of elytra length to width
**HW** Head width
**HW/DI** Ratio of head width to dorsal interocular distance
**HW/VI** Ratio of head width to ventral interocular distance
**PL** Pronotum length
**PW** Pronotum width
**PL/PW** Ratio of pronotum length to width
**VI** Ventral interocular distance

**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.

Morphological and molecular data suggest *Pharaxonotha* contains many more undescribed species than are presented in the key below. A regional fauna of *Pharaxonotha* has been published for those species inhabiting *Dioon* (Skelley et al. 2022) and others are currently in progress for *Ceratozamia* and *Zamia* and will be published elsewhere. The treatments of *P. taylori* Skelley and Tang and *P. kirschii* Reitter are modified from Skelley and Tang (2020) and Skelley et al. (2022) to present details of relevance to Panama.

## Results

Taxonomic groups of *Pharaxonotha* presented below for Panama are here recognized based on morphology and supported with geographic distributions, host ranges, analyses of the 16S rRNA gene from almost all Panamanian *Zamia* species (Tang et al. 2018b, 2020) and by analysis of 368 nuclear genes from a subset of these populations (Salzman et al., unpub. data). Figure 2 displays the geographic distribution of where these species have been found in Panama.

### *Pharaxonotha* Reitter of Panama and *Zamia* L. hosts

**clarkorum** species group
- *P. clarkorum* Pakaluk
  - *Z. hamannii* A.S.Taylor, J.L.Haynes and Holzman
  - *Z. nesophila* A.S.Taylor, J.L.Haynes and Holzman
  - *Z. neurophyllidia* D.W.Stev.
- *P. fortunensis* Tang, Skelley and Taylor, **new species**
  - *Z. lindleyi* Warsz.
- *P. holzmani* Tang, Skelley and Taylor, **new species**
  - *Z. imperialis* A.S.Taylor, J.L.Haynes and Holzman
  - *Z. skinneri* Warsz.
- *P. pseudoparasitica* Tang, Skelley and Taylor, **new species**
  - *Z. pseudoparasitica* J. Yates

**confusa** species group
*P. confusa* Pakaluk
*Z. fairchildiana* L.D.Gómez
*Z. pseudomonticola* L.D.Gómez ex D.W. Stev. and Sabato
*P. panamensis* Tang, Skelley and Taylor, **new species**
*Z. dressleri* D.W.Stev.
*Z. elegantissima* D.W.Stev.
*Z. nana* A.Lindstr., Calonje, D.W.Stev. and A.S.Taylor
*Z. obliqua* A. Braun
*Z. stevensonii* A.S.Taylor and Holzman
**manicatae** species group
*P. manicatae* Tang, Skelley and Taylor, **new species**
*Z. manicata* Linden x Regal
**taylori** species group
*P. taylori* Skelley and Tang
*Z. cunaria* Dressler and D.W.Stev.
*Z. ipetiensis* D.W.Stev.
**kirschii** species group
*P. kirschii* Reitter

## *Pharaxonotha* Reitter

**Type species.** *Pharaxonotha kirschii* Reitter, by monotypy.

**Diagnosis.** *Pharaxonotha* can be distinguished from other members of the Pharaxonothinae by the following combination of characters: antennal club of 3 antennomeres; eyes large, encroaching upon gular area; submental-gular suture apparently lacking; transverse occipital line distinct; stridulatory files at base of head separated by distance ≈ width of scutellar shield; anterior pronotal margin lacking marginal line; lateral pronotal carina narrow, same thickness along entire length; elytra with basal bead; internal abdominal calli absent; male genitalia with median lobe cylindrical and tegmen laterally flattened, but not twisted; known distribution includes the Caribbean Basin from the U.S.A. (Florida, Louisiana and Texas), Bahamas, Greater Antillean islands of Cayman Islands, Cuba, Jamaica, Hispaniola and Puerto Rico; Mexico, Central America into South America as far south as Bolivia.

**Description.** Length 1.59–5.09 mm, width 0.60–1.89 mm. Body in dorsal view elongate, somewhat cylindrical, greatest width at middle of elytra; in lateral view weakly convex dorsally. Body color usually entirely pale yellow-brown to medium brown, but in a few species elytra black to dark brown or elytra and ventral tergites with black to dark brown maculation; dorsal and ventral surfaces punctate, weakly alutaceous to smooth, shining, procumbent setae usually associated with punctation, setal length ranging from short, not reaching distance to nearest puncture, to long and extending beyond nearest puncture.

**Head.** Not broad, width = 0.65–0.80× 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 0.40–1.07 mm; dorsal interocular distance 0.26–0.68 mm, head width/dorsal interocular distance ratio 1.55–1.91, ventral interocular distance 0.14–0.58 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 punctation 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, usually with small denticle at angle; lateral margin evenly shallowly arcuate medially, more strongly arched 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 ⅛ 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. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate, convex; length/width 1.66–1.78, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ 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, ½ size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with fine indistinct punctation. Metaventrite glossy, with weak lateral punctation separated by 4–5× own diameter; medial surface indistinctly punctured; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite 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.** Ventrite apical margin bearing short, sparse setae; internal abdominal calli absent; 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 = 104) dorsoventrally flattened, in repose oriented upside down inside abdomen with tegmen positioned ventrad of the median lobe [while it is common in the Cucujoidea for the male genitalia to be rotated 90 degrees while retracted into the abdomen (McHugh et al. 1997), 180 degrees is unusual]; tegmen not flattened, basal piece broadened and ring-like to hold coiled flagellum, parameres in dorso-ventral view with sides parallel or bulging on outer side, apices symmetrical or asymmetrical; median lobe elongate, cylindrical; flagellum long, hair-like and coiled. Female genitalia (n = 131) gonostylus cylindrical with width equal throughout its length or widest at apex, tapering slightly and gradually to base, in both cases set apically on oblique apex of gonocoxite, or gonostylus ovate and short, length < 3× width and inserted laterally below a truncated gonocoxite apex. Spermatheca (see Fig. 1 for definition of structures and orientations) either slightly arcuate, hook-shaped or C-shaped, with spermathecal duct and glandular ducts inserted on dorsal side of basal third, in pits or on swellings; apical third and basal third symmetrical or with asymmetric swellings dorsally; apical third or basal third either longer, shorter than each other, or of equal length, with annulations, longitudinal or oblique wrinkles or smooth; these structures highly diagnostic for distinguishing species and species groups.

## Key to species of *Pharaxonotha* in Panama

Because of variable and overlapping morphological character states with some species, it is desirable, and in some cases necessary, to have a series of specimens and both sexes to properly identify a species. Also, this key relies heavily on the morphology of spermatheca in female genitalia (see Fig. 1A for spermathecal structures and orientations used in this key). Published keys to regional faunas of *Pharaxonotha* are available for some *Ceratozamia* and *Zamia* (Skelley and Tang 2020; Tang and Gomez Dominguez 2022) and *Dioon* (Skelley et al. 2022) hosts. To help

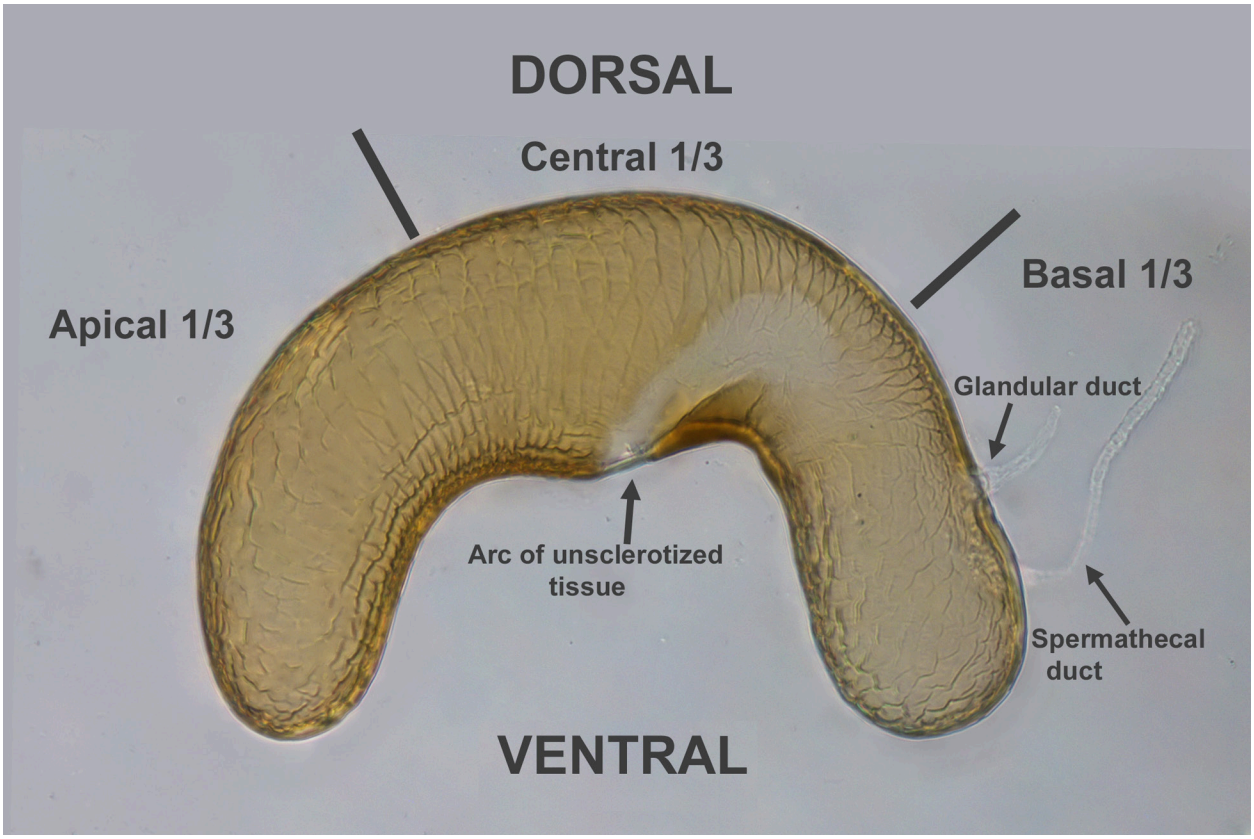


**Figure 1.** Spermatheca of *Pharaxonotha fawcettae* Skelley, Tang and Pérez-Farrera from Jalpan de Serra, Querétaro, Mexico indicating the diagnostic structures and regions used in the key.

facilitate accurate identifications, biological and distributional data are included here. More complete keys for *Ceratozamia* and *Zamia* hosts in other regions are currently in progress and will be published elsewhere.

1. Head in lateral view robust, convex dorsally especially anteriorly (Fig. 12E); post-ocular ridge present (temple), tooth-like in dorsal view; male with small tooth at apex of last abdominal ventrite (Fig. 12G); 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; associated with cycad cones ..... **2**

2(1). Body length 1.59–2.08 mm; pronotal hind angle and elytral humerus rounded, lacking angulation or small denticle; female with basal third of spermatheca wider than apical third (Fig. 11J); Panamá province on *Z. cunaria* and *Z. ipetiensis* ..... ***P. taylori* Skelley and Tang**

— Body length 1.99–3.80 mm; pronotal hind angle and elytral humerus with angulation or small denticle; female with basal third of spermatheca narrower than apical third; inhabiting other species of *Zamia* ..... **3**

3(2). Body length 2.03–2.31 mm; pronotum relatively long, pronotal length/width (PL/PW) = (0.77) 0.80–0.88, pronotal length/elytral length (PL/EL) = 0.34–0.40 (multiple specimens required); female with length of spermatheca ≈ 3× own maximum width; Darien province on *Z. manicata* ..... ***P. manicatae* Tang, Skelley and Taylor, n. sp.**

— Body length 1.99–3.80 mm; pronotum shorter, PL/PW = 0.60–0.80 (0.85), PL/EL = 0.29–0.37 (0.39) (multiple specimens required); female with length of spermatheca > 4× own maximum width; inhabiting other *Zamia* and various provinces ..... **4**

4(3). Spermatheca length > 6× maximum width of basal third; inhabiting NW portion of Panama, primarily in Atlantic drainage from Bocas del Toro to Coclé province [clarkorum species group] ..... **5**

— Spermatheca length < 6× maximum width of basal third; inhabiting southwest portion of Panama in Chiriqui province and eastern portion from Colón and Coclé to Darien provinces … [confusa species group] ..... **8**

5(4). Mean EL/EW = 1.70 (range = 1.63–1.75); mean PL/PW = 0.72 (range = 0.69–0.75); PL/EL strongly sexually dimorphic, in females = 0.309–0.329 (mean = 0.331), in males = 0.332–0.360 (mean = 0.345) (multiple specimens required); apical third of spermatheca swollen; inhabiting the epiphyte *Z. pseudoparasitica* in forest canopy generally 7–20 m above the forest floor in lowland forest from 50–1000m above sea level ..... ***P. pseudoparasitica* Tang, Skelley and Taylor, n. sp.**

— Mean EL/EW = 1.78–1.85 [6 populations sampled; range for all individuals = (1.58)1.67–2.06]; mean PL/PW = 0.73–0.76 (6 populations sampled, range for all individuals = 0.69–0.85); PL/EL moderately to non- sexually dimorphic (means for 6 populations: females = 0.325–0.336, in males = 0.330–0.356) (multiple specimens required); apical third of spermatheca swollen or not swollen; inhabiting non-epiphytic *Zamia* from littoral zone to cloud forest, 0–1200 m elevation ..... **6**

6(5). Body length 2.94–3.79 mm; head narrow relative to pronotal width, HW/PW = 0.66-0.72; fore and middle legs notably more robust than hind leg, protibia broadly triangular, protarsal pads enlarged with dense ventral brush of setae, male protarsal pad width notably > half width of eye in ventral view; male fore legs and tarsi notably more dilated than female; inhabiting *Z. lindleyi* in northern Chiriqui and southern Bocas del Toro provinces in montane and cloud forest from 600–1200 m ..... ..... ***P. fortunensis* Tang, Skelley and Taylor, n. sp.**

— Body length 1.99–2.68 mm; HW/PW = 0.73-0.81; fore and middle legs not notably more robust than hind leg, protibia narrowly triangular, protarsal pads moderately or not enlarged with ventral brush of setae normal, male protarsal pads width half width or less of eye in ventral view; male fore legs and tarsi weakly more dilated than female; inhabiting other *Zamia* species from Coclé to Bocas del Toro provinces, 0–600 m ..... **7**

7(6). Spermatheca shorter = 0.14 mm, apical third with only a slight gradual bend, swollen, width approximately twice the minimum width of basal third, apex rounded; inhabiting *Z. hamannii*, *Z. nesophila* and *Z. neurophyllidia*, in western Bocas del Toro, Panama and nearshore islands to northern Costa Rica ..... ***P. clarkorum* Pakaluk**

— Spermatheca longer = 0.17–0.19 mm, apical third with pronounced angulate bend, not swollen, only slightly wider than minimum width of basal third, apex subtruncate; inhabiting *Z. imperialis* and *Z. skinneri* from eastern Bocas del Toro eastward to Coclé Province ..... ..... ***P. holzmani* Tang, Skelley and Taylor, n. sp.**

8(4). Mean head width/ventral interocular distance (HW/VI) = 2.52–2.68 [5 populations sampled; range for all individuals sampled = (2.19) 2.30–2.83]; mean head width/dorsal interocular distance (HW/DI) = 1.79–1.87 (5 populations sampled; range for all individuals sampled = 1.73–1.97) (multiple specimens required); basal third of spermatheca with insertion point of spermathecal and glandular ducts flat, not raised, smooth portion of spermatheca at basal end usually abruptly transitioning to wider, annulated section, annulations at basal third at 90° angle to margins; southeastern Costa Rica (Puntarenas) and southwestern Panama (Chiriqui) in Pacific drainage south of Continental Divide with *Z. fairchildiana* and *Z. pseudomonticola* ..... ***P. confusa* Pakaluk**

— Mean HW/VI = 2.36–2.46, [6 populations sampled; range for all individuals sampled = (2.13) 2.32–2.75]; mean HW/DI = 1.74–1.77 (6 populations sampled; range = 1.68–1.88) (multiple specimens required); basal third of spermatheca with insertion point of spermathecal and glandular ducts bulging, not flat, smooth portion of spermatheca at basal end usually gradually transitioning to wider, annulated section, annulations at basal third at oblique angle to margins; central and eastern Panama (Coclé, Colón, Darien, Kula Yala, Panamá) with on *Z. dressleri*, *Z. elegantissima*, *Z. nana*, *Z. obliqua* and *Z. stevensonii* ..... ***P. panamensis* Tang, Skelley and Taylor, n. sp.**

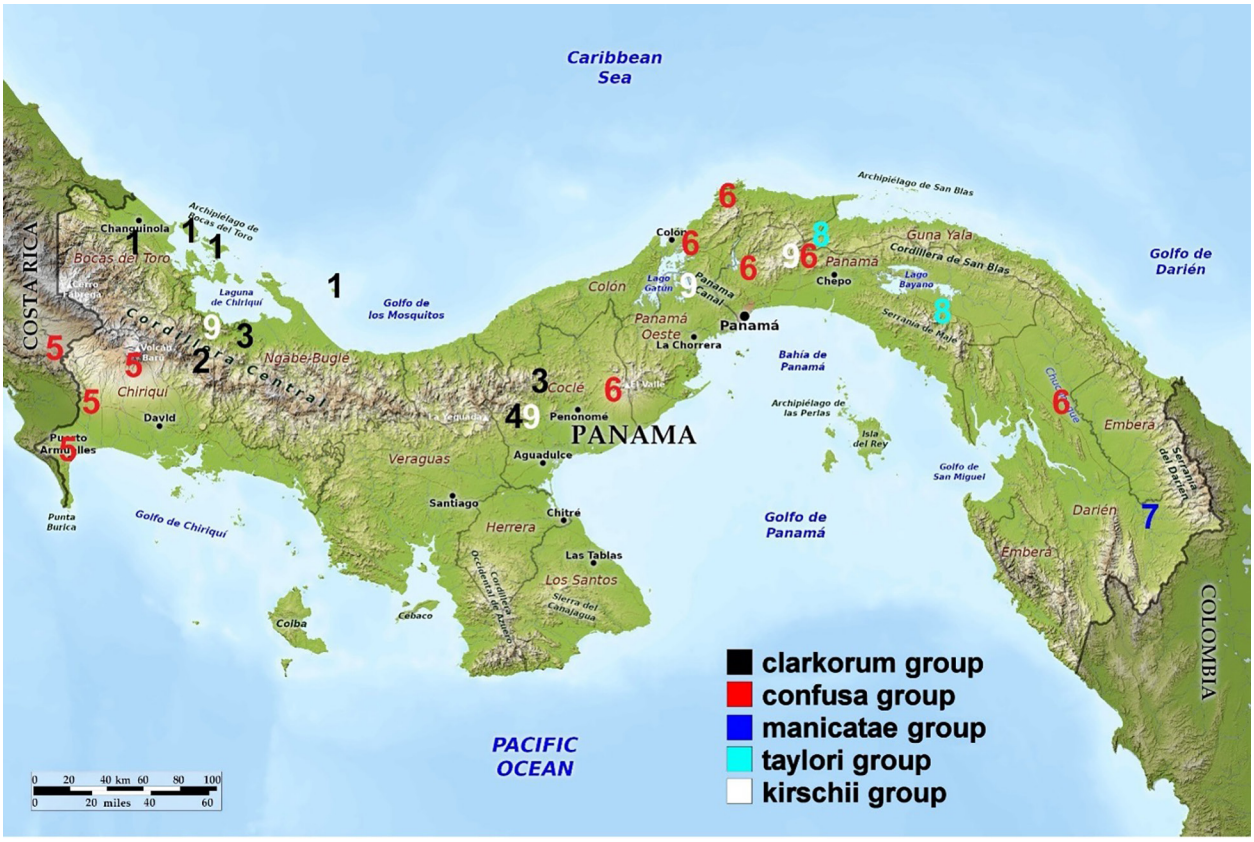


**Figure 2.** Relief map of Panama with localities where *Pharaxonotha* species have been found. Clarkorum group (black numbers): 1) *P. clarkorum*; 2) *P. fortunensis*; 3) *P. holzmani*; 4) *P. pseudoparasitica*. Confusa group (red numbers): 5) *P. confusa*; 6) *P. panamensis*. Manicatae group (dark blue number): 7) *P. manicatae*. Taylori group (light blue numbers): 8) *P. taylori*. Kirschii group (white numbers): 9) *P. kirschii*.

# Taxonomic accounts

## Clarkorum species group

**Adult diagnosis.** Spermatheca total length > 6× the maximum width of spermatheca basal third; head width/pronotal width (HW/PW) = 0.66–0.88 (mean for each species = 0.68–0.78); head width/dorsal interocular distance (HW/DI) = 1.61–1.86 (mean for each species = 1.70–1.78); ventral interocular distance/head width (HW/VI) = 2.05–2.59 (mean for each species = 2.22–2.41).

**Remarks.** Genetic analysis of the 16S rRNA gene places the clarkorum species group within the recent radiations of *Pharaxonotha* (Tang et al. 2018, 2020). Within the Panamanian fauna, the clarkorum species group is quite similar to the confusa species group in external morphology and currently they can be most effectively distinguished using spermatheca shape or DNA analysis of the 16S rRNA gene. The clarkorum species group is formed based on their similar elongate spermatheca, by analysis of the 16S rRNA mitochondrial gene for *Pharaxonotha* populations throughout its range (Tang et al. 2018, 2020) and analysis of 368 nuclear genes of a subsample of these populations (Salzman et al. unpublished data). There is pronounced sexual dimorphism in body proportions and leg development in several species in this group. Distribution of the clarkorum species group in Panama is along the Atlantic drainage from Coclé Province to Bocas del Toro. Diverse species of *Zamia* serve as hosts, including those in the *Z. skinneri* complex with their wide (up to 21 cm) plicate leaflets, *Z. lindleyi*, a premontane forest-cloud forest species with narrow, strap-shaped leaflets, and *Z. pseudoparasitica,* with long pendant leaves

and the only true epiphytic cycad. DNA analysis (Tang et al. 2018, 2020; Salzman et al. unpublished data) suggests this group extends into Colombia, in the coastal population of *Z. obliqua* in the department of Chocó and cloud forest in the Andes on *Z. oligodonta*. Morphology, particularly of the spermatheca, indicates the group also extends northward into contiguous Atlantic drainage of Costa Rica on *Z. neurophyllidia* and possibly as far north as Mexico, on *Ceratozamia*. Geographic reconstructions of Central America and northern Colombia during the Miocene and Pliocene (Coates 1997) indicates the region consisted of a series of islands, especially in northwestern Panama where this group and its hosts have radiated.

### *Pharaxonotha clarkorum* Pakaluk

Figures 3A–J, 4A–J (illustrations 2, 5, 8 in Pakaluk 1988)

*Pharaxonotha clarkorum* Pakaluk 1988: 448–449; Chaves and Genaro 2005: 143 (species list); Skelley and Segalla 2019: 188 (discussion); Skelley and Tang 2020: 4 (key).

**Diagnosis.** *Pharaxonotha clarkorum* is distinguished from other members of the genus by a combination of characters: body length 1.98–2.63 mm, among the smallest members of the clarkorum species group; pronotal length/width (PL/PW) = 0.68–0.79; head width/dorsal interocular length = 1.65–1.86; head width/ventral interocular length = 2.21–2.61; spermatheca with width of apical third about twice the minimum width of the basal third.

**Redescription.** Length 1.98–2.63 mm, width 0.61–0.99 mm (n = 86). Body in dorsal view elongate-oval (Fig. 3A–C, 4A–C), greatest width at middle of elytra; in lateral view convex dorsally (Fig. 3B, 4B). General body color entirely orange-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesosternum and abdomen mostly covered with short procumbent setae.

**Head** not broad, width = 0.72–0.82× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.47–0.60 mm; dorsal interocular distance 0.27–0.34 mm, head width/dorsal interocular distance ratio 1.65–1.86, ventral interocular distance 0.20–0.25 mm, head width/ventral interocular distance ratio 2.21–2.61. Eye with large black facets, about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV–VIII small, width equals length; club fairly large, IX and X similar in length; XI enlarged, 1.6× longer than X, globular with rounded apex (Fig. 3D, 4D). Clypeus weakly concave anteriorly, moderately punctate. Mentum (Fig. 3E, 4E) finely punctate, submentum more coarsely punctured, 2–3× diameter of those on mentum, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. 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 0.68–0.79; with distinct marginal beads laterally and basally, anteriorly with fine marginal bead medially; convex; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral carina parallel-sided or evenly shallowly arcuate for entire length; 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 of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process expanded apically, truncate and convex at apex. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate-oval, convex; length/width ratio1.78–1.96, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, weakly impressed; intervals of striae with fine, shallow punctures, 1.2× size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctation separated by 2–3× own diameter; medial surface

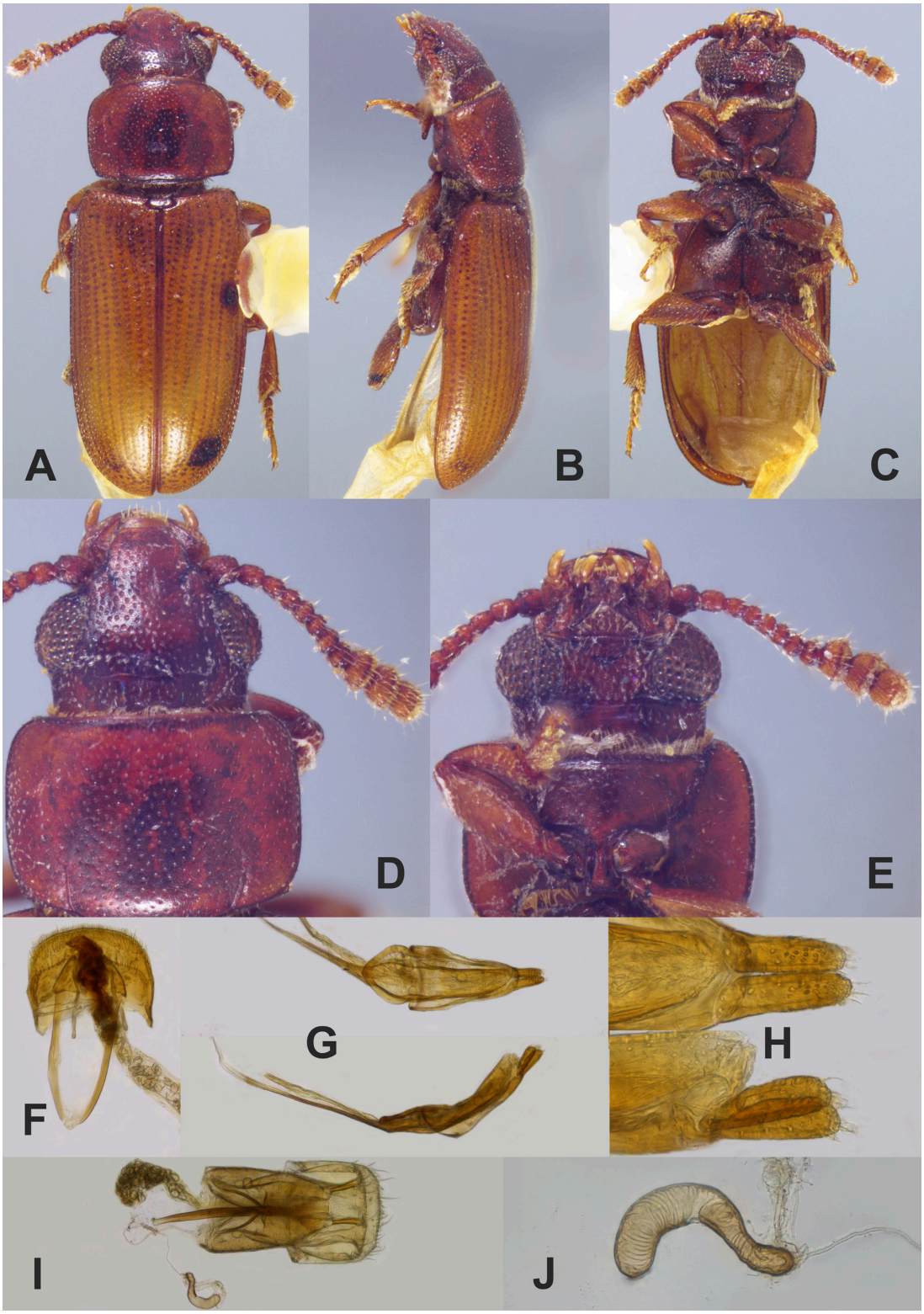


**Figure 3.** *Pharaxonotha clarkorum* paratypes from Costa Rica, Heredia Province, Puerto Viejo de Sarapiquí, Finca La Selva (A–I: male). **A–C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Male genital capsule, ventral view. **G)** Tegmen attached to median lobe, (top to bottom) ventral and lateral views. **H)** Parameres of tegmen, (top to bottom) ventral and lateral views. **I)** Retracted ovipositor with spermatheca, ventral view. **J)** Spermatheca.

finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, moderately compressed laterally; tibiae shorter than femora, gradually dilated to obliquely truncate apices; protibia with apical lateral tooth distinct, with apical fringe of short spinules of concave ventral apical margin usually lacking near lateral tooth; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite I with intercoxal process narrow, with triangular point anteromedially; lateral edges slightly projected, lateral and posterior margins arcuate, converging posteriorly; anterior and posterior margins of ventrites more or less straight; ventrite I longer medially than II; II–IV subequal in length; V slightly longer than IV with lateral margins converging posteriorly to a rounded apex; apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation across surface, distance to nearest puncture approximately 2× 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 similar to all others in the genus (Fig. 3F–H, 4F–H), with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum.

**Female.** Similar to male, no sexual dimorphism observed. Genitalia elongate (Fig. 3I, 4I); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width. Spermatheca with basal third narrow, length > 8× maximum width of basal third, apical third swollen, nearly 2× maximum width of basal third (Fig. 3J, 4J).

**Type locality.** Costa Rica, Heredia Province, Puerto Viejo de Sarapiquí, Finca La Selva.

**Range.** The type locality for *Pharaxonotha clarkorum* is in northern Costa Rica, some 160 km from the Panama border. The host of the type specimens, *Z. neurophyllidia*, as currently understood, has a widespread and historically nearly continuous distribution along the Atlantic drainage of Costa Rica to across the border of Panama into Bocas del Toro province (M. Calonje and W. Tang, unpub. data). In central Bocas del Toro, *Z. neurophyllidia* is replaced by closely related species, *Z. nesophila* and *Z. hamannii* (Taylor et al. 2008). Morphologically the beetles inhabiting the cones of all three hosts within this range appear identical and are here considered conspecific and placed together within *P. clarkorum*.

**Materials examined.** Holotype male of *Pharaxonotha clarkorum* with the following labels: 1) [rectangular; white; printed in black ink] "COSTA RICA: Heredia Prov., Puerto Viejo de Sarapiqui, Finca La Selva, 19.XI.82, in cone of Zamia skinneri [*Z. neurophyllidia*], David B. Clark coll. 1". 2) [rectangular; red; printed in black ink, except as noted] "HOLOTYPE, Pharaxonotha, clarkorum [handwritten], Pakaluk". Deposited in the USNM.

**Additional materials (124).** Six paratypes with same label data as holotype (USNM). **COSTA RICA: Alajuela,** P.N.V. Arenal, end Ceiba Tr., 630m, [GPS coord. omitted], *Z. neurophyllidia* ♂ cone, 10.X.2022, W. Tang (38); **Heredia**, La Virgen, Tirimbina res., 10.416, −84.12, cone ♂ *Z. neurophyllidia*, 1-X-2022, W. Tang (26); **Limon,** Aguas Frias, 70m, 10.45, -83.56, ♂ cone *Z. neurophyllidia*, 4-X-2022, W. Tang (9). **PANAMA: Bocas del Toro**, Isla Colón, 0–10 m asl, Jul-8-2000, A. Taylor, #9, *Zamia neurophyllidia*, wet, lowland tropical for. (6); Teribe Bonyic, ex ♂ cone *Zamia neurophyllidia*, Dec 2019, I. Rayo (1); [island name omitted], *Zamia nesophila* ♂ cone, 18 Oct 2012, G. Holzman (21); [island name omitted], 0-5 m asl, Sept-19-2004, A. Taylor, #17, *Zamia* sp. [*Z. hamannii*], wet lowland tropical forest (5); [island name omitted], ex ♂ cone *Zamia hamannii*, early 2021, A. Ibañez, SMS20-165 (12). Specimens to be deposited in: ANIC, FSCA, NHMUK, NZAC, RHTC, SEMC, STRI, MIUP, TAMU, USNM.

**Remarks.** *Pharaxonotha clarkorum* is placed here in the "recent radiations" of *Pharaxonotha* based on analysis of the 16S rRNA gene (Tang et al. 2018b, 2020). Within the clarkorum species group *P. clarkorum* appears most closely related to *P. holzmani,* which is distinguished from the former by the longer length, greater curvature and narrower apical width of its spermatheca, and is found further east in more inland habitats on *Z. imperialis* and *Z. skinneri*. Unlike *P. pseudoparasitica*, but similar to all other members of the clarkorum species group, it does not co-occur with *Notorhopalotria* weevils, either in Costa Rica or Panama (O'Brien and Tang 2015; W. Tang unpublished data; D. Clark personal communication). It appears to be the sole beetle pollinator of *Z. neurophyllidia, Z. nesophila and Z. hamannii*.

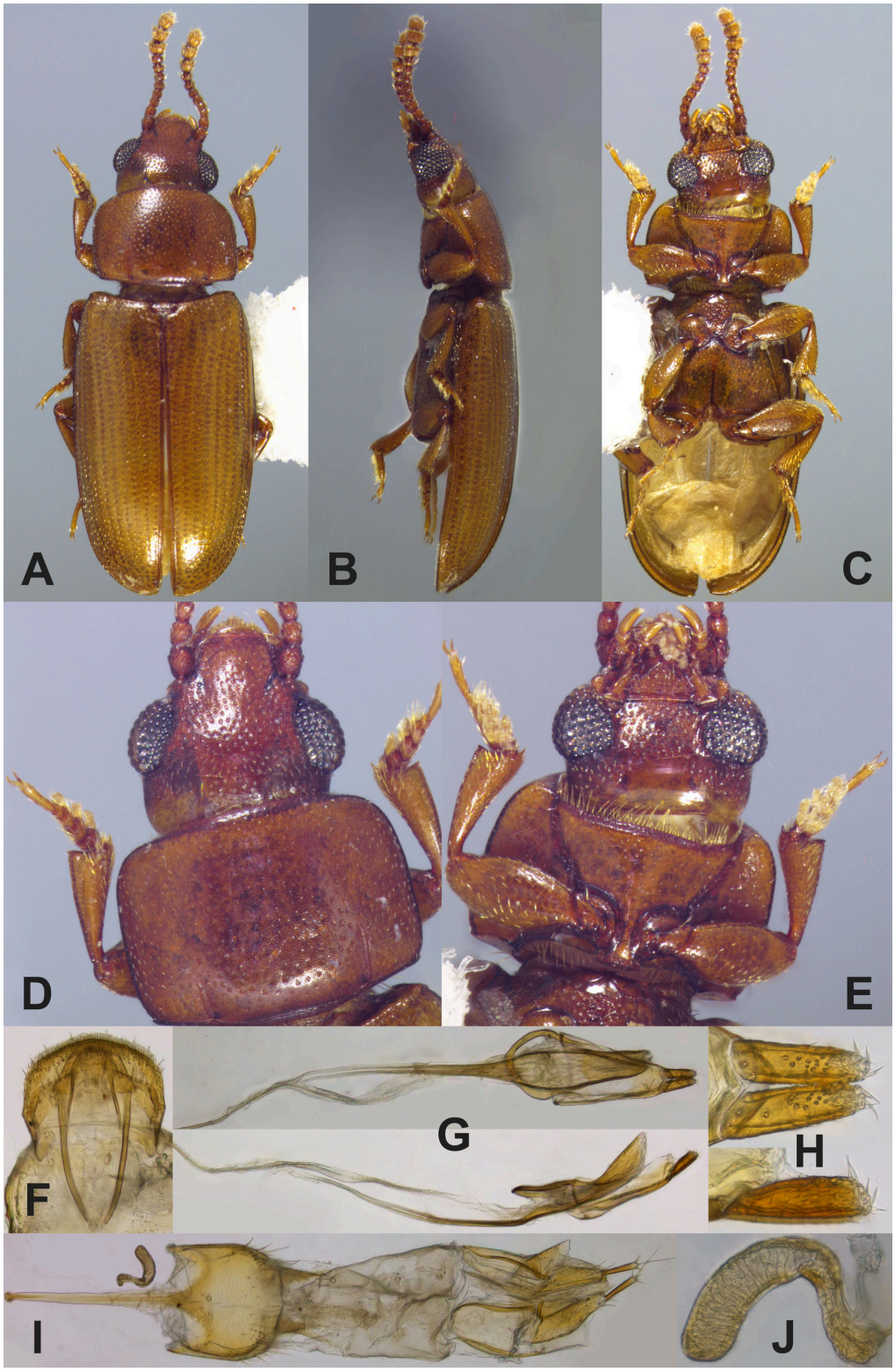


**Figure 4.** *Pharaxonotha clarkorum* found on *Zamia hamannii* in Bocas del Toro, Panama (A–H: male). **A–C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Genital capsule, ventral view. **G)** Tegmen attached to median lobe, (top to bottom) ventral and lateral views. **H)** Parameres of tegmen, (top to bottom) ventral and lateral views. **I)** Extended ovipositor with spermatheca, ventral view. **J)** Spermatheca.

### ***Pharaxonotha fortunensis*** **Tang, Skelley and Taylor, new species**

Figures 5A–I

**Diagnosis.** *Pharaxonotha fortunensis* can only be distinguished from other members of the genus by a combination of characters: Body length 2.94–3.79 mm, on average larger than other Panamanian species found on *Zamia*; head width/pronotal width (HW/PW) = 0.66-0.72, on average less than other Panamanian species; elytra length/width (EL/EW) = 1.78–2.05 (population mean = 1.85), on average larger than other members of the clarkorum species group; fore and middle legs notably more robust than hind leg, protibia broadly triangular, protarsal pads enlarged with dense ventral brush of setae, male protarsal pad width notably > half width of eye in ventral view; male fore legs and tarsi notably more dilated than in female; apical third of spermatheca swollen (Fig. 5I); inhabiting *Z. lindleyi* in northern Chiriqui and southern Boca del Toro at high elevations.

**Description.** Length 2.94–3.79 mm, width 0.99–1.42 mm (n = 20). Body in dorsal view elongate-oval (Fig. 5A–C), greatest width at middle of elytra; in lateral view convex dorsally (Fig. 5B). General body color entirely orange-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesosternum and abdomen mostly covered with short procumbent setae.

**Head** not broad, width = 0.66–0.72× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.58–0.76 mm; dorsal interocular distance 0.35–0.45 mm, head width/dorsal interocular distance ratio 1.61–1.78, ventral interocular distance 0.26–0.37 mm, head width/ventral interocular distance ratio 2.05–2.36. Eye with large black facets, about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV–VIII small, width equals length; club fairly large, IX and X similar in length; XI enlarged, 1.6× longer than X, globular with rounded apex (Fig. 5D). Clypeus weakly concave anteriorly, moderately punctate. Mentum (Fig. 5E) finely punctate, submentum more coarsely punctured, 2–3× diameter of those on mentum, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. 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 0.70–0.77; with distinct marginal beads laterally and basally, anteriorly with fine marginal bead medially; convex; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral carina parallel-sided or evenly shallowly arcuate for entire length; 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 of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process expanded apically, truncate and convex at apex. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate-oval, convex; length/width ratio1.78–2.05, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, weakly impressed; intervals of striae with fine, shallow punctures, 1.2× size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctation separated by 2–3× own diameter; medial surface finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow, fore and middle legs notably more robust than hind leg, protibia broadly triangular, protarsal pads enlarged with dense ventral brush of setae, male protarsal pad width notably > half width of eye in ventral view; male fore legs and tarsi notably more dilated than in female. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, moderately compressed laterally; tibiae shorter than femora, gradually dilated to obliquely truncate apices; protibia with apical lateral tooth

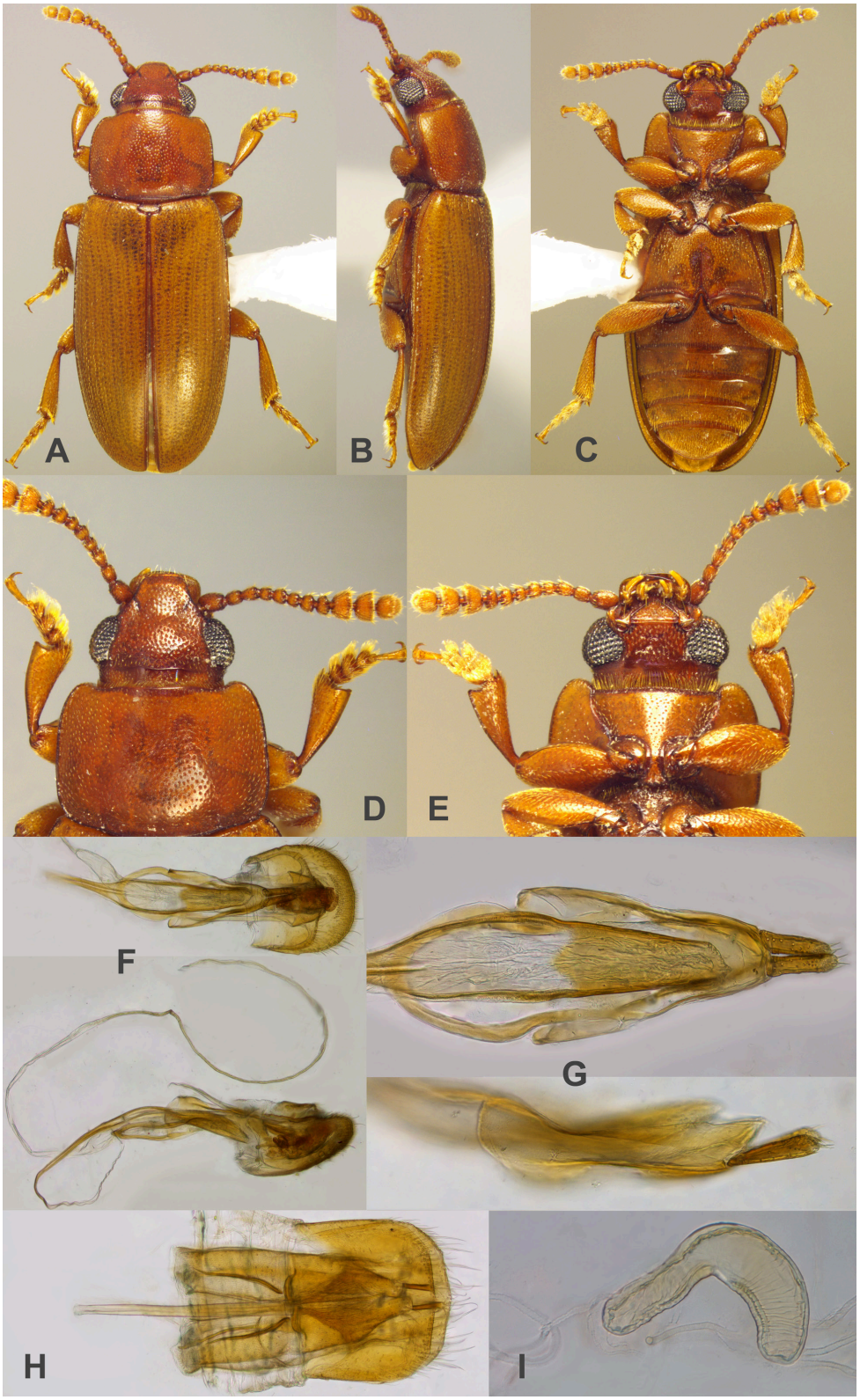


**Figure 5.** *Pharaxonotha fortunensis* (A–E: male holotype). **A–C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Male genital capsule, ventral view. **G)** Tegmen attached to median lobe, (top to bottom) ventral and lateral views. **H)** Retracted female genitalia, ventral view. **I)** Spermatheca.

distinct, with apical fringe of short spinules of concave ventral apical margin usually lacking near lateral tooth; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite I with intercoxal process narrow, with triangular point anteromedially; lateral edges slightly projected, lateral and posterior margins arcuate, converging posteriorly; anterior and posterior margins of ventrites more or less straight; ventrite I longer medially than II; II–IV subequal in length; V slightly longer than IV with lateral margins converging posteriorly to a rounded apex; apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation across surface, distance to nearest puncture approximately 2× 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 similar to all others in the genus (Fig. 5F–G), with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum.

**Female.** Similar to male, no sexual dimorphism observed. Genitalia elongate (Fig. 5H); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width. Spermatheca with basal third narrow, length > 7× maximum width of basal third, apical third swollen, nearly 2× maximum width of basal third (Fig. 5I).

**Type locality.** Panama, Chiriquí Province, Fortuna Dam.

**Range.** Known from the watershed of Fortuna Dam in Chiriquí province in cloud forest and montane forest. Its host, *Zamia lindleyi*, ranges into the neighboring Province of Bocas del Toro (Stevenson 1993) and this beetle likely extends there as well.

**Materials examined.** Holotype (by designation) male of *Pharaxonotha fortunensis* with the following labels: 1) [rectangular; white; printed in black ink] "PANAMA: Chiriquí Prov., Fortuna Dam, ♂ cone *Zamia lindleyi*, 30-IX-2010, C. Espinoza". 2) [rectangular; red; printed in black ink] "HOLOTYPE ♂ *fortunensis* Tang, Skelley and A.S. Taylor 2024". Deposited in the FSCA.

**Additional paratypes (37).** Allotype (FSCA) and 36 paratypes same label data as holotype, to be deposited in: ANIC, FSCA, NHMUK, NZAC, RHTC, SEMC, STRI, MIUP, TAMU, USNM.

**Etymology.** This beetle was collected in the watershed of Fortuna Dam, in the Reserva Forestal Fortuna. The adjectival species epithet means "from Fortuna".

**Remarks.** *Pharaxonotha fortunensis* belongs in the "recent radiation" of *Pharaxonotha* based on analysis of the 16S rRNA gene (Tang et al. 2018b, 2020). As a member of the clarkorum species group it appears most similar to *P. pseudoparasitica* and *P. clarkorum*, based on the swollen apical third of the spermatheca. Unlike *P. pseudoparasitica* and like most members of the confusa species group, it does not co-occur with *Notorhopalotria* weevils. It appears to be the sole beetle pollinator of *Z. lindleyi*.

### *Pharaxonotha holzmani* Tang, Skelley and Taylor, new species

Figures 6A–J

**Diagnosis.** *Pharaxonotha holzmani* can be distinguished from other members of the genus by a combination of characters: Body length 1.99–2.68 mm, among the small members of the clarkorum species group; head width/pronotal width = 0.73–0.88, ranging higher than the majority of Panamanian species; pronotal L/W = 0.70–0.85 (mean = 0.75) intermediate in range for Panamanian species; elytra L/W = 1.69–1.88 (mean = 0.78) intermediate in range for Panamanian species; spermatheca elongated with apical third not swollen (Fig. 6J); inhabiting cones of *Zamia imperialis* and *Z. skinneri*, from eastern Bocas del Toro to Coclé at elevations from 1–750 m asl.

**Description.** Length 1.99–2.68 mm, width 0.77–1.01 mm (n = 55). Body in dorsal view elongate-oval (Fig. 6A–C), greatest width at middle of elytra; in lateral view convex dorsally (Fig. 6B). General body color entirely orange-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesosternum and abdomen mostly covered with short procumbent setae.

**Head** not broad, width = 0.73–0.88× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.48–0.59 mm; dorsal interocular distance 0.27–0.34 mm, head width/dorsal

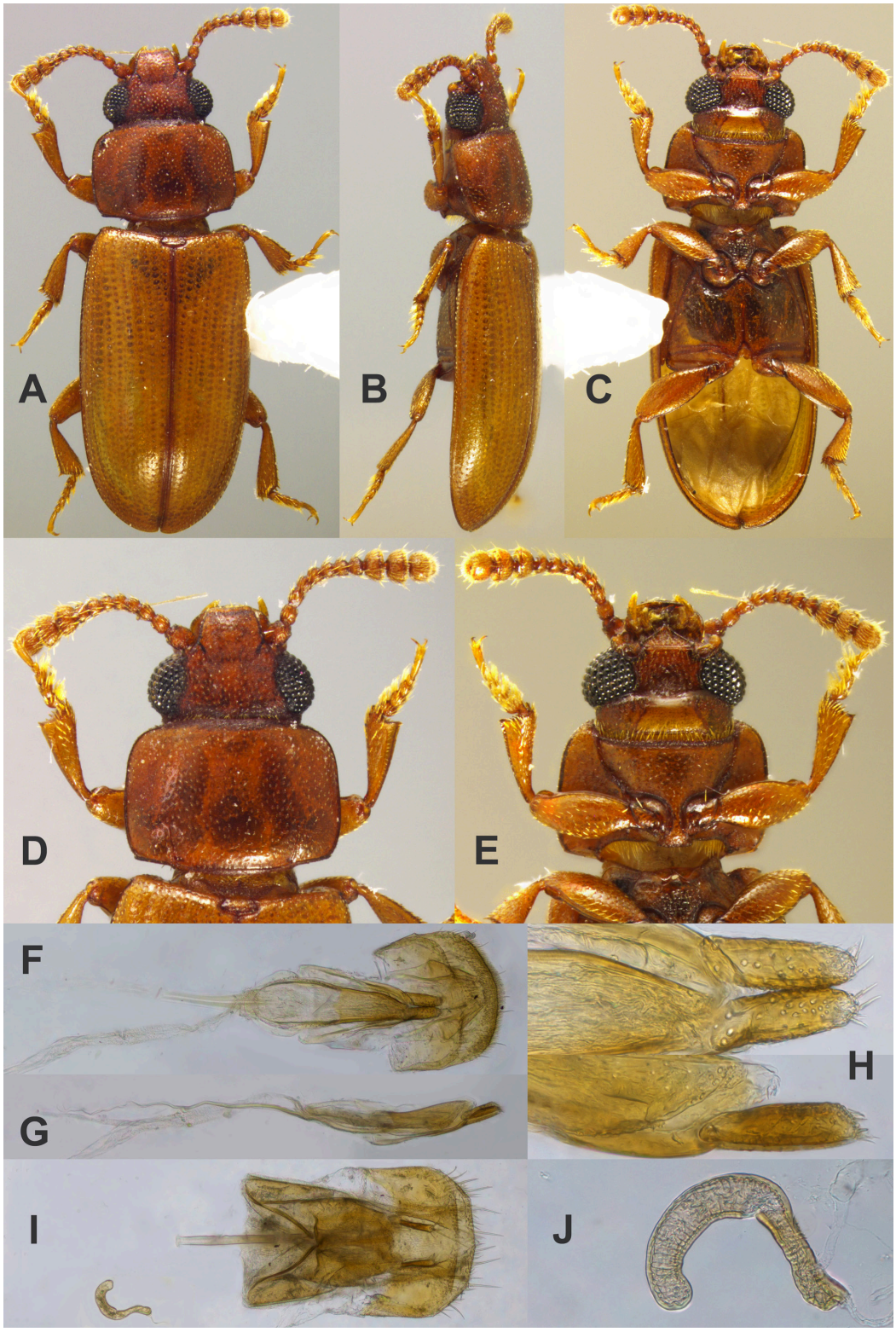


**Figure 6.** *Pharaxonotha holzmani* from *Zamia imperialis* (A-H: male holotype). **A–C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Genital capsule attached to tegmen and median lobe, ventral view. **G)** Tegmen attached to median lobe, lateral view. **H)** Parameres of tegmen, (top to bottom) ventral and lateral views. **I)** Retracted ovipositor with spermatheca, ventral view. **J)** Spermatheca.

interocular distance ratio 1.67–1.84, ventral interocular distance 0.20–0.27 mm, head width/ventral interocular distance ratio 2.15–2.59. Eye with large black facets, about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV–VIII small, width equals length; club fairly large, IX and X similar in length; XI enlarged, 1.6× longer than X, globular with rounded apex (Fig. 6D). Clypeus weakly concave anteriorly, moderately punctate. Mentum (Fig. 6E) finely punctate, submentum more coarsely punctured, 2–3× diameter of those on mentum, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. 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 0.70–0.85; with distinct marginal beads laterally and basally, anteriorly with fine marginal bead medially; convex; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral carina parallel-sided or evenly shallowly arcuate for entire length; 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 of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process expanded apically, truncate and convex at apex. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate-oval, convex; length/width ratio 1.63–1.73, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, weakly impressed; intervals of striae with fine, shallow punctures, 1.2× size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctation separated by 2–3× own diameter; medial surface finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, moderately compressed laterally; tibiae shorter than femora, gradually dilated to obliquely truncate apices; protibia with apical lateral tooth distinct, with apical fringe of short spinules of concave ventral apical margin usually lacking near lateral tooth; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite I with intercoxal process narrow, with triangular point anteromedially; lateral edges slightly projected, lateral and posterior margins arcuate, converging posteriorly; anterior and posterior margins of ventrites more or less straight; ventrite I longer medially than II; II–IV subequal in length; V slightly longer than IV with lateral margins converging posteriorly to a rounded apex; apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation across surface, distance to nearest puncture approximately 2× 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 similar to all others in the genus (Fig. 6F–H), with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum.

**Female.** Similar to male. Genitalia elongate (Fig. 6I); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width. Spermatheca with basal third narrow, length > 8× maximum width of basal third, apical third not swollen (Fig. 6J).

**Type locality.** PANAMA: Coclé.

**Range.** Known only from Panama, in Coclé province and at Rambala, Bocas del Toro Province. Hosts also occur in Veraguas province (Stevenson 1993) and this beetle likely occurs in this region as well.

**Materials examined.** Holotype (by designation) male of *Pharaxonotha holzmani* with the following labels: 1) [rectangular; white; printed in black ink] "PANAMA, Coclé Prov., [locality name omitted], ex male cone *Zamia*

*imperialis*, Alberto Taylor 11-XI-2016". 2) [rectangular; red; printed in black ink] "HOLOTYPE ♂ *Pharaxonotha holzmani* Tang, Skelley and A.S. Taylor 2024". Deposited in the FSCA.

**Additional paratypes (91).** Allotype (FSCA) and 49 adult paratypes same label data. **PANAMA: Bocas del Toro Prov.**, Chiriquí Grande, Rambala; ex ♂ cone *Zamia skinneri*, 15-X-2012, A. Taylor & G. Holzman (19); **Coclé Prov.**, [locality name omitted], 600 m asl, Nov-18-2004, A. Taylor, *Zamia skinneri*, Vial #10,13, wet, premountain tropical forest (20); [locality name omitted], 800 m asl, Nov-22-2003, A. Taylor, #4, *Zamia skinneri*, wet, premountain tropical forest (2). Paratypes to be deposited in: ANIC, FSCA, NHMUK, NZAC, RHTC, SEMC, STRI, MIUP, TAMU, USNM.

**Additional specimens examined but not included in type series.** Mainland costal materials studied and considered to be potential hybrids between *P. clarkorum* and *P. holzmani*, not designated as paratypes: **PANAMA: Bocas del Toro**, Punta Pargo, ex male cone *Zamia* sp. aff. *nesophila,* 18-X-2012, A. Taylor & G. Holzman (41).

**Etymology.** Named for Greg Holzman, for his field and taxonomic work with author A. Taylor on the *Zamia skinneri* complex.

**Remarks.** *Pharaxonotha holzmani* is placed here in the "recent radiations" of *Pharaxonotha* based on analysis of the 16S rRNA gene (Tang et al. 2018b, 2020). As a member of the clarkorum species group it appears most similar to *P. clarkorum*, based on the general external body proportions. Like other members of the clarkorum species group (with the exception of *P. pseudoparasitica*) it does not co-occur in the male cones of its hosts with *Notorhopalotria* weevils, in contrast with most members of the confusa species group (O'Brien and Tang 2015).

### *Pharaxonotha pseudoparasitica* Tang, Skelley and Taylor, new species

Figures 7A–J

**Diagnosis.** *Pharaxonotha pseudoparasitica* can only be distinguished from other members of the genus by a combination of characters: Body length 2.27–3.24 mm, on average greater than most members of the clarkorum species group, except *P. fortunensis*; head width/pronotal width = 0.72–0.77, within the range typical for the majority of Panamanian species; pronotal L/W = 0.69–0.75 (mean = 0.72) on average smaller than other Panamanian species; elytra L/W with a strong tendency to be larger in females, in males = 1.63–1.73, in females = 1.71–1.75; apical third of spermatheca swollen (Fig. 7J); inhabiting cones of *Zamia pseudoparasitica*, a true epiphyte living on branches of trees, typically 7-20 m above the forest floor at elevations from 100–1000 m asl.

**Description.** Length 2.27–3.24 mm, width 0.91–1.27 mm (n = 20). Body in dorsal view elongate-oval (Fig. 7A–C), greatest width at middle of elytra; in lateral view convex dorsally (Fig. 7B). General body color entirely orange-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesoventrite and abdomen mostly covered with short procumbent setae.

**Head** not broad, width = 0.72–0.77× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.53–0.71 mm; dorsal interocular distance 0.31–0.40 mm, head width/dorsal interocular distance ratio 1.66–1.80, ventral interocular distance 0.21–0.32 mm, head width/ventral interocular distance ratio 2.19–2.53. Eye with large black facets, about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV–VIII small, width equals length; club fairly large, IX and X similar in length; XI enlarged, 1.6× longer than X, globular with rounded apex (Fig. 7E). Clypeus weakly concave anteriorly, moderately punctate. Mentum (Fig. 7E) finely punctate, submentum more coarsely punctured, 2–3× diameter of those on mentum, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. 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 0.69–0.75; with distinct marginal beads laterally and basally, anteriorly with fine marginal bead medially; convex; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral carina parallel-sided or evenly shallowly arcuate for entire length; posterior margin slightly projecting medially,

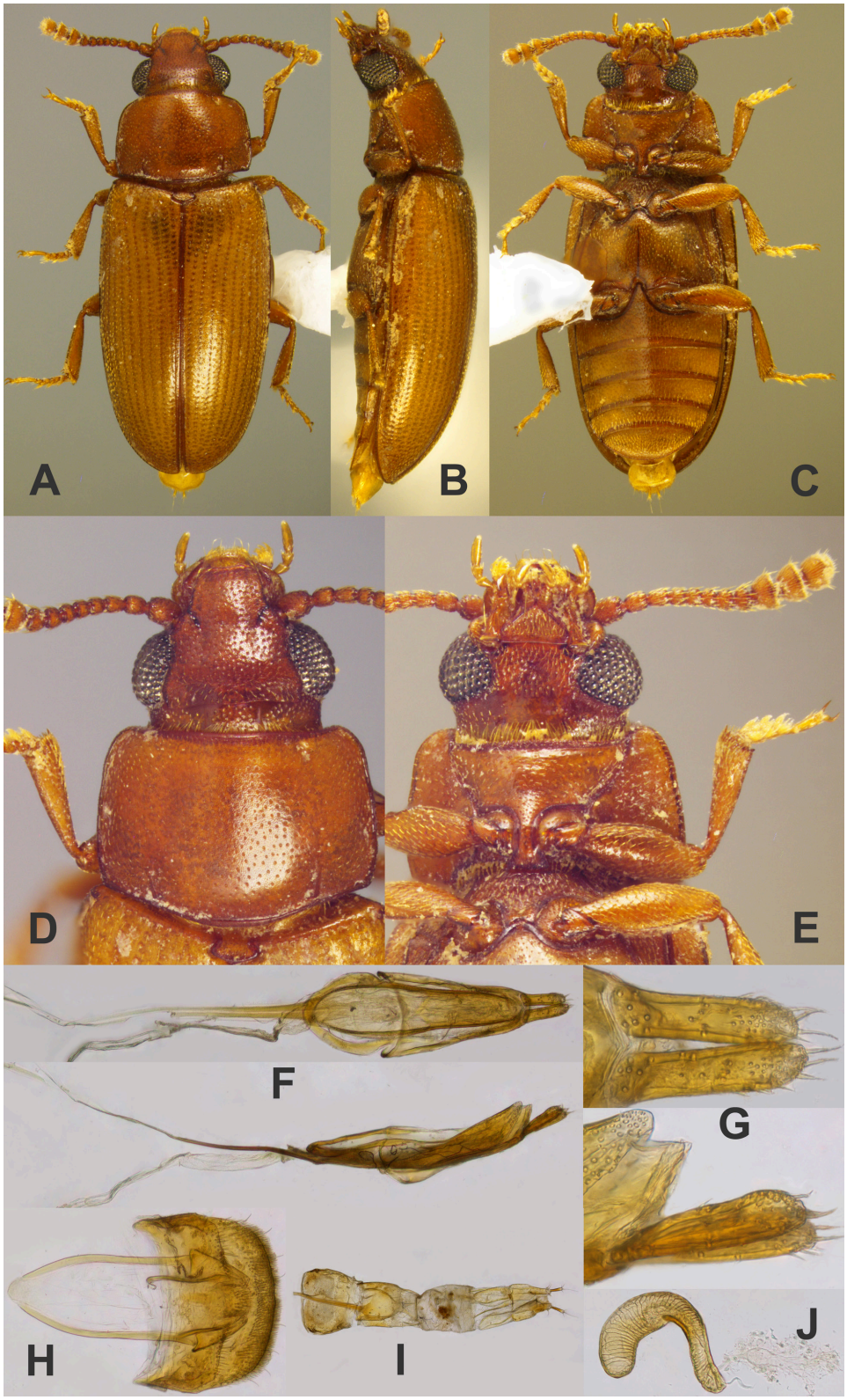


**Figure 7.** *Pharaxonotha pseudoparasitica* (A–E: female allotype). **A-C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Tegmen attached to median lobe, (top to bottom) ventral and lateral views. **G)** Parameres of tegmen, (top to bottom) ventral and lateral views. **H)** Male genital capsule, ventral view. **I)** Extended ovipositor. **J)** Spermatheca.

projection beginning approximately by pair of small, dark pores in margin located ¼ width from posterior angles, each pore marks base of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process expanded apically, truncate and convex at apex. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate-oval, convex; length/width ratio 1.63–1.73, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, weakly impressed; intervals of striae with fine, shallow punctures, 1.2× size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctation separated by 2–3× own diameter; medial surface finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, moderately compressed laterally; tibiae shorter than femora, gradually dilated to obliquely truncate apices; protibia with apical lateral tooth distinct, with apical fringe of short spinules of concave ventral apical margin usually lacking near lateral tooth; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite I with intercoxal process narrow, with triangular point anteromedially; lateral edges slightly projected, lateral and posterior margins arcuate, converging posteriorly; anterior and posterior margins of ventrites more or less straight; ventrite I longer medially than II; II–IV subequal in length; V slightly longer than IV with lateral margins converging posteriorly to a rounded apex; apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation across surface, distance to nearest puncture approximately 2× 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 similar to all others in the genus (Fig. 7F–H), with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum.

**Female.** Similar to male, except elytral length/width (EL/EW) = 1.71–1.75, with strong tendency to be larger in females. Genitalia elongate (Fig. 7I); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width. Spermatheca with basal third narrow, length > 9× maximum width of basal third, apical third swollen, nearly 2× maximum width of basal third (Fig. 7J).

**Type locality.** PANAMA: Coclé, El Copé.

**Range.** Known from Panama, Coclé province, El Copé. Host range extends into Bocas del Toro, Colón and Veraguas provinces (Stevenson 1993) and this beetle likely occurs in these regions as well.

**Materials examined.** Holotype (by designation) male of *Pharaxonotha pseudoparasitica* with the following labels: 1) [rectangular; white; printed in black ink] "PANAMA, Coclé Prov., El Copé, ex male cone *Zamia pseudoparasitica*, Alberto Taylor IX-22-2004". 2) [rectangular; red; printed in black ink] "HOLOTYPE ♂ *Pharaxonotha pseudoparasitica* Tang, Skelley and A.S. Taylor 2024". Deposited in the FSCA.

**Additional paratypes (184).** Allotype (FSCA) and 91 Paratypes same label data. **PANAMA: Coclé Prov.**, El Copé, ex male cone *Zamia pseudoparasitica*, Alberto Taylor, 800m asl, wet premountain forest, IX-2-2002 (12); IX-22,28-2003 (23); IX-24-2004 (16); X-2-2016 (41). Paratypes to be deposited in: ANIC, FSCA, NHMUK, NZAC, RHTC, SEMC, STRI, MIUP, TAMU, USNM.

**Etymology.** The host plant, *Zamia pseudoparasitica*, is an epiphyte appearing to parasitize trees on which it lives, but have a commensal relationship with them. These beetles appear to parasitize the cones of the host plant, but instead act as pollinators. Thus, as with the host species, the specific epithet is a feminine adjective reflecting the beetles' role as a false parasite.

**Remarks.** *Pharaxonotha pseudoparasitica* is placed here in the "recent radiation" of species using *Zamia* cycads as hosts (Tang et al. 2018b, 2020). As a member of the clarkorum species group it appears most similar to *P.*

*fortunensis*, based on the swollen apical third of the spermatheca. Unlike other members of the clarkorum species group, *P. pseudoparasitica* co-occurs in the male cones of its host with a species of *Notorhopalotria* weevil, *N. taylori* Tang and O'Brien (O'Brien and Tang 2015).

## Confusa species group

**Adult diagnosis.** Spermatheca not elongate, total length < 6× the maximum width of the basal third, C-shaped, width throughout its length not varying more than about 1.5X the central thickness of the basal third; head width/pronotal width (HW/PW) = 0.66–0.86 (mean for each species = 0.76–0.78); head width/dorsal interocular distance (HW/DI) = 1.68–1.97 (mean for each species = 1.76–1.86); ventral interocular distance/head width (HW/VI) = 2.13–2.83 (mean for each species = 2.36–2.58).

**Remarks.** Genetic analysis of the 16S rRNA gene places the confusa species group within the recent radiations of *Pharaxonotha* (Tang et al. 2018, 2020). Within the Panamanian fauna, the confusa species group is quite similar to the clarkorum species group in external morphology. The confusa species group is formed based on spermatheca morphology, by analysis of the 16SrRNA gene in *Pharaxonotha* from nearly all *Zamia* species in Panamanian (Tang et al. 2018b, 2020) as well as analysis of 368 nuclear genes in a subsample of these populations (Salzman et al. unpublished data). Distribution of this group is disjunct with one species, *P. confusa*, recognized in the Pacific drainage of the western province of Chiriqui extending into the adjoining Costa Rican province of Puntarenas on the *Z. fairchildiana-Z. pseudomonticola* complex. Another member of this species group, *P. panamensis*, is recognized on the Atlantic drainage from central to eastern Panama on five morphologically diverse hosts: *Z. nana, Z. dressleri, Z. obliqua*, *Z. elegantissima* and *Z. stevensonii*.

### *Pharaxonotha confusa* Pakaluk

Figures 8A–J (illustrations 6, 9 in Pakaluk 1988)

*Pharaxonotha confusa* Pakaluk 1988: 449; Chaves and Genaro 2005: 143 (species list); Skelley and Segalla 2019: 188 (discussion); Skelley and Tang 2020: 4 (key).

**Diagnosis.** *Pharaxonotha confusa* can only be distinguished from other members of the genus by a combination of characters: Body length 2.13–3.38 mm, among the intermediate-sized members of Panamanian *Pharaxonotha*; head width/pronotal width = 0.67–0.80, within the range typical for the majority of Panamanian species; pronotal L/W = 0.60–0.80 (mean = 0.74) intermediate in range for Panamanian species; elytra L/W = 1.66–1.87 (mean = 1.79) intermediate in range for Panamanian species; spermatheca with insertion point of spermathecal and glandular ducts flat, not raised, smooth portion at basal end usually abruptly transitioning to wider, annulated section, annulations at basal third at 90° angle to margins; inhabiting cones of *Zamia fairchildiana* and *Z. pseudomonticola*, in western Chiriqui province and across the border to Puntarenas province, Costa Rica, at elevations from 1–1500 m asl.

**Description.** Length 2.13–3.38 mm, width 0.84–1.29 mm (n = 116). Body in dorsal view elongate-oval (Fig. 8A–C), greatest width at middle of elytra; in lateral view convex dorsally (Fig. 8B). General body color entirely orange-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesoventrite and abdomen mostly covered with short procumbent setae.

**Head** not broad, width = 0.66–0.81× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.51–0.77 mm; dorsal interocular distance 0.29–0.41 mm, head width/dorsal interocular distance ratio 1.73–1.97, ventral interocular distance 0.20–0.31 mm, head width/ventral interocular distance ratio 2.19–2.83. Eye with large black facets, about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV–VIII small, width equals length; club fairly large, IX and X similar in length; XI enlarged, 1.6× longer than X, globular with rounded apex (Fig. 8C). Clypeus weakly concave anteriorly, moderately punctate. Mentum (Fig. 8E) finely punctate, submentum more coarsely punctured, 2–3× diameter of those on mentum, distance between nearest punctures approximately 1× own diameter, each puncture with a

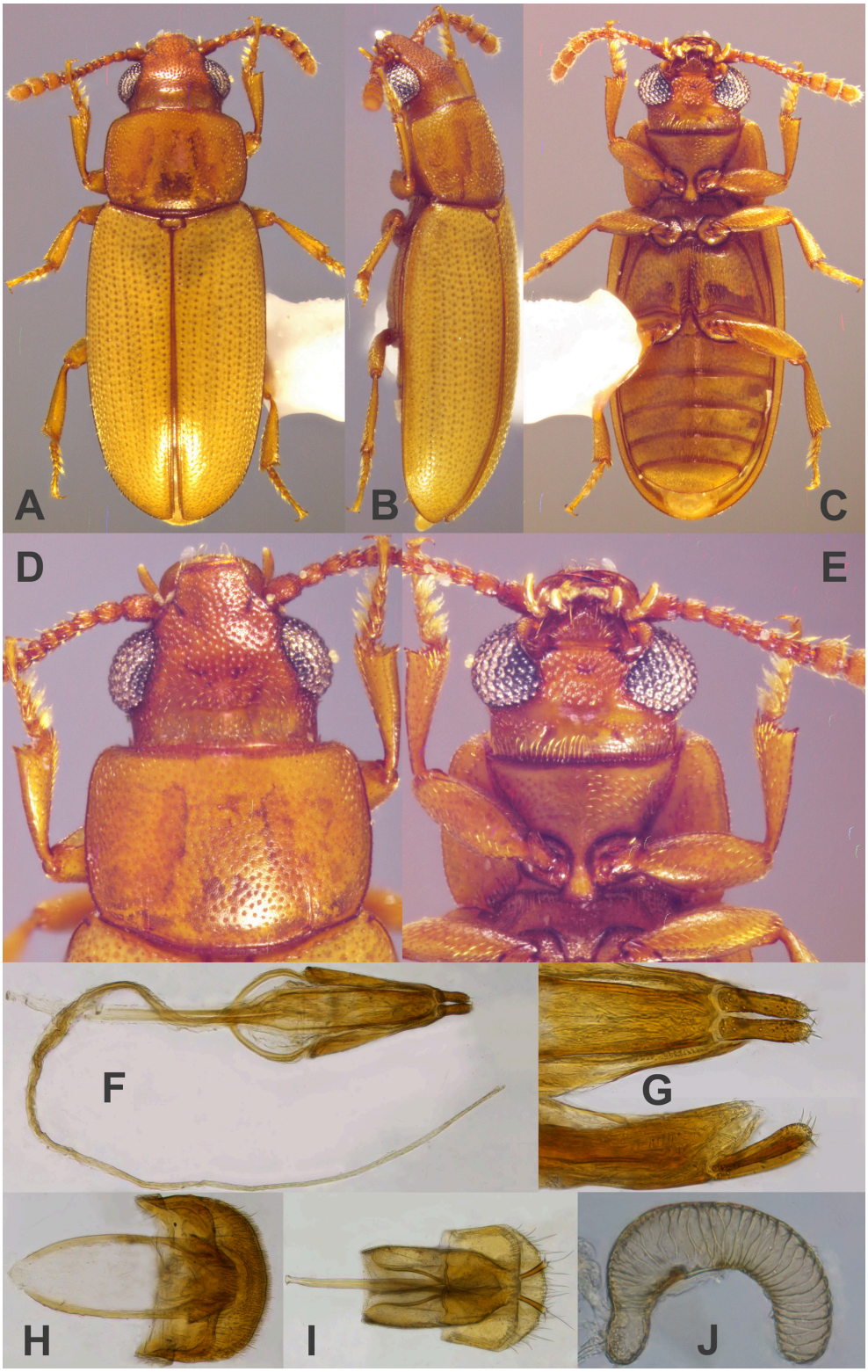


**Figure 8.** *Pharaxonotha confusa* from *Z. fairchildiana* from Burica Peninsula (A–H, J). **A–C)** Female dorsal, lateral and ventral habitus. **D–E)** Female head, dorsal and ventral views. **F)** Tegmen attached to median lobe, ventral view. **G)** Parameres of tegmen, (top to bottom) ventral and lateral views. **H)** Male genital capsule, ventral view. **I)** Retracted ovipositor from *Z. pseudomonticola* from Porton, ventral view. **J)** Spermatheca.

short seta. 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 0.60–0.80; with distinct marginal beads laterally and basally, anteriorly with fine marginal bead medially; convex; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral carina parallel-sided or evenly shallowly arcuate for entire length; 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 of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process expanded apically, truncate and convex at apex. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate-oval, convex; length/width ratio 1.66–1.91, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, weakly impressed; intervals of striae with fine, shallow punctures, 1.2× size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctation separated by 2–3× own diameter; medial surface finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, moderately compressed laterally; tibiae shorter than femora, gradually dilated to obliquely truncate apices; protibia with apical lateral tooth distinct, with apical fringe of short spinules of concave ventral apical margin usually lacking near lateral tooth; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite I with intercoxal process narrow, with triangular point anteromedially; lateral edges slightly projected, lateral and posterior margins arcuate, converging posteriorly; anterior and posterior margins of ventrites more or less straight; ventrite I longer medially than II; II–IV subequal in length; V slightly longer than IV with lateral margins converging posteriorly to a rounded apex; apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation across surface, distance to nearest puncture approximately 2× 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 similar to all others in the genus (Fig. 8F–H), with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum.

**Female.** Similar to male. Genitalia elongate (Fig. 8I); gonostylus set apically on gonocoxite, gonostylus length = 5–6× width. Spermatheca C-shaped, evenly curved, approximately equal width for most of length, except slightly narrower at its basal ⅕–⅙, length < 6× maximum width of basal third, apical third not more swollen than maximum width of basal ⅓ (Fig. 8J).

**Type locality.** Costa Rica, Puntarenas province, San Vito de Coto Brus, Las Cruces, Wilson Botanical Garden.

**Range.** As delimited here, known from Chiriqui province, Panama extending west into Puntarenas province, Costa Rica in cones of *Zamia fairchildiana* and *Z. pseudomonticola*, at elevations from 1–1500 masl. *Zamia fairchildiana* occurs as far northwest as San José province, Costa Rica and this beetle likely occurs there as well.

**Materials examined.** Holotype male of *Pharaxonotha confusa* with the following labels: 1) [rectangular; white; printed in black ink] "COSTA RICA: Puntarenas, Prov., San Vito de Coto Brus, Las Cruces, Wilson Botanical Garden, ex., male cones of Zamia fairchildeana [sic, see Remarks] 25.II.85, G. E. Schatz coll.". 2) [rectangular; red; printed in black ink, except as noted] "HOLOTYPE, Pharaxonotha, confusa [handwritten], Pakaluk". Deposited in the USNM.

**Additional materials (987).** Two paratypes with same label data as holotype (USNM). **COSTA RICA: Puntarenas**: Las Cruces, Coto Brus, 1100m, II-1994, Luis D. Gomez, ex male *Zamia*, #94767 (111); Osa Pen., Corcovado

Nat. Park, Pop#1, 8-XII-2005, C. Lopez Gallego, *Zamia fairchildiana* ♂ cones (57); Las Cruces, Loop Trail, ♂ cone *Z. pseudomonticola,*1300m, [GPS coord. Omitted], W. Tang, XI-24-2010 (177); Wilson Botanical Garden, ex ♂ cone *Z. pseudomonticola,* N8°47.150′ W47°57.570′, 1235m, W. Tang, XI-24-2010 (54); Golfo Dulce, beach nr. Rincon, ♂ cone *Zamia fairchildiana*, [GPS coord. Omitted], W, Tang, XI-26-2011 (238); **PANAMA: Chiriquí**, Burica Pen., San Bartolo Limite, 13.5 km WNW of Puerto Armuelles, 440m, [GPS coord. omitted], ♂ cone *Zamia fairchildiana*, I-8-2008, M. Calonje et al. (206); Santa Clara, Finca Hartmann, *Z. pseudomonticola,* Alberto Taylor 29-XII-2001 (93); 30-XII-2001 (21); Hartman-Enders, 1500m asl, 30-XII-2001(10); Porton, ex ♂ cone *Zamia*. sp. aff. *pseudomonticola*, 7-XII-2013, A. Taylor (18). Specimens to be deposited in: ANIC, FSCA, NHMUK, NZAC, RHTC, SEMC, STRI, MIUP, TAMU, USNM.

**Remarks.** Describing *P. confusa*, Pakaluk (1988) cited the host as best understood at the time with the advice of regional botanists. *Zamia* from various localities are planted in Wilson Botanical Garden, so the cone from which type specimens of *P. confusa* were collected may have been a cultivated *Zamia fairchildiana*. However, that individual cycad will never be known to confirm that identification.

In the 1980s, there was taxonomic confusion on the identity of "*fairchildiana*" and "*pseudomonticola*" (Calonje et al. 2023). Gómez (1982) described both *Z. fairchildiana* and *Z. pseudomonticola* in the same paper. Prior to this, there was no official name for any *Zamia* in southeastern Costa Rica. Unfortunately, Gómez (1982) did not clearly cite holotypes, thus *Z. pseudomonticola* did not become an available name until Stevenson and Sabado (1986) provided additional information to make it valid. For many years afterward confusion continued, with the name "*Zamia fairchildiana*" being used for all the common arborescent understory *Zamia* in the region, while the identity of *Z. pseudomonticola* remained unclear. Although Stevenson and Sabado (1986) claimed to have found and examined the type for *Z. pseudomonticola* and validated the name, the issue was not fully resolved until Acuña and Gómez (2009) designated a lectotype (from the Osa peninsula) for *Z. fairchildiana*. Years later, after more field work, morphological studies and DNA analyses, it is generally understood that *Z. fairchildiana* is the lowland form, while *Z. pseudomonticola* is the highland form which occurs naturally around the Wilson Botanical Garden. Thus, the natural host for the nominal population of *P. confusa* is *Z. pseudomonticola*.

As may be expected from a beetle that occurs within a wide range of elevations and diverse habitats (lowland rainforest and beach habitat to premontane forest), *P. confusa* exhibits some variation. Lowland populations inhabiting *Z. fairchildiana* are on average smaller (mean length = 2.47 mm) than highland forms inhabiting *Z. pseudomonticola* (mean length = 2.69–3.00 mm). However, DNA analysis (Tang et al. 2018b, 2020; Salzman et al. unpublished data) did not detect sufficient genetic differences among populations to warrant demarcation into more than one species. The elevational ranges of the two host species meet and appear continuous (Calonje, personal communication) and there does not appear to have been any recent geographic barriers to prevent gene flow from lowland to highland populations. The male cones of host *Z. pseudomonticola* are larger than those of *Z. fairchildiana* and the difference in available nutrition may account for differences in beetle size. The lowland and highland forms are otherwise nearly identical in their external morphological proportions. Until definitive characters are found to separate them, we treat the lowland form as a variety of the nominal highland form. As a member of the confusa species group, *P. confusa* appears most similar to *P. panamensis*, based on the overall shape of the spermatheca and genetic analysis (Tang et al. 2018b, 2020; Salzman et al. unpublished data). Like most other members of the confusa species group, this beetle co-occurs in the male cones of its hosts with *Notorhopalotria* weevils, in this case with *N. montgomeryensis* O'Brien and Tang (O'Brien and Tang 2015).

### *Pharaxonotha panamensis* Tang, Skelley and Taylor, new species

Figures 9A–J

**Diagnosis.** *Pharaxonotha panamensis* can be distinguished from other members of the genus by the following combination of characters: Body length 2.18–2.96 mm, among the intermediate-sized members of Panamanian *Pharaxonotha*; head width/pronotal width = 0.73–0.86 (mean for 5 populations = 0.76–0.78), within the range typical for the majority of Panamanian species; pronotal L/W = 0.69–0.81 (mean = 0.74–0.76) intermediate in range for Panamanian species; elytra L/W = 1.66–1.92 (mean = 1.74–1.78) intermediate in range for Panamanian species; spermatheca with insertion point of spermathecal and glandular ducts bulging, not flat, smooth portion at basal end usually gradually transitioning to wider, annulated section, annulations at basal third at oblique angle

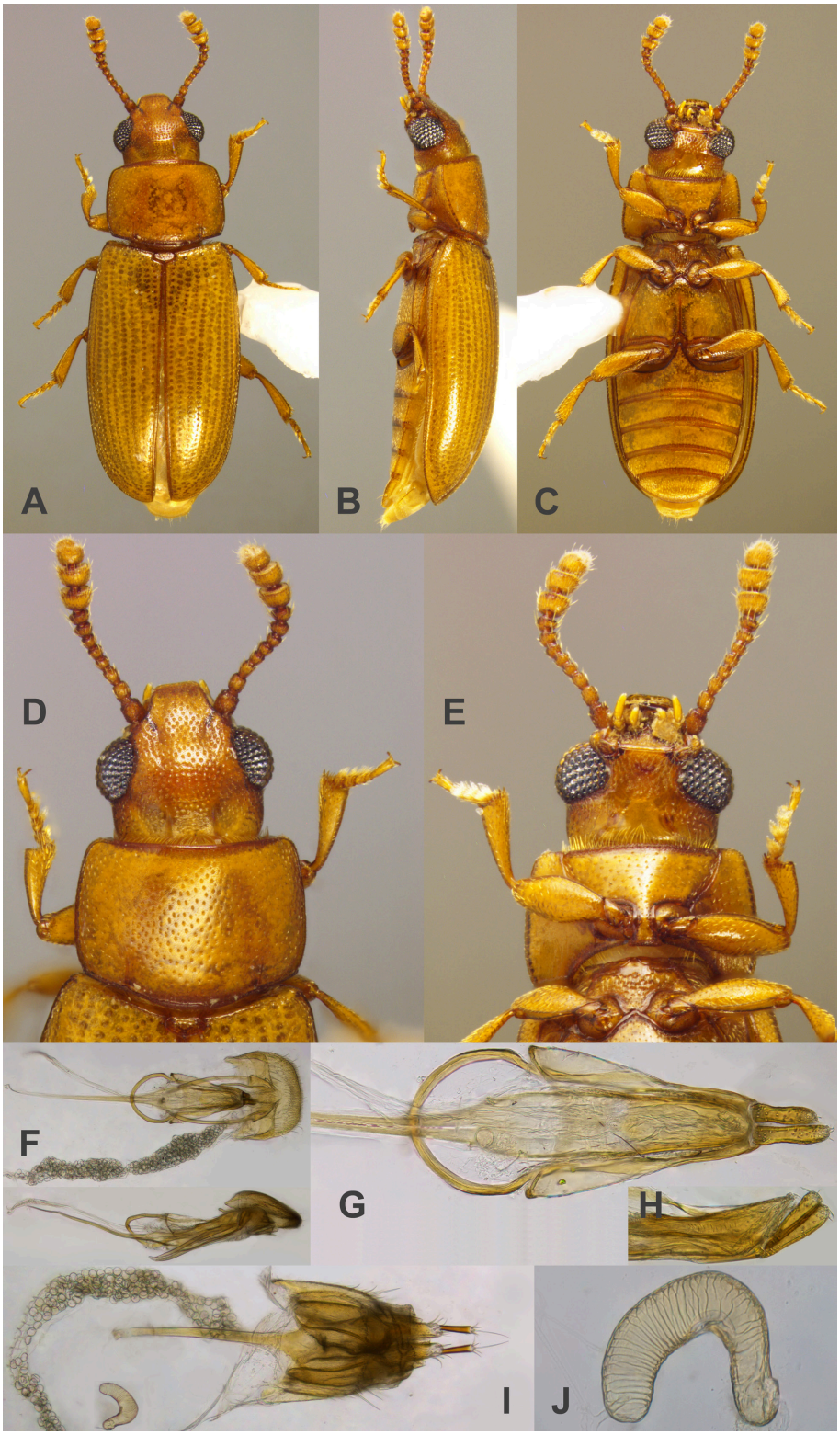


**Figure 9.** *Pharaxonotha panamensis* from *Z. stevensonii* (A-E: female allotype). **A–C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Male genital capsule and tegmen attached to median lobe, (top to bottom) ventral and lateral views. **G)** Tegmen, ventral view. **H)** Parameres of tegmen, lateral view. **I)** Retracted ovipositor and spermatheca, ventral view. **J)** Spermatheca (partially inflated).

to margins (Fig. 9J); inhabiting cones of *Z. dressleri*, *Z. elegantissima*, *Z. nana* and *Zamia stevensonii* in Coclé, Colón, Kula Yala, and Panamá provinces.

**Description.** Length 2.18–2.96 mm, width 0.81–1.12 mm (n = 80). Body in dorsal view elongate-oval (Fig. 9A–C), greatest width at middle of elytra; in lateral view convex dorsally (Fig. 9B). General body color entirely orange-brown; dorsal surface punctate, shining and appearing glabrous, short procumbent hairs associated with punctation on pronotum and elytra, ventrally shining and appearing glabrous except mesoventrite and abdomen mostly covered with short procumbent setae.

**Head** not broad, width = 0.73–0.86× pronotal width; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.54–0.67 mm; dorsal interocular distance 0.30–0.38 mm, head width/dorsal interocular distance ratio 1.68–1.88, ventral interocular distance 0.20–0.20 mm, head width/ventral interocular distance ratio 2.13–2.75. Eye with large black facets, about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV–VIII small, width equals length; club fairly large, IX and X similar in length; XI enlarged, 1.6× longer than X, globular with rounded apex (Fig. 9D). Clypeus weakly concave anteriorly, moderately punctate. Mentum (Fig. 9E) finely punctate, submentum more coarsely punctured, 2–3× diameter of those on mentum, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. 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 0.69–0.81; with distinct marginal beads laterally and basally, anteriorly with fine marginal bead medially; convex; anterior angles broadly rounded, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral carina parallel-sided or evenly shallowly arcuate for entire length; 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 of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process expanded apically, truncate and convex at apex. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate-oval, convex; length/width ratio 1.66–1.92, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, weakly impressed; intervals of striae with fine, shallow punctures, 1.2× size of strial punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctation separated by 2–3× own diameter; medial surface finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, moderately compressed laterally; tibiae shorter than femora, gradually dilated to obliquely truncate apices; protibia with apical lateral tooth distinct, with apical fringe of short spinules of concave ventral apical margin usually lacking near lateral tooth; meso- and metatibia with apical fringe of short spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite I with intercoxal process narrow, with triangular point anteromedially; lateral edges slightly projected, lateral and posterior margins arcuate, converging posteriorly; anterior and posterior margins of ventrites more or less straight; ventrite I longer medially than II; II–IV subequal in length; V slightly longer than IV with lateral margins converging posteriorly to a rounded apex; apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctation across surface, distance to nearest puncture approximately 2× 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 similar to all others in the genus (Fig. 9F–H), with dorsoventrally flattened tegmen, elongate cylindrical median lobe, and long coiled flagellum.

**Female.** Similar to male. Genitalia elongate (Fig. 9I); gonostylus set apically on gonocoxite, gonostylus length = 5–7× width. spermatheca with insertion point of spermathecal and glandular ducts bulging, not flat, smooth portion at basal end usually gradually transitioning to wider, annulated section, annulations at basal third at oblique angle to margins (Fig. 9J).

**Type locality.** Panama: Panamá Province, Chagres National Park.

**Range.** Currently known from five provinces in central and eastern Panama: Coclé, Colón, Darien, Kula Yala, and Panamá.

**Materials examined.** Holotype (by designation) male of *Pharaxonotha panamensis* with the following labels: 1) [rectangular; white; printed in black ink] "PANAMA, Panama Prov., Chagres Nat. Park, ex ♂ cone *Zamia stevensonii*, l5-XII-Dec 2010, A. Taylor". 2) [rectangular; red; printed in black ink] "HOLOTYPE ♂ *Pharaxonotha panamensis* Tang, Skelley and A.S. Taylor 2024". Deposited in the FSCA.

**Additional paratypes (380).** Allotype (FSCA) and 39 adult paratypes same label data as holotype. **PANAMA: Coclé,** El Valle, 726m asl, Mar-18-2005, A. Taylor #23, *Zamia acuminata* [*Z. nana*], wet, premountain tropical for. (24); El Valle, *Z. nana* ♂ cone, 21-I-2008, W. Tang & A. Taylor (14); **Colón**, 2 km. S Sabanitas, 120 m., II-29-2000, M. Akers, ex. cycad inflorescences (4); Akers-Colón, 100 m asl, Nov.-22-2001, A. Taylor #1, *Zamia pseudomonticola* [cultivated], wet, lowland tropical forest (20); Akers-Colón, 100 m asl, Dec.-5-2001, A. Taylor #23, *Zamia acuminata* [*Z. nana* cultivated], wet, lowland tropical forest (10); Colón, 200 m asl, Dec.-13-2001, A. Taylor #18, *Zamia dressleri,* wet, lowland tropical forest (24); Santa Rita Arriba, ex ♂ cone *Z. dressleri*, A. Taylor, Oct-Nov-2002 (18); Santa Rita Arriba, ex ♂ cone *Z. dressleri*, A. Taylor, Akers gard. by forest, 19Aug 2012 (39); Portobello, Buenaventura, *Z. elegantissima* cone ♂, 25-XII-2010, A. Taylor (20); **Darien**, [locality name omitted] 200 m asl, Jan-26-2004, A. Taylor #8, *Zamia obliqua,* wet, lowland tropical forest (6); **Kuna Yala**, Llano Carti, ex ♂ cone *Z. elegantissima*, A. Taylor, 8-II-2004 (8); 4-2-2007 (14); **Panamá**, Calzada Larga, 125 m asl, [date?], A. Taylor, Vial #26, *Zamia* cf. *elegantissima*, wet, lowland tropical forest (22); Campo Chagres, 100m asl, lowland tropical forest, A. Taylor #16, Feb-2000, *Zamia* cf. *elegantissima* [*Z. stevensonii*] (12); #20, Dec-5-2002, *Zamia acuminata* [*Z. nana*] in population of *Z.* cf. *elegantissima* [*Z. stevensonii*] (7); #11, Nov-3-2004, *Zamia obliqua* in population of *Z.* cf. *elegantissima* [*Z. stevensonii*] (14); #12, Oct-29-2004, *Zamia dressleri* in population of *Z.* cf. *elegantissima* [*Z. stevensonii*] (20); Chagres Nat. Park, ex ♂ cone *Zamia stevensonii*, 19-12-2001, A. Taylor (28); XII-2003 (7); 3-IX-2012 (27); 16-IX-2012 (14); Cerro Azul, 700m asl, Oct-3-2003, A. Taylor #6, *Zamia elegantissima* [*Z. stevensonii*], wet premountain tropical for. (2); Llano Carti Road, ex ♂ cone *Zamia elegantissima*, 8-11-2004, A. Taylor (25); Nov-2,8-2004 (22); #6, *Zamia elegantissima* Llano Carti, 300-400m asl, wet lowland tropical forest, A. Taylor #14, Sept-11-2004, *Zamia dressleri* [bait cone] in population of *Z. cunaria* (20); #27, Oct-16-2004, *Zamia* cf. *elegantissima* [bait cone] in population of *Z. cunaria/Z. elegantissima* (7). Paratypes to be deposited in: ANIC, FSCA, NHMUK, NZAC, RHTC, SEMC, STRI, MIUP, TAMU, USNM.

**Additional specimens examined, but not included in type series: COLOMBIA: Chocó**, Piedra-Piedra (Nuqui), ex: cone *Zamia obliqua*, 3-9-07, C. Lopez Gallego (15 FSCA).

**Etymology.** The adjectival specific epithet refers to the wide distribution of the species in central and eastern Panama.

**Remarks.** *Pharaxonotha panamensis* is placed here in the "recent radiations" of *Pharaxonotha* based on analysis of the 16S rRNA gene (Tang et al. 2018b, 2020). One of its host species, *Z. obliqua*, as currently circumscribed, has a range which extends west into western Panama and east in the Chocó of Colombia. In one dissected female specimen of *P. panamensis* from a Darien population inhabiting *Z. obliqua,* the spermatheca was more elongated than typical for the species, however, this character was not consistent in that population. Genetic analysis using 368 nuclear genes (Salzman et al., unpub.) supports the inclusion of this Darien population within this species, however, those collected from *Z. obliqua* inhabiting Chocó, Colombia appear to belong to another species within the clarkorum species group. The Colombian population is excluded from *P. panamensis*, until more definitive genetic or morphological evidence refutes this. Additionally, any *Pharaxonotha* that may inhabit *Z. obliqua* in western Panama and Costa Rica, must be evaluated before inclusion in this species. Like most members of the confusa species group (with the exception of *P. panamensis* on *Z. nana*) *P. panamensis* co-occurs in the male cones of its hosts with *Notorhopalotria* weevils, namely *N. panamensis* O'Brien and Tang 2015 (O'Brien and Tang 2015).

## Manicatae species group

**Adult diagnosis.** *Pharaxonotha manicatae* is the second smallest member of the genus in Panama, length 2.03–2.31 mm (mean = 2.19 mm, n = 17). Other distinguishing characters include the relatively long pronotum, with pronotal width/pronotal length = (0.77) 0.80–0.88 mm (mean = 0.83 mm, n = 17); spermatheca with the basal third wider than the apical third; and known distribution in eastern Darien province on *Zamia manicata*.

**Remarks.** This is the sole representative of the manicatae species group in Panama. The unique spermatheca shape of this species does not match any in the numerous populations so far surveyed in the recent or Caribbean radiations of *Pharaxonotha* (Franz and Skelley 2008; Skelley and Segalla 2019; Tang unpublished data) and although DNA evidence is not yet available, the group is placed tentatively among the early diverging lineages, where there is a wide diversity of spermatheca morphologies.

### *Pharaxonotha manicatae* Tang, Skelley and Taylor, new species

Figures 10A–J

**Adult diagnosis.** *Pharaxonotha manicatae* is the second smallest member of the genus in Panama, length 2.03–2.31 mm (mean = 2.19 mm, n = 17). Other distinguishing characters include the relatively long pronotum, with pronotal width/pronotal length = (0.77) 0.80–0.88 mm (mean = 0.83 mm, n = 17); and known distribution in eastern Darien province on *Zamia manicata*. Host and thus very likely this beetle extends into neighboring Antioquia and Chocó departments of Colombia.

**Description.** Type series length 2.03–2.31 mm, width 0.74–1.08 mm. Body (Fig. 10A–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. 10D–E), width = 0.76–0.81× 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 0.49–0.56 mm; dorsal interocular distance 0.29–0.33 mm, head width/dorsal interocular distance ratio 1.59–1.83, ventral interocular distance 0.21–0.24 mm, head width/ventral interocular distance ratio 2.27–2.50. 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 0.77–0.88; 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 ⅛ 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. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate, convex; length/width 1.45–1.89, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ elytral length, with 10–15 punctures;

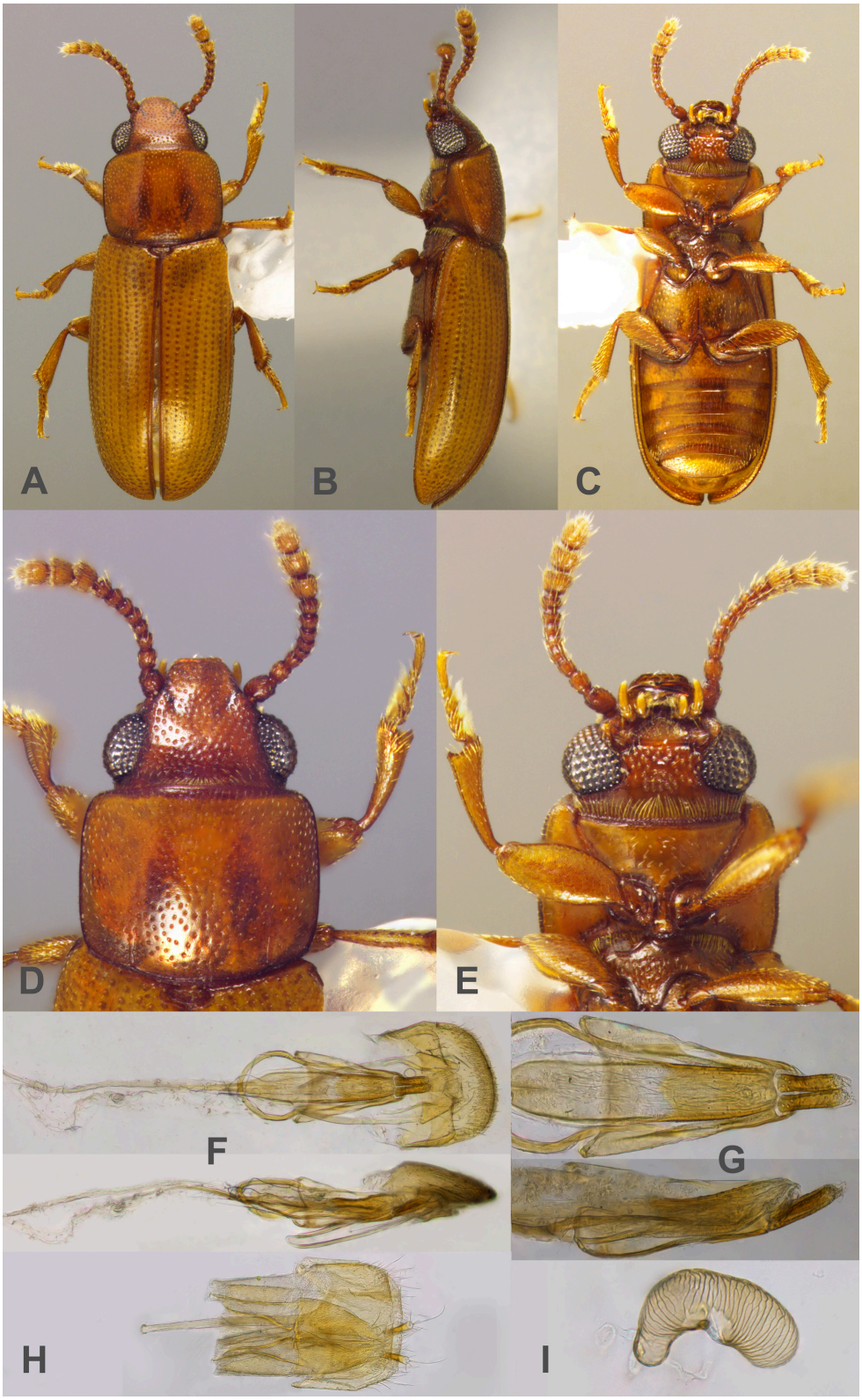


**Figure 10.** *Pharaxonotha manicatae* (A-E: male holotype). **A–C)** Dorsal, lateral and ventral habitus. **D–E)** Head, dorsal and ventral views. **F)** Genital capsule and tegmen attached to median lobe, (top to bottom) ventral and lateral views. **G)** Tegmen attached to median lobe, (top to bottom) ventral and lateral view. **H)** Retracted ovipositor, ventral view. **I)** Spermatheca.

punctures of elytral striae slightly larger than pronotal punctures, striae not impressed; intervals of striae with fine, shallow punctures, ½ size of strial 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. Metaventrite glossy, with weak lateral punctation separated by 4–5× own diameter; medial surface indistinctly punctured; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite 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.** Ventrite 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 = 1) 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. 10F–H).

**Female.** Similar to male, no sexual dimorphism observed. Genital tube elongate, length past abdominal segment VIII = 4× width (n = 1); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width (Fig. 10I). Spermatheca C-shaped, apical third annulated and swollen, length ≈ 3× maximum width of apical third, basal third tapering to rounded base (Fig. 10J).

**Type locality.** Panama: Darien province.

**Range.** Known from easternmost Panama, in Darien Province, in male cones of *Zamia manicata*. The host occurs in the neighboring Antioquia and Chocó departments of Colombia (Stevenson 1993) and this beetle is likely found into these areas as well.

**Materials examined.** Holotype (by designation) male of *Pharaxonotha manicatae* with the following labels: 1) [rectangular; white; printed in black ink] "PANAMA: Darien, ex *Zamia manicata* ♂ cone, April 2016, A. Taylor". 2) [rectangular; red; printed in black ink] "HOLOTYPE ♂ *Pharaxonotha manicatae* Tang, Skelley and A.S. Taylor 2024". Deposited in the FSCA.

**Additional paratypes (20).** Allotype (FSCA) and 19 adult paratypes same data as holotype. Paratypes to be deposited in: FSCA, MIUP, NHMUK, STRI.

**Etymology.** Name based on the host species, *Zamia manicata*; in adjectival form "*manicata-e*", meaning 'of manicata'.

**Remarks.** Based on spermatheca morphology and its elongated pronotum, *Z. manicata* does not fit in any of the other four species groups currently recognized in Panama and is placed in its own species group. Although DNA analysis has not yet been conducted, spermatheca shape does not fit any in the recent radiations found throughout the range of *Pharaxonotha* and this lineage is currently placed among the early diverging lineages. No *Notorhopalotria* weevils have been detected to co-occur with *P. manicatae* in cones of *Z. manicata*, and this *Pharaxonotha* is currently considered to be the sole pollinator in this host.

## Taylori species group

**Adult diagnosis.** *Pharaxonotha taylori* is the smallest member of the genus in Panama, length 1.59–2.08 mm (mean = 1.79 mm, n = 17). 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; spermatheca with basal third much wider than apical third; male terminalia not distinctly dorsoventrally flattened; and known distribution in central Panama on *Zamia cunaria* and *Z. ipetiensis*.

**Remarks.** This is the sole representative of the taylori species group in Panama and analysis of the 16S rRNA gene (Tang et al. 2018b, 2020) places it among the early diverging lineages of *Pharaxonotha* and indicates that a closely

related or conspecific species occurs on *Zamia pyrophylla* in the neighboring Chocó department of Colombia. Analysis of 368 nuclear genes of the populations on *Z. pyrophylla* confirms the placement of this group among the early diverging lineages (Salzman et al. unpublished data).

### *Pharaxonotha taylori* Skelley and Tang

Figures 11A–J (photographs 1A–J in Skelley and Tang 2020)

*Pharaxonotha taylori* Skelley and Tang 2020: 4–7.

**Diagnosis.** *Pharaxonotha taylori* is the smallest known member of the genus, length 1.59–2.08 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.** [Reprinted with minor changes from Skelley and Tang (2020)]. Type series length 1.59–2.08 mm, width 0.60–0.81 mm. Body (Fig. 11A–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. 11D–E), width = 0.78–0.84× 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 0.40–0.51 mm; dorsal interocular distance 0.23–0.29 mm, head width/dorsal interocular distance ratio 1.55–1.91, ventral interocular distance 0.14–0.21 mm, head width/ventral interocular distance ratio 2.37–2.86. 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 0.71–0.81; 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 ⅛ 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. Hypomeron laterally with few minute punctures, medially lacking distinct longitudinal striations. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate, convex; length/width 1.66–1.87, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ¼ 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, ½ size of strial 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. Metaventrite glossy, with weak lateral punctation separated by 4–5× own diameter; medial surface indistinctly punctured; entire surface convex, metathoracic discrimen extending approximately ¾ metaventrite length. Legs narrow,

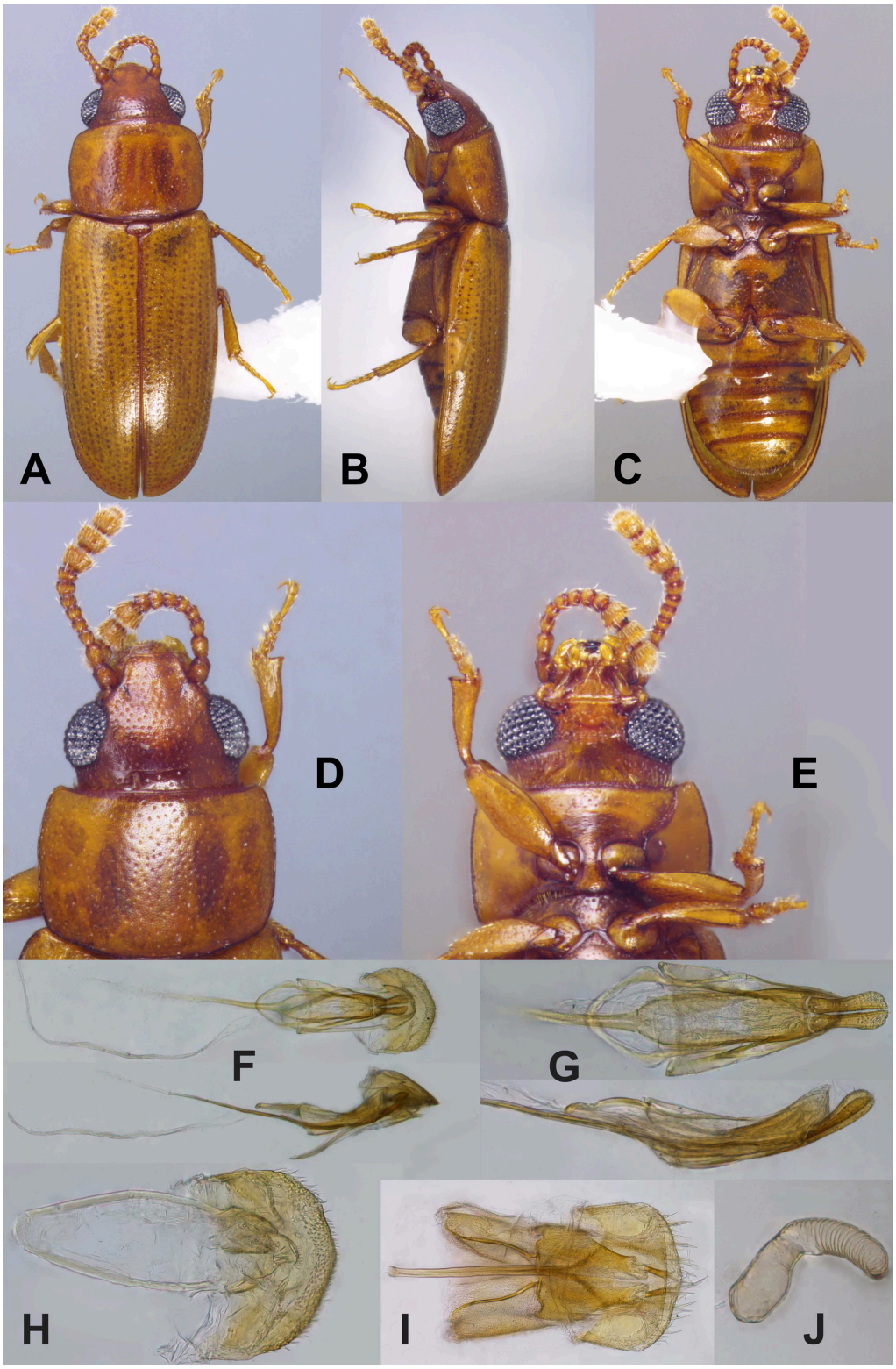


**Figure 11.** *Pharaxonotha taylori.* **A–C)** Dorsal, lateral and ventral habitus. **D–E**) Head, dorsal and ventral views. **F)** Genital capsule and tegmen attached to median lobe, (top to bottom) ventral and lateral views. **G)** Tegmen attached to median lobe, (top to bottom) ventral and lateral views. **H)** Male genital capsule. **I)** Retracted ovipositor, ventral view. **J)** Spermatheca. Images F–J reproduced from Skelley and Tang (2020).

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.** Ventrite 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. 11F–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. 11I). Spermatheca C-shaped, length > 4× width, basal third smooth, slightly swollen and wider than apical third, apex annulated (Fig. 11J).

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

**Materials examined.** There are 62 specimens of the type series of *P. taylori* as reported by Skelley and Tang (2020): **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, 300 m asl (holotype, allotype, 14); same locality, Sept-2-2003, A. Taylor, #25, *Zamia ipetiensis* in population of *Z. cunaria*, wet, lowland tropical forest (11); same locality, 300-400 m asl, Sept-2-2003, A. Taylor, #5; *Zamia ipetiensis* in population of *Z. cunaria*, wet, lowland tropical forest (9); same locality, ♂ bait cone *Zamia ipetiensis* (*Z. cunaria* habitat), 26-VIII-2011, A. Taylor (21); 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). Repositories are reported in Skelley and Tang (2020). 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: Chocó**, 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".

**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 (Stevenson 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 the beetles from these two host *Zamia* were treated by Skelley and Tang (2020) 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. These Colombian beetles are treated as a potentially separate species from *P. taylori* and were exclude them from the type series (Skelley and Tang 2020). No *Notorhopalotria* weevils have been detected to co-occur with *P. taylori* and this *Pharaxonotha* is currently considered to be the sole pollinator in its hosts.

## Kirschii species group

**Adult diagnosis.** The kirschii species group can be distinguished from other *Pharaxonotha* by a more robust head that has a temple behind the eye, and male with a small tooth or denticle at apex of terminal abdominal ventrite.

**Remarks.** This species group was established by Skelley et al. (2022) based on analysis of the 16S rRNA gene of two populations that are part of the early diverging lineages in Tang et al. (2018b, 2020). Although no representatives of this group were detected on *Zamia* in Panama during this study, members of this group have been collected from cones of *Ceratozamia*, *Dioon* and *Zamia* in Mexico and *P. kirschii* is known to occur in Panama (see Skelley et al. 2022 and Materials examined under *P. kirschii* below). Members of this group likely represent a complex of species. Further work is needed on both the cycad associated and the free-living populations.

### *Pharaxonotha kirschii* Reitter

Figures 12A–L

*Pharaxonotha kirschii* Reitter 1875: 44 ~ Sharp 1900: 598; Chittenden 1911: 8–13; Hinton 1945: 189–192; Pakaluk 1988: 450; Skelley et al. 2022: 33–39.
*Pharaxonotha kirschi* ~ emendation of various authors.
*Thallisella condradti* Gorham 1898: 249 ~ Champion 1904: 36 [synonymy].

**Diagnosis.** A member of the kirschii group, this species is diagnosed by the uniformly dark coloration of both sexes. an enlarged antennomere XI compared to IX, the lateral pronotal marginal bead of many is weakly angulate near the middle, and the male abdominal ventrite apical tooth is more pronounced. *Pharaxonotha kirschii* is widespread from the southern US to Panama, is not associated with cycads. It is a known as the "Mexican grain beetle", a pest in stored plant products which has been intercepted in many countries.

**Description.** [Reprinted with some modification from Skelley et al. (2022)]. Length 3.37–4.11 mm, width 1.22–1.56 mm. General body color (Fig. 12A–C) dark brown to black. Dorsal surface glossy, with very short setae in puncture.

**Head.** Not broad, width = 0.62–0.67× pronotal width (Fig. 12D–F); in lateral view robust, clypeus to base of head dorsally convex; in dorsal view conical, gradually narrowed anteriorly, surface convex, coarsely punctured, average distance between closest punctures 2–3× width of puncture; head width 0.72–0.86 mm; dorsal interocular distance 0.51–0.60 mm, head width/dorsal interocular distance ratio 1.36–1.42, ventral interocular distance 0.41–0.51 mm, head width/ventral interocular distance ratio 1.68–1.79. Eye with large black facets, similar diameter of head punctures; head posterior of eye with a small tooth (temple) in dorsal profile. Antennal length slightly shorter than pronotal width, 1.4× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II same length as III; IV circular; V–VII same length as IV, gradually becoming wider with VIII weakly transverse and flattened apically; club fairly large, IX and X similar in length; XI enlarged, 1.5× longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] distinct nearly from eye to eye. Mentum and submentum coarsely punctured, ½–¾× diameter of facet, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. Gular area smooth, without punctation or setae, border with submentum marked by change in punctation.

**Thorax.** With pronotum transversely rectangular in dorsal view, length/width ratio 0.69–0.80; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles sharply rounded, projecting forward; posterior angles developed, with small denticle at angle; lateral margin weakly angulate 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 ¼ width from posterior angles, each pore marks base of a distinct sulcus extending anteriorly onto disc ¼ 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 ⅓ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few punctures. Scutellar shield distinctly transverse pentagonal, posterior margin weakly rounded. Elytra in dorsal view elongate, flattened dorsally; length/width 1.72–1.90, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striole extending ⅕ elytral length, with 7–10 punctures; punctures of elytral striae 2× larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, indistinct shallow punctures, ⅕ size of strial punctures; all punctures of elytral bearing a single very short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with

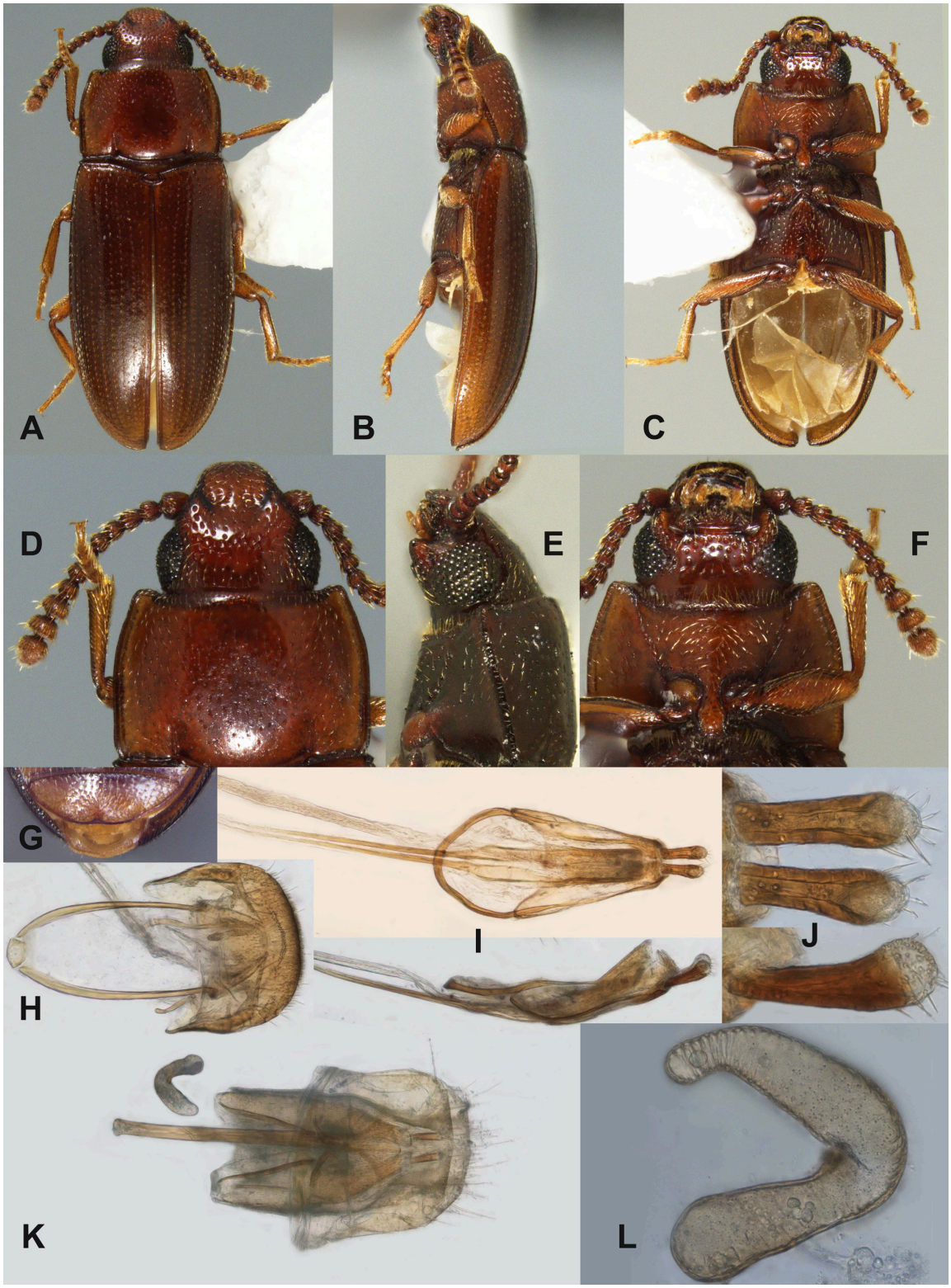


**Figure 12.** *Pharaxonotha kirschii* from Costa Rica, Guanacaste Province (A–J: male). **A–C)** Dorsal, lateral and ventral habitus. **D–F)** Head, dorsal, lateral and ventral views. **G**) Terminal segment of male abdomen. **H)** Genital capsule. **I)** Tegmen attached to median lobe, (top to bottom) ventral and lateral views. **J)** Parameres of tegmen, (top to bottom) ventral and lateral views. **K)** Retracted ovipositor with spermatheca, ventral view. **L)** Spermatheca.

strong lateral punctation separated by 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrimen extending approximately ½ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora narrowly oblong, compressed laterally; tibiae shorter than femora, weakly dilated to obliquely truncate apices; 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× 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 ventrite 5 with distinct denticle at apex. Male genitalia (n = 4) similar to all others in the genus with widened tegmen, elongate cylindrical median lobe, and long coiled flagellum (Fig. 12G–J).

**Female.** Similar to male. Female differs with narrow protibia and protarsus, male have weakly dilated protibia and basal protarsomeres. Female lacking apical denticle on terminal abdominal ventrite. Genital tube shortened, length past abdominal segment VIII = 1.5× width (n = 5); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width (Fig. 12K). Spermatheca base asymmetrically rounded with curvature extending further on ventral side, basal third broadest at basal end, narrowing until unsclerotized arc at central third, apical third usually narrowing apically and usually curving abruptly near apex to a broadly rounded point (Fig. 12L).

**Materials examined.** The present location of the type(s) is unknown (not examined). The types of *Thallisella condradti* was collected in Vera Paz, Guatemala (Gorham 1898), present location of type material is the NHMUK (examined) (Skelley et al. 2022).

**Additional materials examined (641).** Data for all materials studied of *P. kirschii* are presented in Skelley et al. (2022). For Panama, we studied eight specimens here considered to be *P. kirschii*: **PANAMA:** Canal Zone, 12-V-1952, F. S. Blanton, at light (1 USNM); **Chiriquí:** Chiriquicito, 18-V-1996, R. Turnbow, mv + bl (1 RHTC); **Coclé:** 5.6 km. N. Pan Amer. Hwy, El Copé Rd, 08°37′N, 80°35′W, 7-VI-1995, J. Ashe, R. Brooks, #141 ex slash (2 SEMC); **Panama:** 11-15 km. N. El Llano, 13-V-1991, R. Turnbow (1 RHTC); Fort Kobbe, 27-V-1965 (1 USNM); same locality, 12-V-1985, A. J. Gilbert, P. H. Sullivan, and F. T. Hovore (1 FSCA); same locality, 23-V-1991, R. Turnbow, mv + bl (1 RHTC).

**Remarks.** Based on the volume of data for *P. kirschii* discussed in Skelley et al. (2022), it appears to be a more free-living species, occurring more commonly in leaf litter in the wild in many areas where there are no native or ornamental cycads. It is possible that cryptic species reside within the materials considered *P. kirschii*. We leave their analysis for future work when molecular grade materials are available for study.

*Pharaxonotha kirschii* was described from specimens collected in eastern Europe from Mexican plant products. Since then, it has been intercepted in many countries and mentioned many times in regional lists, regional reports, taxonomic catalogues, phylogenetic studies, keys to taxa, natural history accounts, etc., and now a growing number of websites. As the "Mexican grain beetle", *P. kirschii* has been discussed in references including Chittenden (1895, 1911), Hinton (1945), Anderson (1987), Kingsolver (1987), Booth et al. (1990), and Lawrence (1991) and many others. For a further discussion of the natural and taxonomic history of this species and recently described, closely related species see Skelley et al. (2022).

# Discussion

Geographic reconstructions of Panama and nearby lands of Costa Rica and Colombia during the last 10 million years (Coates 1997; Pindell and Kennan 2009) indicate a shifting mosaic of islands rising from the ocean with repeatedly changing connections to larger landmasses to the south and north. Genetic analysis of *Zamia* throughout its range (Calonje et al. 2019) points to a history of rapid diversification in Panama within this geographic scenario, with contributions from a radiation within Central America as well as one from South America and isolation within islands likely contributing to this speciation process in *Zamia*. Given this geographic history and pattern of evolution in the host genus, some questions about *Zamia-Pharaxonotha* coevolution can be addressed

based on the taxonomic conclusions of this paper: 1) is there a one to one correspondence of each *Zamia* species with a unique *Pharaxonotha* species; 2) what are some situations conducive to the pairing of a unique *Pharaxonotha* with a unique *Zamia*; and 3) alternatively, what are likely situations where a species of *Pharaxonotha* occurs on multiple hosts? Answer 1: with only nine species of *Pharaxonotha* detected and 17 host *Zamia* species, the answer to this question is clearly no strict one-to-one correspondence of each beetle to a particular host in all situations. Answer 2: in this paper we present three examples where a *Pharaxonotha* species is found only on a single host *Zamia* species. Two of these are situations with some form of habitat isolation and likely restricted gene flow. For example, the high altitude *Z. lindleyi* and epiphytic *Z. pseudoparasitica* likely subject their cone beetles to genetic isolation via the island effect of tropical mountain tops (Merckx et al. 2015) or habitat isolation offered by a canopy niche versus a forest floor niche (Sutton et al. 1983; Basset et al. 1992; Wolda et al. 1998; Cruz-Angón et al. 2009). Answer 3: there are at least five examples of *Pharaxonotha* that are found on multiple hosts. One example is *P. confusa* in southwestern Panama on *Z. fairchildiana* and *Z. pseudomonticola*, two closely related host species with contiguous distributions that apparently offer no barriers to gene flow in their shared *Pharaxonotha*. A second example of a shared *Pharaxonotha* is *P. panamensis* on *Z. dressleri*, *Z. elegantissima*, *Z. nana*, *Z. obliqua* and *Z. stevensonii*, five hosts that exhibit strikingly different leaf morphologies. The close geographic proximity of these hosts in central Panama would suggest few barriers to dispersal of beetles among these hosts in the recent past. Choice experiments with cones of *Z. obliqua, Z. pseudomonticola* and *Z. stevensonii* in *Z. dressleri* habitat have shown that the *Pharaxonotha* that lives in *Z. dressleri* habitat will congregate on cones of all these species, indicating similar attraction of this species of beetle on all these *Zamia* and the absence of any visitation barriers (Terry et al. 2012). A second cone visitor, the weevil *Notorhopalotria panamensis,* is also shared by four of the same natural hosts as *P. panamensis* (O'Brien and Tang 2015; Tang, unpublished data), giving a second example in the same hosts of how close proximity in this host group allows the sharing of the same cone insect. A third example of shared *Pharaxonotha* is *P. holzmani* on *Z. imperialis* and *Z. skinneri*. These two hosts have wide ranges with potential geographic overlap offering the possibility of beetle movement between them and the interbreeding of their beetle populations. There is one exception to this pattern of close host proximity leading to the sharing of cone beetle visitors; *Zamia cunaria* is sympatric with *Z. elegantissima*, often occurring side by side in the same habitat (Chemnick and Hoese 2008), however, no sharing of pollinators has been detected. A likely explanation is that the *Pharaxonotha* inhabiting *Z. cunaria, P. taylori*, is an early diverging lineage of the group (Tang et al. 2018b, 2020) with some pronounced differences in external morphology and genitalia and it probably responds to different attractants or chemical cues. Clearly, *Zamia* and *Pharaxonotha* do not exhibit exact parallel evolution, with pattern of radiation in *Pharaxonotha*, to some extent, occurring independently from the pattern of radiation in their host cycads. The examples above indicate how evolution of hosts and evolution of symbionts may have responded differently to the geologic events that shaped the land mass we know today as Panama.

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