Review of *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting the cycad genus *Dioon* Lindl. (Cycadales), with descriptions of nine new species and comments on *P. kirschii* Reitter

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Robert E. Woodruff Festschrift Contribution  
Date of issue: February 24, 2022

Center for Systematic Entomology, Inc., Gainesville, FL

Published on February 24, 2022 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
http://centerforsystematicentomology.org/

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Review of *Pharaxonotha* Reitter (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting the cycad genus *Dioon* Lindl. (Cycadales), with descriptions of nine new species and comments on *P. kirschii* Reitter

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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 *Dioon* Lindl., *Ceratozamia* Brongn., *Microcycas* (Miq.) A.DC and *Zamia* L. In this paper nine new species found in *Dioon* are described by Skelley, Tang and Pérez-Farrera: *Pharaxonotha* bicolor, *P. dimorpha*, *P. fawcettae*, *P. gigantea*, *P. novoai*, *P. occidentalis*, *P. sclerotiza*, *P. woodruffi*, *P. vovidesi*. A key to described species of *Pharaxonotha* inhabiting *Dioon* is presented, along with an account of *Pharaxonotha kirschii* Reitter for comparison.

**Key words.** Cycad, cone, pollination, Mexico, Mexican grain beetle.

**ZooBank registration.** urn:lsid:zoobank.org:pub:B5B5333E-3467-473F-BFA9-5E5C1CFAC1DA

**Introduction**

The New World beetle genus *Pharaxonotha* Reitter (Erotylidae: Pharaxonothinae) has a close association with cycads (Cycadales), an ancient lineage of gymnosperms (Norstog and Nichols 1997). Except for the type species of *Pharaxonotha*, *P. kirschii* Reitter, which is a minor stored products pest, all other species of the genus that have been described are inhabitants of cycad cones (Pakaluk 1988; Chaves and Genaro 2005; Franz and Skelley 2008; Xu et al. 2015; Skelley et al. 2017; Santiago-Jiménez et al. 2019; Skelley and Segalla 2019; Skelley and Tang 2020). In the New World, almost all cycad populations studied have an associated species or two of *Pharaxonotha*, ranging from the southern US and Caribbean to Bolivia and Brazil. Exclusion experiments on the cycad genus *Zamia* L. indicate that they are pollinators (Tang 1987; Valencia-Montoya et al. 2017; Segalla et al. 2021).

As part of a series of papers describing species on New World cycads, here we describe nine species of *Pharaxonotha* inhabiting cones of the cycad genus *Dioon* Lindl. Although Vovides (1991) and Navarrete-Heredia (2018) reported on the presence of *Pharaxonotha* in *Dioon* cones, this is the first paper to our knowledge, where species inhabiting *Dioon* have been scientifically described. To aid with their identification, an addendum to the
key of Skelley and Tang (2020) for species of Pharaxonotha found on Dioon is presented herein. Additional species of Pharaxonotha occurring with other genera will be the subjects of future papers.

**Material and Methods**

*Pharaxonotha* beetles are available in wild populations of the New World cycad genera, *Ceratozamia* Brongn., *Dioon*, *Microcycas* (Miq.) A.DC. and *Zamia* during the rapid elongation and pollen shedding phase of male cones (Pakaluk 1988; Tang 1987; Tang et al. 2018a, 2020; Chaves and Genaro 2005; Franz and Skelley 2008; Skelley and Tang 2020). Typically, this is a brief window that lasts about one month (Griffith et al. 2012). Therefore, they are rarely collected, and most museum collections have no representatives. The specimens studied are from recent expeditions. To be complete, an account of *Pharaxonotha kirschii* is presented for comparison with other members of the genus and to be available for future studies.

**Materials studied.** When found on a pollinating cone, members of these species are often present in large numbers. Data reported are for specimens cited herein, which will be deposited in the following institutional collections:

- **ANIC** Australia, Australian Capital Territory, Canberra City, CSIRO, Australian National Insect Collection
- **CMNC** Canada, Ottawa, Canadian Museum of Nature
- **CNCI** Canada, Ontario, Ottawa, Canadian National Collection of Insects
- **CSCA** USA, California, Sacramento, California State Collection of Arthropods
- **CUIC** USA, New York, Ithaca, Cornell University
- **CZUG** Mexico, Jalisco, Guadalajara, Universidad de Guadalajara, Centro de Estudios en Zoología, Entomología
- **FMNH** USA, Illinois, Chicago, Field Museum of Natural History
- **FSCA** USA, Florida, Gainesville, Division of Plant Industry, Florida State Collection of Arthropods
- **IEXA** Mexico, Veracruz, Xalapa, Instituto de Ecología
- **MTEC** USA, Montana, Bozeman, Montana State University
- **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, Lawrence, University of Kansas, Snow Entomological Museum
- **UAQM** Mexico, Querétaro, Querétaro, Universidad Autónoma de Querétaro
- **UNAM** Mexico, México D.F., Universidad Nacional Autónoma de México
- **UNSM** USA, Nebraska, Lincoln, University of Nebraska State Museum
- **USNM** USA, Washington D.C., National Museum of Natural History

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

The FSCA is the repository for holotypes, allotypes, a series of paratypes and non-paratypes from each locality of the new species. Paratypes and non-paratypes of collecting events with large numbers will have specimens distributed to the above listed institutions as indicated in the Material examined sections. Because of the voluminous data available for *P. kirschii*, which is rarely collected in large series, individual label data are followed with a parenthetic statement of the number of specimens and the repository for those data.

**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), with genitalic terminology...
Review of *Pharaxonotha* inhabiting the cycad genus *Dioon*

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following McHugh et al. (1997). Spermatheca terminology is illustrated in Figure 2G. Beetles were collected from wild populations and preserved in 75–95% ethanol. Specimen dissection techniques followed that of Hanley and Ashe (2003). Photographs were taken with a Nikon DS-Fi2 camera attached to either a NIKON SMZ-1500 dissecting microscope or NIKON Eclipse 80i compound scope. All pictures are composites produced by taking a series of photographs of each specimen at different levels of focus and integrating them into one picture using the software program Helicon Focus®. Measurements were taken with a calibrated ocular micrometer in a Leica MS5 Stereomicroscope.

Abbreviations used throughout the keys and text include:

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>DI</td>
<td>Dorsal interocular distance</td>
</tr>
<tr>
<td>EL</td>
<td>Elytral length</td>
</tr>
<tr>
<td>EW</td>
<td>Elytral width</td>
</tr>
<tr>
<td>EL/EW</td>
<td>Ratio of elytral length to width</td>
</tr>
<tr>
<td>HW</td>
<td>Head width</td>
</tr>
<tr>
<td>HW/DI</td>
<td>Ratio of head width to dorsal interocular distance</td>
</tr>
<tr>
<td>HW/VI</td>
<td>Ratio of head width to ventral interocular distance</td>
</tr>
<tr>
<td>PL</td>
<td>Pronotal length</td>
</tr>
<tr>
<td>PW</td>
<td>Pronotal width</td>
</tr>
<tr>
<td>PL/PW</td>
<td>Ratio of pronotum length to width</td>
</tr>
<tr>
<td>VI</td>
<td>Ventral interocular distance</td>
</tr>
</tbody>
</table>

**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 more undescribed species than are presently described (Tang et al. 2018b, 2020). Regional faunas and/or reviews of those species inhabiting the cycad genera *Ceratozamia* and *Zamia* are currently in progress and will be published elsewhere.

Some species have all specimens studied designated as paratypes. In three cases, we restrict paratype designation to a single population or local region because of our concern there may be cryptic species residing in these materials. For these species, the type series has many paratypes which will be dispersed to many institutions for reference by future workers.

**Results**

Within the genus *Pharaxonotha* these groups of species inhabiting *Dioon* are recognized here based on morphological analyses provided below and supported with analyses of the 16S rRNA gene in Tang et al. (2018b, 2020).

*Pharaxonotha* Reitter on *Dioon*

**bicolor species group**

*P. bicolor* Skelley, Tang and Pérez-Farrera, **new species**

**vovidesi species group**

*P. fawcettae* Skelley, Tang and Pérez-Farrera, **new species**

*P. vovidesi* Skelley, Tang and Pérez-Farrera, **new species**

**occidentalis species group**

*P. gigantea* Skelley, Tang and Pérez-Farrera, **new species**

*P. novoa* Skelley, Tang and Pérez-Farrera, **new species**

*P. occidentalis* Skelley, Tang and Pérez-Farrera, **new species**

*P. woodruffi* Skelley, Tang and Pérez-Farrera, **new species**

**kirschii species group**

*P. dimorpha* Skelley, Tang and Pérez-Farrera, **new species**

*P. sclerotiza* Skelley, Tang and Pérez-Farrera, **new species**
Pharaxonotha Reitter


**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; stridulatory files at base of head separated by distance approximately equal to width of scutellar shield; anterior pronotal margin lacking or with very fine marginal line; lateral pronotal carina narrow, same thickness along entire length; elytra with basal bead; internal abdominal calli absent; male genitalia straight, not twisted, median lobe and tegmen rotated 180 degrees when retracted into the abdomen [see Fig. 10G and Tang et al. 2020 for examples; 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]; median lobe cylindrical; flagellum long hair-like; tegmen flattened or not flattened, basal piece broadened and ring-like to hold coiled flagellum. Known distribution includes the Caribbean Basin from Florida and Bahamas to Greater Antillean islands of the Cayman Islands, Cuba, Jamaica, Hispaniola and Puerto Rico; mainland from southern US and Mexico to South America as far south as Bolivia.

**Key to species of Pharaxonotha Reitter on Dioon**

1. Head in lateral view robust, thick, prominent ventrally, convex dorsally (Fig. 1A); post-ocular ridge present (temple), small, tooth-like in dorsal view (Fig. 1A, 2A); male with small tooth or denticle at apex of last abdominal ventrite (Fig. 2D); body strongly glossy, robust, dark red-brown to black; southern US to Central America, occasionally associated with cycads [kirschii group] ........................................ 2

2. — Head in lateral view narrowed, more flattened anteriorly, not prominent ventrally, flattened dorsally and ventrally (Fig. 1B–D); post-ocular ridge indistinct, mostly lacking (Fig. 2B–C); male lacking modified last abdominal ventrite; body weakly glossy to distinctly dulled, flattened, red-brown to yellow-brown, rarely dark brown to black; widespread in the Neotropics, associated with cycad cones ................................................................................................................................. 4

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2(1). Antennomere XI visibly larger, more robust than the small antennomere IX (Fig. 2E); body of most dark-brown to nearly black; male with distinct denticle on last abdominal ventrite; USA (Texas, Louisiana) to Panama in nature, Europe and elsewhere in plant products, free living .......................... \textit{P. kirschii} Reitter

— Antennomere XI visible smaller than the robust antennomere IX (Fig. 2F); body of most red-brown, rarely black; male with indistinct denticle on last abdominal ventrite; Mexico, associated with cycads ........................................... 3

3(2). On female, fuscous spot on elytra covering < ½ area of elytra (Fig. 11A); spermatheca apex gradually curving to a rounded point; male paramere width in lateral view > 3.4× own length (Fig. 11I); inhabiting the Dioon angustifolium Miq. complex in Tamaulipas, Mexico ........................ \textit{P. sclerotiza}, \textbf{new species}

— On female, fuscous spot on elytra covering > ¾ area of elytra (Fig. 10A); spermatheca apex abruptly curving to a truncated point; male paramere width in lateral view < 3.4× own length (Fig. 10J); inhabiting Dioon edule Lindl. in Veracruz, Mexico .................. \textit{P. dimorpha}, \textbf{new species}

4(1). Dorsally, hairs emerging from punctures visible under low magnification (< 30×), procumbent, length nearly equaling or exceeding distance to nearest puncture; inhabiting Dioon spp. in Mexico .......................... 5

— Dorsally, body appearing glabrous under low magnification (< 30×) or, when visible, length of hairs associated with punctures distinctly less than distance to nearest puncture; inhabiting Zamia spp., Ceratozamia spp., and Microcycas sp. from Florida and the Caribbean, and Mexico south to Bolivia .......................... \textbf{Go to couplet 2 in Skelley and Tang (2020)}

5(4). Eyes small, finely facetted, 3–4 facets = length of antennomere II (Fig. 1B); eyes widely separated, head width/dorsal interocular distance (HW/DI) = 1.33–1.44 (1.54); head width/ventral interocular distance (HW/VI) < 1.73; anterior pronotal angles broadly rounded, not projecting forward beyond anterior margin; body alutaceous, strongly dulled, some populations bicolored with elytra black to dark brown and contrasting with orange-brown pronotum; inhabiting Dioon califanoi De Luca & Sabato, Dioon caputoi De Luca & Sabato, Dioon purpusii Rose in northern Oaxaca and Puebla [biclor group] .......................... \textit{P. bicolor}, \textbf{new species}

— Eyes larger, encroaching on frons and gular region, coarsely facetted, 2–3 facets = length of antennomere II (Fig. 1C–D); eyes more narrowly separated, HW/DI = 1.48–1.72; HW/VI > 1.92; anterior pronotal angles sharply rounded, projecting forward beyond anterior margin; body weakly dulled, uniformly orange-brown to yellow-brown or pronotum slightly darker than elytra .......................... \textit{P. gigantea}, \textbf{new species}

6(5). Body large, length > 4.7 mm; pronotal punctures large, impressed, sharply defined (Fig. 6D); inhabiting Dioon stevensonii Nic.-Mor. & Vovides in Guerrero, Mexico [occidentalis group, in part] .......................... \textit{P. holmgrenii} De Luca & Sabato, Dioon caputoi De Luca & Sabato, Dioon purpusii Rose in northern Oaxaca and Puebla [biclor group] .......................... \textit{P. gigantea}, \textbf{new species}

— Body smaller, length < 4.5 mm; pronotal punctures small, not sharply defined; inhabiting other species of Dioon in other Mexican states .......................... \textit{P. gigantea}, \textbf{new species}

7(6). Head more flattened between eyes, in lateral view hardly visible above and below eyes (Fig. 1C); transverse occipital line [vertexal line] absent, with row of punctures that may appear as line (Fig. 2B); male protarsus and metatibia distinctly more swollen than female; male meso- and metatibia median margin slightly concave with small inwardly directed tooth at apex; inhabiting Pacific drainage in Jalisco, Oaxaca and Chiapas or in northeastern Oaxaca [occidentalis group, part] .......................... \textit{P. dimorpha}, \textbf{new species}

— Head convex between eyes, in lateral view readily visible above and below eyes (Fig. 1D); transverse occipital line [vertexal line] present (Fig. 2C); male protarsus and metatibia weakly swollen compared with female; male meso- and metatibia median margin straight to weakly convex and lacking tooth at apex; inhabiting Atlantic drainage in Hidalgo, Nuevo Leon, Querétaro, San Luis Potosí, Tamaulipas and northern Veracruz [vovidesi group] .......................... \textit{P. gigantea}, \textbf{new species}

8(7). Posterior lateral margin of eye with small distinct fringe of setae separated from facets (Fig. 2B), best visible from dorsal profile; pronotal length/elytral length (PL/EL) = 0.27–0.33; male tegmen with parameres in dorsal view with pronounced bulge on outer margin; inhabiting Dioon holmgrenii De
Luca, Sabato & Vázq. Torres, Dioon merolae De Luca, Sabato & Vázq. Torres, Dioon tomasellii De Luca, Sabato & Vázq. Torres in Chiapas, Jalisco and western and southern Oaxaca .......................... 9

— Posterior lateral margin of eye without distinct fringe of setae; (PL/EL) = 0.32–0.37; male tegmen with parameres in dorsal view with margins nearly straight; inhabiting Dioon spinulosum Dyer ex Eichler in northeastern Oaxaca .................................................. P. woodruffi, new species

9(8). Elytral setae fine, short, reaching next puncture in length (Fig. 8A–B); HW/DI = 1.54–1.67, HW/VI = 1.92–2.44; inhabiting Dioon holmgrenii and Dioon merolae in western Oaxaca and Chiapas .......................... P. occidentalis, new species

— Elytral setae prominent, long, surpassing next puncture in length (Fig. 7A–B); HW/DI = 1.69–1.72, HW/VI = 2.64–2.82; inhabiting Dioon tomasellii in Jalisco ......................... P. novoai, new species

10(7). Head with transverse occipital line [vertexal line] long laterally in most, most with line surpassing half distance between stridulatory file and eye, often curving anteriorly near eye; mean pronotal length/width (PL/PW) = 0.69–0.70 (multiple specimens required); in females spermatheca elongate, ratio of spermatheca length to width at basal third > 4.5, base not abruptly swollen (see Fig. 2G); inhabiting the Dioon angustifolium complex north of the Mexican Transvolcanic Belt in Hidalgo, Nuevo Leon, Querétaro, San Luis Potosi and Tamaulipas .......................... P. fawcettae, new species

— Head with transverse occipital line [vertexal line] short laterally in most, most with line stopping about half distance between stridulatory file and eye, not curving anteriorly; mean PL/PW = 0.71–0.74 (multiple specimens required); in females spermatheca short and compact, ratio of spermatheca length to width at basal third < 3.5, base abruptly swollen, swelling often quadrate-shaped; inhabiting Dioon edule south of the Mexican Transvolcanic Belt in Veracruz .... P. vovidesi, new species

Taxonomic accounts

Bicolor species group

Adult diagnosis. This is the only known group of Pharaxonotha where adults have an elytral color that contrasts distinctly with the pronotum and the rest of the body. In this group the elytra are usually completely black to dark brown, contrasting with the completely orange-brown pronotum, head and ventral surfaces. In teneral specimens and some apparently fully sclerotized adults, elytra and pronotum may be concolorous light brown, however, punctures of the elytra usually retain their dark coloration. In all other known species of Pharaxonotha the elytra and pronotum share similar coloration, with the pronotum sometimes slightly darker than the elytra. As in most Pharaxonotha inhabiting Dioon, the dorsal surface of the head, pronotum and elytra have long setae emerging from punctures, with setal length reaching or exceeding the distance to nearest puncture. The bicolor species group can also be distinguished from Pharaxonotha inhabiting other Dioon species by their small eyes and relatively large interocular distances, with the four populations examined exhibiting mean dorsal head width/interocular distance/ (HW/DI) = 1.39 [range = 1.33–1.44 (1.54)] and mean ventral interocular distance/head width (HW/VI) = 1.56–1.59 (range = 1.47–1.69). Other Pharaxonotha inhabiting Dioon, described in this paper, have mean HW/DI = 1.47–1.69 (range = 1.47–1.72) and mean HW/VI = 1.69–2.78 (range = 1.67–2.86).

Remarks. Analysis of the 16S rRNA gene places this group among the recent radiation of Pharaxonotha as described by Tang et al. (2018b, 2020) and also indicates that three of the four known populations are conspecific. Materials of P. bicolor analyzed by Tang et al. (2018b: 8, fig.4; 2020: 18, fig. 3) are presented in their trees labeled as follows: "D0235 Santa Catarina, Oax. D. purpusii"; "D0238 Coatepec, Puebla, D. caputoi"; "D0243 Teotitlan, Puebla, D. califanoi". The fourth population falls within the morphological variation of the other three and these are all placed within a single species. As currently known this group is restricted to northern Oaxaca and adjacent southern Puebla on Dioon califanoi, D. caputoi and D. purpusii, however, other possible hosts in this region include D. argenteum T.I.Greg., Chemnick, Salas-Mor. & Vovides and D. planifolium Salas-Mor., Chemnick & T.I.Greg which may harbor this or additional species. Dissected adult specimens usually have the gut packed with the distinctive monosulcate pollen grains of cycads, indicating that this is a major food source.
**Pharaxonotha bicolor** Skelley, Tang and Pérez-Farrera, new species
Figures 1B, 3A–K, illustration 1D in Vovides (1991)

**Diagnosis.** *Pharaxonotha bicolor* is easily distinguished from all members of the genus by the distinct long elytral setation, elytral surface dulled with striae weakly impressed; pronotal anterolateral angles not projecting forward, broadly rounded in dorsal and lateral view; eyes small, not or barely encroaching the gula or frons, HW/DI < 1.45 and HW/VI < 1.73; protibia narrow to apex; and with a known distribution in Mexico [Oaxaca, Puebla] on *Dioon califanoi, D. caputoi* and *D. purpusii*.

**Description.** Type series length 2.72–3.97 mm, width 1.07–1.63 mm. General body color (Fig. 3A–C) orange-brown, elytra usually black to dark brown; dorsal surface punctate, alutaceous, shining, procumbent hairs associated with punctation on pronotum and elytra, hair length reaching or exceeding nearest punction; ventrally shining.

**Head.** Not broad (Fig. 3D–F), width = 0.66–0.75× 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 0.62–0.78 mm; dorsal interocular distance 0.45–0.58 mm, head width/dorsal interocular distance ratio 1.33–1.44 (1.54), ventral interocular distance 0.40–0.51 mm, head width/ventral interocular distance ratio 1.48–1.72. Eye small, finely facetted, 3–4 facets = length of antennomere II; facets about 3× diameter of head punctures. Antennal length slightly shorter than pronotal width, 2× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV circular; IV–VIII small, width slightly less than length, gradually widening to a nearly circular VIII; club fairly large, IX and X similar in length; XI not enlarged, slightly longer than X, width ¾ length, globular with acuminete apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] distinct medially, absent laterally. Mentum and submentum moderately punctured, half diameter of facet, distance between nearest punctures approximately 1× own diameter, each puncture with a long seta. 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 rectangular in dorsal view, length/width ratio 0.68–0.76; with distinct marginal carina laterally and basally, anteriorly lacking marginal carina; surface convex; anterior angles broadly rounded in dorsal and lateral view, not projecting forward; posterior angles weakly developed, with small denticle at angle; lateral margin medially parallel-sided or converging slightly posteriorly, evenly shallowly arcuate basally, broadly inwardly arcuate anteriorly; 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 ½ length of eye; prosternal process convex apically, expanded and truncate at apex. Hypomeron laterally with indistinct seta bearing punctures, medially with few longitudinal striations. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal. Elytra in dorsal view elongate-oval, convex; length/width 1.66–1.89, greatest width near midlength; with distinct marginal line basally; 8 complete striae of moderate puncture size, striae IV–X hidden in alutaceous surface; scutellary stria almost length, with 10–15 punctures; punctures of elytral striae slightly larger than pronotal punctures, striae visibly impressed; intervals of striae with fine, shallow punctures, ½ size of striae; all punctures of elytra bearing a single prominent long seta, extending past next puncture in series. Mesoventrite with strong punctation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite weakly glossy, with moderate lateral punctation separated by 2–3× own diameter; medial surface finely punctured, separated by 5–6× own diameter; entire surface convex, metathoracic discrimin 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 narrowly robust, moderately compressed laterally; tibiae shorter than femora, parallel-sided to obliquely truncate apices; protibia with apical lateral tooth small, with apical fringe of (~5–6) long stout spinules on concave ventral apical margin continuous to lateral tooth; meso- and metatibia with apical fringe of long spinules on anterior and posterior margins.
Abdomen. Ventrite apical margin bearing long setae; all ventrites bearing moderate, shallow evenly distributed punctuation across surface, distance to nearest puncture approximately 2× diameter of puncture, punctures bearing mostly reclining setae; ventrite V with setae length nearly uniformly approximately 4× diameter of puncture; if I–IV each with 2 or more median pairs of longer, semi-erect sensory hairs, they are obscured in other setation. Male genitalia (n = 4) not distinctly dorsoventrally flattened; tegmen in dorsal view with basal piece ring-like; parameres in dorsal view gradually widening to a rounded apex, lateral margins approximately straight, in lateral view length = 3.9–4.7× width (Fig. 3H); elongate cylindrical median lobe narrowing apically; long coiled flagellum (Fig. 3G–I).

Female. Similar to male. Sexual dimorphism present with male protibia weakly triangularly dilated apically, female protibia parallel-sided, narrow to truncate apex; and basal protarsomeres of male more robust than female. Genitalia (n = 5): gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonocoxite, gonostylus length = 3.4–4.5× greatest width (Fig. 3J). Spermatheca C-shaped, length = 3.0–4.4× maximum width, asymmetric, widest in apical third, basal third with longitudinal wrinkles, apical third with weakly annuated, semi-reticulated texture, dorsally swollen in basal portion of apical third (Fig. 3K).

Distribution. Known from subhumid to arid habitats at elevations between 1300–1900m on Dioon califanoi, D. caputoi, D. purpusii in northern Oaxaca and southern Puebla (Gutiérrez-Ortega et al. 2018).

Material examined. Holotype (by designation) male of Pharaxonotha bicolor with the following labels: 1) [rectangular; white; printed in black ink] “MEX, Oax., San Andrés Pápalo, ♀ cone Dioon sp. aff. purpusii, late Oct 2016, M. A. Perez Farrera. 2) [rectangular; red; printed in black ink] “HOLOTYPE ♀ Pharaxonotha bicolor Skelley, Tang and Pérez-Farrera 2022” Deposited in the FSCA.

Paratypes (total 170). Allotype (FSCA) and 50 paratypes with same data as holotype: MEXICO: Oaxaca: Santa Catarina, [GPS omitted], 1400m, Dioon purpusii ♀ cone, 5-XI-2012, W. Tang (21); Teotitlán, 1600m, 25-II-1989, A. Vovides, ex male cone of Dioon califanoi (1); Teotitlán, 12-X-1991, A. Vovides, 20A, Dioon califanoi (4); Teotitlán de camino, 12-X-1991, A. Vovides, 24A, Dioon califanoi (1); MEXICO: Oaxaca, Teotitlán de Flores, Magón, 24-VIII-1991, A. Vovides, 36A, Dioon califanoi (2); same data only, 44A (3); Teotitlán de Flores, Magón, 15-IX-1999, A. Vovides, 8A, unknown cycad (8). Puebla: Coatepec, [GPS omitted], 1842m, ex Dioon caputoi, 6-XI-2012, W. Tang (10); Santiago, Coatepec, 13-X-1993, A. Vovides, C. Iglesias & P. Aguilar, Dioon caputoi cone debris (8); same locality except, IX-2004, F. Nicolalde, Dioon caputoi (3); Oax. border, Teotitlán, [GPS omitted], 1890m, ex Dioon califanoi ♀ cone, 7-XI-2012, W. Tang (58). Paratypes to be deposited in ANIC, CUIC, CZUG, FSICA, IEXA, NHMUK, NZAC, UAQM, UNAM, USNM.

Etymology. The species epithet refers to the usually contrasting colors of the black to dark brown elytra and the orange pronotum.

Remarks. This species has been found together in the male cones of two of its hosts, Dioon califanoi and D. purpusii, with two species of Allocorynina weevils, Parallocorynus (P.) gregoryi O’Brien and Tang and P. (Eocorynus) chemnicki Tang and O’Brien. On another host species, D. caputoi, this species occurs with Parallocorynus (P.) bicolor (Voss) (O’Brien and Tang 2015; Tang unpub. data). These weevils have an orange pronotum and black to dark brown elytral color scheme similar to that of Pharaxonotha bicolor, suggesting that there may be a mimicry complex in these associated insects. More intensive sampling from this host complex may also reveal the presence of P. bicolor in D. argenteum and D. planifolium, which have adjacent ranges to these other hosts.

Vovidesi species group

Adult diagnosis. In the vovidesi species group the dorsal surface is yellow-brown to orange-brown, with the pronotum often being slightly darker than the elytra, and the head in lateral view is flattened anteriorly and more convex between the eyes. As in most Pharaxonotha inhabiting Dioon, the dorsal surface of the head, pronotum and elytra have long setae emerging from punctures, with setal length reaching or exceeding the distance to nearest puncture. Length ranges from 2.48–3.91 mm.

Remarks. This species group is established based on analyses of the 16S rRNA gene from five populations sampled from both species described herein and are part of the early diverging lineages in Tang et al. (2018b, 2020). Materials of P. vovidesi analyzed by Tang et al. (2018b: 8, fig. 4; 2020: 18, fig. 3) are presented in their trees labeled
as follows: "D0250 Farallon, D. edule"; "D0324 Palm Sola, D. edule" and "D0253 Mt. Oscuro, D. edule". Materials of *P. fawcettae* analyzed by Tang et al. (2018b: 8, fig. 4; 2020: 18, fig. 3) are presented in their trees labeled as follows: "D0322 SLP, D. angustifolium" and "D0323 Tamaulipas D. angustifolium".

The group is distributed widely along the Atlantic drainage of eastern Mexico, in Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas and central Veracruz on the *Dioon edule-angustifolium* complex. Dissected adult specimens from both species of the vovidesi group usually have their guts packed with the distinctive monosulcate pollen grains of cycads, indicating that this is a major food source.

**Pharaxonotha fawcettae** Skelley, Tang and Pérez-Farrera, new species

Figures 2G, 4A–K

**Diagnosis.** *Pharaxonotha fawcettae* is distinguished from other species in the genus by the pronotum and elytra with long, distinct setae; head flattened anteriorly and convex between eyes, head with transverse occipital line [vertexal line] long laterally with line surpassing half distance between stridulatory file and eye, often curving anteriorly near eye; sexual dimorphisms indistinct, and pronotum with mean pronotal length/width (PL/PW) ranges from 0.69–0.70 (multiple specimens required). In females the spermatheca is elongate, ratio of spermatheca length to width at basal third > 4.5, and base is not abruptly swollen (see Fig. 2G). It is known to inhabit male cones of the *D. angustifolium* complex north of the Mexican Transvolcanic Belt in Hidalgo, Nuevo Leon, Querétaro, San Luis Potosí and Tamaulipas.

**Description.** Length 3.03–3.91 mm, width 1.17–1.63 mm. General body color entirely pale yellowish brown (Fig. 4A–C); dorsal surface punctate, strongly alutaceous, dulled, long procumbent hairs associated with punctuation on pronotum and elytra; ventrally alutaceous, dull, covered with scattered long procumbent setae.

**Head.** Not broad, width = 0.65–0.73× pronotal width (Fig. 4D–F); in lateral view flattened anteriorly, convex between eyes; in dorsal view, conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, moderately punctured, average distance between closest punctures 1–2× width of puncture; head width 0.64–0.82 mm; dorsal interocular distance 0.40–0.52 mm, head width/dorsal interocular distance ratio 1.50–1.68, ventral interocular distance 0.29–0.39 mm, head width/ventral interocular distance ratio 2.00–2.39. Eye with large black facets, about 2× diameter of head punctures. Antennal length slightly shorter than pronotal width, 1.3× head width; antennomere I ( scape) fairly large, slightly elongate; antennomere II equal in length to III; IV circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, 1.3× longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] long laterally in most, most with line surpassing half distance between stridulatory file and eye, often curving anteriorly near eye. Mentum and submentum somewhat coarsely punctured, 1/3–½ diameter of facet, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation.

**Thorax.** With pronotum transversely rectangular in dorsal view, length/width ratio 0.66–0.72; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles narrowly rounded in dorsal view, projecting forward; posterior angles obtuse, with small denticule at angle; lateral margin evenly shallowly arcuate for length, 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 ½ length of eye; prosternal process convex apically, expanded and truncate at apex. Hypomeron smooth, few minute punctures.

Scutellar shield distinctly transverse, posterior margin weakly roundly pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.67–1.84, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary stipe extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae 1.5× larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, shallow punctures, ¼ 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 punctuation, distance between nearest punctures approximately equal to diameter of puncture, puncture depth moderate. Metaventrite glossy, with strong lateral punctuation separated by 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrinen extending approximately ¾ metaventrite length. Legs broadened, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora narrowly robust, compressed laterally; tibiae shorter than femora, narrowly triangularly dilated to obliquely truncate apices, obliquely truncate apical margin; protibia with apical lateral tooth small, with complete apical fringe of very short stout spinules on straight ventral margin; metaseta 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 punctuation 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 genitalia (n = 7): not distinctly dorsoventrally flattened; tegmen in dorsal view with basal piece ring-like; parameres in dorsal view gradually narrowing to narrowest point between ½–⅓ of length from base than expanding toward apex, inner margin straight, outer margin with slight curvature on apical half, apex rounded to slightly truncate, in lateral view length = 4.2–4.9× width; elongate cylindrical median lobe narrowing apically; long coiled flagellum (Fig. 4G–I).

**Female.** Similar to male, sexual dimorphism weakly evident with male protarsomere I more broadly dilated and male femora, tibia and protarsi slightly more robust. Genitalia (n = 7): gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonocoxite, gonostylus length = 3.1–3.8× greatest width (Fig. 4J). Spermatheca C-shaped, approximately symmetrical, central third not rigid and easily deforming or collapsing during dissection, length = 4.7–5.8× width of basal third, basal third with faint longitudinal wrinkles, apical third weakly annulated, apical and basal ends rounded, apical end with slight taper (Fig. 2G, 4K).

**Distribution.** This species occurs in northeastern Mexico along the Atlantic drainage north of the Mexican Trans-volcanic Belt in Querétaro, Nuevo León, San Luis Potosí and Tamaulipas on populations of *Dioon* recognized here for convenience as a single species, *D. angustifolium*, but also as *D. edule* and *D. edule* var. *angustifolium* by others (González-Astorga et al. 2005; Gutiérrez-Ortega et al. 2018). Ongoing genetic analysis of these northeastern *Dioon* populations indicate that these may consist of two species, one in Nuevo León and Tamaulipas and another in Hidalgo, Querétaro, San Luis Potosí (Gutiérrez-Ortega, pers. comm.).

**Material examined.** Holotype (by designation) male of *Pharaxonotha fawcettae* with the following labels: 1) [rectangular; white; printed in black ink] “MEXICO, N.L., 2400’, 16 mi. W. Linares, Hwy. 58, IX-11-1982, C.W. & L. O’Brien & G. Wibmer”; 2) [rectangular; white; printed in black ink] “ex male strobile Dioon edule” [D. angustifolium]; 3) [rectangular; red; printed in black ink] “HOLOTYPE ♂ Pharaxonotha fawcettae Skelley, Tang and Pérez-Farrera 2022”. Deposited in the FSCA.

**Paratypes (total 58).** Female allotype (FSCA) and 54 paratypes with same data as holotype; MEXICO: Nuevo León: 16 mi. W. Linares 3600’, VIII-15-1971, O’Brien & Marshall (1); 29 km. W. Linares, 3.VI.1983, S. & J. Peck, 730m, ravine oak forest litter Berlese (2). Paratypes to be deposited in ANIC, CNCI, CUIC, FSCA, IEXA, MTEC, NHMUK, NZAC, UNAM, USNM.


** Intercepted specimens. **Texas: Laredo, XI-7-1947, on cycad plants ex. Tampa Mex., #47-16298 (2 USNM).

**Etymology.** Named for the late Priscilla Fawcett, the first to unravel the life cycles and feeding habits of some New World cycad beetles, *Rhopalotria slossoni* (Schaeffer) and *R. mollis* (Sharp) (now *R. furfuracea* O’Brien and
Tang) (Belidae) (Norstog and Fawcett 1989; Norstog et al. 1992). She was a professional botanical illustrator with exceptional observational skills. The beetle named for her occurs together on the same host with a beetle named for her late husband, Knut Norstog. Together their work helped to establish the foundations of cycad reproductive biology and pollination.

Remarks. The five populations placed within Pharaxonotha fawcettae in this description possess wide interpopulational variation. Their widely distributed host populations also display substantial morphological and genetic variation (González-Astorga et al. 2005; Gutiérrez-Ortega et al. 2018; Gutiérrez-Ortega, pers. comm.). We treat P. fawcettae as a complex in which varieties or possibly subspecies may be recognized in the future, if or when more detailed analyses become available. Pharaxonotha fawcettae has been found together on the male cones of D. angustifolium with two species of Allocorynina weevils, Parallocorynus (P.) norstogi O’Brien and Tang and P. (Neocorynus) inexpectatus O’Brien and Tang (O’Brien and Tang 2015).

Pharaxonotha vovidesi Skelley, Tang and Pérez-Farrera, new species
Figures 1D, 2C, 5A–K
Diagnosis. Pharaxonotha vovidesi is distinguished from other species in the genus by the pronotum and elytra with long, distinct setae; head flattened anteriorly and convex between eyes, head with transverse occipital line short, indistinct laterally, sexual dimorphisms indistinct, and pronotum with mean PL/PW ranges from 0.71–0.74 (multiple specimens required). In females the spermatheca is short and compact, ratio of spermatheca length to width at basal third < 3.5, and base abruptly swollen, swelling often quadrate-shaped. It is known to inhabit D. edule south of the Mexican Transvolcanic Belt in Veracruz, Mexico.

Description. Length 2.48–3.80 mm, width 0.96–1.47 mm. General body color entirely pale yellowish brown (Fig. 5A–C); dorsal surface punctate, strongly alutaceous, dulled, long procumbent hairs associated with punctuation on pronotum and elytra; ventrally alutaceous, dull, covered with scattered long procumbent setae.

Head. Not broad, width = 0.67–0.77× pronotal width (Fig. 5D–F); in lateral view flattened anteriorly, convex between eyes; in dorsal view conical, gradually narrowed anteriorly, moderately punctured, average distance between closest punctures 1–2× width of puncture; head width 0.57–0.81 mm; dorsal interocular distance 0.40–0.52 mm, head width/dorsal interocular distance ratio 1.48–1.65, ventral interocular distance 0.30–0.39 mm, head width/ventral interocular distance ratio 1.94–2.29. Eye with large black facets, about 2× diameter of head punctures. Antennal length slightly longer than pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, 1.3× longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] short laterally in most, most with line stopping about half distance between stridulatory file and eye, not curving anteriorly. Mentum and submentum moderately punctured, 1/3–½ diameter of facet, distance between nearest punctures approximately 1–2× own diameter, each puncture with a long seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation and with a shallow transverse depression.

Thorax. With pronotum rectangular in dorsal view, length/width ratio 0.67–0.77; with distinct marginal carina laterally and basally, anteriorly lacking marginal carina medially; surface convex; anterior angles narrowly rounded in dorsal and lateral view, projecting forward; posterior angles obtuse, with small denticle at angle; lateral margin evenly shallowly arcuate for 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 ½ length of eye; prosternal process convex apically, weakly truncate and truncate at apex. Hypomeron smooth, with indistinct seta bearing punctures. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal. Elytra in dorsal view elongate-oval, convex; length/width 1.69–1.88, greatest width near middlend; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellar striole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae as large as pronotal punctures, striae not impressed; intervals of striae with
fine, distinct punctures, ½ size of strial punctures; all punctures of elytra bearing a single prominent long seta, extending past next puncture in series. Mesoventrite with strong punctuation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite weakly glossy, with moderate lateral punctuation separated by 2–3× own diameter; medial surface finely punctured, separated by 3–4× own diameter; entire surface convex, metathoracic discriment extending approximately ⅓ metaventrite length. Legs narrow, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora narrowly robust, moderately compressed laterally; tibiae shorter than femora, narrowly dilated to obliquely truncate apices; protibia with apical lateral tooth small, distinct, with apical fringe of long stout spinules on concave ventral apical margin slight gap present between last spinule and lateral tooth; meso- and metatibia with apical fringe of long spinules on anterior and posterior margins.

**Abdomen.** Ventrite apical margin bearing long setae; all ventrites bearing moderate, shallow evenly distributed punctuation across surface, distance to nearest puncture approximately 2× diameter of puncture, punctures bearing mostly reclining setae; ventrite V with setae length nearly uniformly approximately 4× diameter of puncture; I–IV each with 2 or more median pairs of longer, semi-erect sensory hairs, they are obscured in other setation. Male genitalia (n = 6): not distinctly dorsoventrally flattened; tegmen in dorsal view with basal piece ring-like; parameres in dorsal view narrowed at center, apical half slightly asymmetric with slight bulge on outer margin, in lateral view length = 3.8–4.5× width; elongate cylindrical median lobe narrowing apically; long coiled flagellum (Fig. 5G–I).

**Female.** Similar to male, except male femora, tibia and protarsi slightly more robust. Female genitalia (n = 8): gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonoxocite, gonostylus length = 3.3–4.0× greatest width (Fig. 5). Spermatheca C-shaped, slightly asymmetric, widest in basal third, length = 3.0–3.4× greatest width, base abruptly swollen, swelling often quadrate-shaped, basal third with longitudinal wrinkles, apical third weakly annulated (Fig. 5K).

**Distribution.** As currently circumscribed, this species is known to occur near Actopan, Colorado, El Farallón and Monte Oscuro in eastern Veracruz, Mexico.

**Material examined.** Holotype (by designation) male of *Pharaxonotha vovidesi* with the following labels: 1) [rectangular; white; printed in black ink] “MEXICO, Veracruz, Monte Oscuro, ex Dioon edule ♂ cone, 2-XI-2012, A. Vovides; 2) [rectangular; red; printed in black ink] “HOLOTYPE ♂ Pharaxonotha vovidesi Skelley, Tang and Pérez-Farrera 2022” . Deposited in the FSCA.

**Paratypes (total 274).** Allotype (FSCA) and 183 paratypes with same data as holotype: MEXICO: Veracruz: Monte Oscuro, Municipio Emiliano Zapata, 20–VIII-1993, A. Vovides, C. Iglesias & P. Aguilar, Dioon edule male cone (9); same locality except, X-2002, A. Vovides, 34A, Dioon edule (8); same locality except, X-2002, A. Vovides, C. Iglesias & P. Aguilar, Dioon edule male cone (73). Paratypes to be deposited in ANIC, CUIC, CZUG, FSCA, IEXA, NHMUK, NZAC, UAQM, UNAM, USNM.

**Additional specimens (total 308).** Material studied presently considered to be *P. vovidesi*, but not designated as paratypes: MEXICO: Veracruz: Mun. Actopan, Rancho del Niño, 8-X-2002, A. Vovides, C. Iglesias, & P. Aguilar, Dioon edule (66); Colorado, [GPS omitted], Dioon edule ♂ cone, 17-XI-2014, W. Tang (14); Farallón, [GPS omitted], ex ♂ cone Dioon edule, 16-XI-2012, W. Tang (122). These will be deposited in institutions stated above.

**Etymology.** The species honors Andrew Vovides for his accomplishments in cycad taxonomy, systematics, ecology and conservation as well as his contributions to the study of cycad pollination.

**Remarks.** Genetic analysis of the host Dioon populations south of the Mexican Transvolcanic Belt by Gutiérrez-Ortega et al. (2018) suggests long genetic isolation of different populations, despite relatively close geographic proximity. We consider *P. vovidesi* as a complex in which varieties or possibly subspecies may be recognized in the future, if or when more detailed analyses become available. *Pharaxonotha vovidesi* has been found together on male Dioon edule cones with species of Allocorynina weevils: *Parallocorynus (P.) perezfarreri* Tang and O’Brien and *P. (Neocorynus) iglesiasi* Tang and O’Brien (O’Brien and Tang 2015).
Occidentalis species group

**Adult diagnosis.** In the occidentalis species group the head is more flattened in lateral view, even between the eyes, the transverse occipital line [vertexal line] is absent (except in *P. gigantea*), sexual dimorphisms more pronounced, and the dorsal surface is uniformly yellow-brown to orange-brown, with the pronotum often being slightly darker than the elytra. As in the majority of *Pharaxonotha* inhabiting *Dioon*, the dorsal surface of the head, pronotum and elytra have long setae emerging from punctures, with setal length reaching or exceeding the distance to nearest puncture (slightly shorter in *P. gigantea*). In *Pharaxonotha* inhabiting other cycad genera, dorsal hairs are shorter, not reaching the nearest puncture.

**Remarks.** This species group is proposed based on analysis of the 16S rRNA gene of three populations of one species that are part of the early diverging lineages in Tang et al. (2018b; 2020). Materials of *P. occidentalis* analyzed by Tang et al. (2018b: 8, fig.4; 2020: 18, fig. 3) are presented in their trees labeled as follows: “D0177 Loxicha, D. holmgrenii”; “D0246, Rancho Limon, D. holmgrenii”; “D0286 Campanario, D. merolae”.

Four species are placed within the group based on geographic proximity and selected morphological characters. This group is distributed along the Pacific drainage of western Mexico, in the states of Chiapas, Guererro, Jalisco, and Oaxaca on *Dioon holmgrenii*, *D. merolae*, *D. stevensonii* and *D. tomaselli* and includes one member in eastern Oaxaca, on *D. spinulosum*, which is within the Atlantic drainage of Mexico. It is likely that members of this species group also inhabit *Dioon* in other western states of Mexico, such as Durango, Michoacán, Nayarit, Sinaloa, and Sonora. Dissected adult specimens from all four species of the occidentalis group usually have their guts packed with the distinctive monosulcate pollen grains of cycads, indicating that this is a major food source.

*Pharaxonotha gigantea* Skelley, Tang and Pérez-Farrera, new species

**Figures 6A–H**

**Diagnosis.** This is the largest known *Pharaxonotha* with a length of 5.08 mm. Other distinguishing characters include the wide, transversely rectangular pronotum (length/width = 0.71) with punctures large, impressed, sharply defined.

**Description.** Length 5.08 mm, width 1.95 mm. General body color (Fig. 6A–C) red-brown, pronotum slightly darker than elytra; dorsal surface punctate, with a procumbent hair associated with each punctuation on head, pronotum and elytra, length of hairs reaching or nearly reaching nearest puncture (many hairs may have been broken off during the cleaning of the specimen, which was originally encased in pollen and other debris).

**Head.** Not broad, width = 0.68× pronotal width (Fig. 6D–E); in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, finely, densely punctured, average distance between closest punctures 1–2× width of puncture; head width 1.07 mm; dorsal interocular distance 0.68 mm, head width/dorsal interocular distance ratio 1.57, ventral interocular distance 0.50 mm, head width/ventral interocular distance ratio 2.14. 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 shorter than III; IV small, circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, 1.3× longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] distinct, laterally nearly reaching eye. Mentum and submentum finely punctured, ½–⅓× diameter of facet, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctation.

**Thorax.** With pronotum transversely rectangular in dorsal view, length/width ratio 0.71; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles narrowly rounded, projecting forward; posterior angles weakly developed, with small denticule at angle; lateral margin parallel-sided in medial half, shallowly arcuate inward anteriorly and posteriorly; posterior margin slightly projecting medially, projection beginning approximately by pair of small, dark pores in margin located 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 fine dense punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately ½ length of eye; prosternal process flattened apically, weakly expanded and truncate at apex. Hypomeron rugose with dense moderate
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punctures. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.71, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striae extending ⅓ elytral length, with 15 punctures; punctures of elytral striae same size as pronotal punctures, striae weakly impressed; intervals of striae with fine, shallow punctures, ⅓ size of striaal punctures; all punctures of elytra bearing a single short seta; seta most visible in profile, extending to reach next puncture. Mesoventrite with strong coarse punctuation, narrowly separated, hidden in rugose surface. Metaventrite glossy, with strong lateral punctuation separated by 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrumen extending approximately ⅔ metaventrite length. Legs broadened, relatively similar in length and shape. Procoxa oval; meso- and metaventrite transversely elongate-oval; trochanters obliquely truncate apically; femora robust, compressed laterally; tibiae shorter than femora, narrowly triangularly 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 punctuation 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 genitalia (n = 1): moderately dorsoventrally flattened; tegmen in dorsal view with basal piece ring-like and wide; parameres in dorsal view narrowing slightly ⅓ of length from the base then expanding gradually to a rounded apex, apical ⅔ slightly asymmetric with inner margin straight and outer margin with slight curvature, in lateral view length = 4.9× width; elongate cylindrical median lobe with strong taper apically; long coiled flagellum (Fig. 6F–H).

**Female.** Not known.

**Distribution.** Currently known only in the Mexican state of Guerrero on *Dioon stevensonii*.

**Material examined.** Holotype (by designation) male of *Pharaxonotha gigantea* with the following labels: 1) [rectangular; white; printed in black ink] "MEXICO, Guerrero, Achatla, oak forest, [GPS omitted], ex: Dioon tomaseli [D. stevensonii] male cone, coll. J. Chemnick, 18May2004, TW2004-18, elev. 1380 m; 2) [rectangular; red; printed in black ink] "HOLOTYPE ♂ *Pharaxonotha gigantea* Skelley, Tang and Pérez-Farrera 2022". Deposited in the FSCA.

**Etymology.** Named for its size; this is the largest *Pharaxonotha* known.

**Remarks.** The sole type specimen of *Pharaxonotha gigantea* was found together on a male cone of *D. stevensonii* with a species of Allocorynina weevil, *Parallocorynus* (*Dysicorynus*) *andrewsi* Tang and O’Brien (O’Brien and Tang 2015). Two specimens of *Pharaxonotha gigantea* were originally collected, however, one was sacrificed for genetic analysis, but did not yield usable DNA.

**Pharaxonotha novoai** Skelley, Tang and Pérez-Farrera, new species

Figures 7A–K, fig. 4 in Navarrette-Heredia (2018)

**Diagnosis.** This species is recognized by the long elytral setae surpassing neighboring punctures and by having a fringe of setae separated from and posterior of the eyes. Also, the eyes strongly encroach the mentum and the ventral interocular distance relative to head width is the shortest for any of the *Pharaxonotha* found on *Dioon* described in this paper, having a head width 2.64–2.82× ventral interocular distance.

**Description.** Length 3.40–3.63 mm, width 0.91–0.95 mm. General body color (Fig. 7A–C) pale brown, pronotum slightly darker; dorsal surface distinctly setose with long setae reaching well beyond neighboring punctures.

**Head.** Not broad, width = 0.70–0.71× pronotal width (Fig. 7D–F); in lateral view notably narrow, flattened; 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 0.65–0.67 mm; dorsal interocular distance 0.38–0.39 mm, head width/dorsal interocular distance ratio 1.69–1.72, ventral interocular distance 0.23–0.25 mm, head width/ventral interocular distance ratio 2.64–2.82. Eye with large black facets,
about $3\times$ diameter of head punctures; posterior lateral margin of eye with small distinct fringe of setae separated from facets. Antennal length slightly shorter than pronotal width, $1.2\times$ head width; antennomere I (sca) fairly large, slightly elongate; antennomere II equal in size to III; IV small, circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, $1.3\times$ longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] absent medially. Mentum and submentum fine punctured, $\frac{1}{2}\times$ diameter of facet, distance between nearest punctures approximately 2–3× own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation.

**Thorax.** With pronotum transversely rectangular in dorsal view, length/width ratio 0.75–0.76; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles narrowly rounded, projecting forward; posterior angles developed, angulate with small denticule at angle; lateral margin slightly arched in medial half, more arcuate inward anteriorly and posteriorly; posterior margin slightly projecting medially, projection beginning approximately by pair of small, dark pores in margin located $\frac{1}{2}$ width from posterior angles, each pore marks base of a distinct sulcus extending anteriorly onto disc $\frac{1}{4}$ length of pronotum. Prosternum in ventral view convex, with few scattered fine punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately $\frac{1}{2}$ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few minute punctures. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.87–2.02, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellar striae extending $\frac{1}{5}$ elytral length, with 12–15 punctures; punctures of elytral striae $2\times$ larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, distinct punctures, $\frac{1}{2}$ size of striae; all punctures of elytra bearing a single long seta, seta extending past neighboring puncture. Mesoventrite with strong close punctuation, surface rugose, distance between nearest punctures approximately equal to diameter of punctures. Metaventrite glossy, with moderate lateral punctuation separated by 2–3× own diameter; medial surface finely distinctly punctured, separated by 4–5× own diameter; surface medially flattened, metathoracic discernment extending approximately $\frac{3}{4}$ metaventrite length. Legs broadened, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, compressed laterally; tibiae shorter than femora, narrowly triangularly 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, dense setae; all ventrites bearing moderate, shallow punctuation evenly distributed across surface, distance to nearest puncture approximately $2\times$ diameter of puncture, punctures bearing long reclining setae; ventrite V with setae length nearly uniformly approximately $2\times$ diameter of puncture; I–IV each with 2 or more median pairs of longer, semi-erect sensory hairs (difficult to see in poor lighting, often abraded). Male genitalia (n = 1): moderately dorsoventrally flattened; tegmen in dorsal view with basal piece ring-like; parameres in dorsal view narrowing slightly $\frac{1}{5}$ of length from the base then expanding noticeably to maximum width at $\frac{3}{5}$ length from base, apical $\frac{3}{5}$ strongly asymmetric with inner margin straight and outer margin with pronounced curvature and noticeably bulging, apex rounded, in lateral view length $= 3.8\times$ width; elongate cylindrical median lobe narrowing apically; long coiled flagellum (Fig. 7G–I).

**Female.** Similar to male, sexual dimorphism weakly evident; femora, protibia and basal protarsomeres of male more broadly dilated. Genitalia (n = 1); gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonocoxite, gonostylus length $= 3.6\times$ width (Fig. 7J). Spermatheca slightly arcuate, but not C-shaped, length $= 3.4\times$ greatest width, asymmetric, wider in apical half, basal third with longitudinal wrinkles, apical third weakly annulated (Fig. 7K).

**Distribution.** Currently known from Jalisco, Mexico. Its host, *Dioon tomaselli*, also occurs in Durango, Michoacan, Nayarit and Sinaloa and this beetle’s distribution may extend to these other Mexican states.

**Material examined.** Holotype (by designation) male of *Pharaxonotha novoai* with the following labels: 1) [rectangular; white; printed in black ink] “MEXICO: Jalisco, Cobo Corrientes, Santuaria de las Guacamayas, [GPS...
omitted], XI-2006 [2016], J. Novoa and A. Flores, cones of Dioon tomaselli, in Quercus forest associated with tropical deciduous forest"; 2) "HOLOTYPE ♂ Pharaxonotha novoai Skelley, Tang and Pérez-Farrera 2022". Deposited in the FSCA.

Paratypes (total 14). Allotype (FSCA) and 13 paratypes with same data as holotype deposited in CUIC, CZUG, FSCA, IEXA, UNAM.

Etymology. The species is named for Jorge Novoa, for his conservation work on cycads and other flora and fauna at Santuaria de Guacamayas in Jalisco, Mexico.

Remarks. Pharaxonotha novoai has been found together on male Dioon tomasellii cones with a species of Allocorynina weevil: Parallocorynus (Dysicorynus) andrewsi Tang and O’Brien (O’Brien and Tang 2015; Navarrette-Heredia 2018).

Pharaxonotha occidentalis Skelley, Tang and Pérez-Farrera, new species
Figures 1C, 2B, 8A–J

Diagnosis. As in most Pharaxonotha inhabiting Dioon, the dorsal surface of the head, pronotum and elytra have long setae emerging from punctures, with setal length reaching to the nearest puncture. Other diagnostic characters include body color a uniform brown, posterior lateral margin of eye with small distinct fringe of setae separated from facets, and pronotum relatively short, pronotal length/width = 0.71–0.79 (mean for each of three populations = 0.75). It is known to inhabit Dioon species on the Pacific drainage of Oaxaca and Chiapas, Mexico.

Description. Length 2.77–4.01 mm, width 0.96–1.56 mm. General body color (Fig. 8A–C) uniform pale brown. Dorsal surface distinctly setose with long setae reaching neighboring punctures.

Head. Not broad, width = 0.68–0.73× pronotal width (Fig. 8D–F); in lateral view notably narrow, flattened; 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 0.54–0.76 mm; dorsal interocular distance 0.34–0.45 mm, head width/dorsal interocular distance ratio 1.54–1.67, ventral interocular distance 0.27–0.36 mm, head width/ventral interocular distance ratio 1.93–2.45. Eye with large black facets, about 2× diameter of head punctures; posterior lateral margin of eye with small distinct fringe of setae separated from facets. Antennal length nearly equal to pronotal width, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV circular; V–VII same length as IV, gradually becoming wider with VIII distinctly transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, 1.3× longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] absent medially. Mentum and submentum fine punctured, 1/3× diameter of facet, distance between nearest punctures approximately 2–3× own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation.

Thorax. With pronotum transversely rectangular in dorsal view, length/width ratio 0.71–0.79; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles narrowly rounded, projecting forward; posterior angles weakly developed, with small denticule at angle; lateral margin weakly arched 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 fine punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately ½ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few minute punctures. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.78–2.38, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellar stirole extending ¼ elytral length, with 10–15 punctures; punctures of elytral striae 1.5× larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, shallow punctures, ¼ size of striae punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending almost to next puncture. Mesoventrite with strong punctuation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite
glossy, with strong lateral punctation separated by 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrmen extending approximately ¾ metaventrite length. Legs broadened, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, compressed laterally; tibiae shorter than femora, narrowly triangularly 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, fine setae; all ventrites bearing moderate, shallow punctuation 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 genitalia (n = 3): moderately dorsoventrally flattened; tegmen in dorsal view with basal piece ring-like; parameres in dorsal view narrowing slightly 1/3 of length from the base then expanding slightly to maximum width at ¾ length from base, apical ¾ slightly to moderately asymmetric with inner margin straight and outer margin curved and slightly bulging, apex rounded, in lateral view length = 3.8× width; elongate cylindrical median lobe narrowing apically; long coiled flagellum (Fig. 8G–H).

**Female.** Similar to male, sexual dimorphism weakly evident in pronotal shape with mean pronotal length/width in males = 0.76–0.77 (range = 0.74–0.79, n = 25) and mean length/width in females = 0.74–0.75 (range = 0.71–0.77, n = 30) in three populations examined, with some overlap between males and females; femora, protibia and basal protarsomeres of male more broadly dilated. Genitalia (n = 8): gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonocoxite, gonostylus length = 3.6–4.7× greatest width (Fig. 8I). Spermatheca arcuate, but not C-shaped, length = 2.9–3.7× greatest width, asymmetric, widest in apical half, basal third with longitudinal wrinkles, apical portion weakly annulated, apex slightly tapering and with slight, abrupt bend ventrally (Fig. 8J).

**Distribution.** Known distribution along the Pacific drainage of Oaxaca and Chiapas on *Dioon holmgrenii* and *D. merolae*.

**Material examined.** Holotype (by designation) male of *Pharaxonotha occidentalis* with the following labels: 1) [rectangular; white; printed in black ink] “MEX., Chiapas, El Campanario, 2k Eijdio Andres Quintana Roo, ♂ cone *Dioon merolae*, XI-2011, M. A. Perez Farrera”; 2) [rectangular; red; printed in black ink] “HOLOTYPE ♂ *Pharaxonotha occidentalis* Skelley, Tang and Pérez-Farrera 2022”. Deposited in the FSCA.

**Paratypes (total 184).** Female allotype (FSCA) and 183 with same data as holotype deposited in ANIC, CUIC, CZUG, FSCA, IEXA, NHMUK, NZAC, UAQM, UNAM, USNM.

**Additional specimens (total 428).** Material studied presently considered to be *P. occidentalis*, but not designated as paratypes: MEXICO: Oaxaca, Buenos Aires [GPS omitted], 1120m, *Dioon merolae* ♂ cone, 11-XI-2012, W. Tang (1); Rancho Limón, ex ♂ cone *Dioon holmgrenii*, [GPS omitted], 620m, 12-XI-2012, W. Tang (411); San Bartolomé Loxicha, ex ♂ cone *Dioon holmgrenii*, 5-XII-2008, F. Maldonado-Ruiz (16). These will be deposited in institutions stated above.

**Etymology.** The species epithet, occidentalis, derives from the Latin for west, referring to distribution in western Mexico, along the Pacific drainage of Oaxaca and Chiapas states.

**Remarks.** *Pharaxonotha occidentalis* lives sympatrically on *D. holmgrenii* with the Allocoynina weevils *Parallocorynus* (*P.* *salasae* Tang and O’Brien and *P. (Eocorynus) schiblii* Tang and O’Brien and on *D. merolae* with *Parallocorynus* (*P.* *jonesi* O’Brien and Tang (O’Brien and Tang 2015, Navarrettea-Heredia 2018). While the 16S rRNA gene used in the phylogenetic analysis of *Pharaxonotha* (Tang et al. 2018b, 2020) has a moderate rate of evolution, it did not detect significant genetic differences between *Pharaxonotha* inhabiting *D. holmgrenii* and *D. merolae*. Nor did we find significant morphological differences. Further studies with a more in-depth analysis using a greater number of genes may result in the taxonomic separation of these populations in the future.
**Pharaxonotha woodruffi** Skelley, Tang and Pérez-Farrera, new species
Figures 9A–K

**Diagnosis.** Distinguished from other *Pharaxonotha* by the more flattened head, posterior lateral margin of eye without distinct fringe of setae; pronotal length/elytral length (PL/EL) = 0.32–0.37; sexual dimorphism with males having robust femora, protibial and protarsomeres, and male parameres in dorsal view with margins nearly straight. Also found inhabiting *Dioon spinulosum* in northeastern Oaxaca.

**Description.** Length 3.05–3.36 mm, width 1.20–1.32 mm. General body color (Fig. 9A–C) pale brown, pronotum slightly darker; dorsal surface with short setae not reaching neighboring punctures.

**Head.** Not broad, width = 0.69–0.71× pronotal width (Fig. 9D–F); in lateral view notably narrow, flattened; in dorsal view conical, gradually narrowed anteriorly, surface flat to slightly convex, moderately punctured, average distance between closest punctures 2–3× width of puncture; head width 0.65–0.73 mm; dorsal interocular distance 0.40–0.48 mm, head width/dorsal interocular distance ratio 1.52–1.63, ventral interocular distance 0.33–0.38 mm, head width/ventral interocular distance ratio 1.92–2.00. Eye with large black facets, about 2× diameter of head punctures; lacking separate fringe of setae posterior of eye. Antennal length slightly longer than pronotal width, 1.6× head width; antennomere I ( scape) fairly large, slightly elongate; antennomere II shorter than III; IV circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI not enlarged, 1.1× longer than X, globular with rounded apex. Clypeus weakly concave anteriorly, moderately punctate. Transverse occipital line [vertexal line] absent medially. Mentum and submentum fine punctured, 1/3× diameter of facet, distance between nearest punctures approximately 2–3× 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 0.72–0.78; with distinct marginal carina laterally and basally, anteriorly with fine marginal carina medially; dorsally flattened; anterior angles narrowly rounded, projecting forward; posterior angles weakly developed, with small denticle at angle; lateral margin weakly arched 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 fine punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately ½ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few minute punctures. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal.

Elytra in dorsal view elongate, flattened dorsally; length/width ratio 1.62–1.77, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate punctuation size; scutellary stria extending ¼ elytral length, with 11–15 punctures; punctures of elytral striae 1.5× larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, shallow punctures, ¼ size of striaal punctures; all punctures of elytra bearing a single short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctuation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with moderate lateral punctuation separated by 2–3× own diameter; medial surface finely distinctly punctured, separated by 4–5× own diameter; surface medially flattened, metathoracic disc extending approximately ¾ of metaventrite length. Legs broadened, relatively similar in length and shape. Procoxa oval; mesocoxa globular; metacoxa transversely elongate-oval; trochanters obliquely truncate apically; femora robust, compressed laterally; tibiae shorter than femora, narrowly triangularly 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 metaventrite with apical fringe of short stout spinules on anterior margin, finer setae on posterior margins.

**Abdomen.** Ventrite apical margin bearing short, fine setae; all ventrites bearing moderate, shallow punctuation 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 genitalia (n = 1): not distinctly dorsoventrally flattened, tegmen in dorsal view with basal piece ring-like; parameres in dorsal view symmetrical, gradually expanding to rounded apex, inner and outer margins approximately straight, without lateral bulge, in lateral view length = 4.5× greatest width; elongate cylindrical median lobe narrowing apically; long coiled flagellum (Fig. 9G–I).

Female. Similar to male; sexual dimorphism weakly evident; femora, protibia and basal protarsomeres of male more broadly dilated. Genitalia (n = 1); gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonocoxite, gonostylus length = 3.5× greatest width (Fig. 9J). Spermatheca arcuate, but not C-shaped, short and compact, length = 2.6× greatest width, slightly asymmetric, widest in apical half, base and apex rounded (Fig. 9K).

Distribution. Known from *D. spinulosum*, which inhabit limestone mogotes in lowland wet forest of northeastern Oaxaca.

Material examined. Holotype (by designation) male of *Pharaxonotha woodruffi* with the following labels: 1) [rectangular; white; printed in black ink] “MEXICO, Oax. Hwy147, 6 mi. SE. Jcn. 175&147, 200‘, 25Aug. 1982, C. & L. O’Brien & G. Wibmer; 2) [rectangular; white; printed in black ink] ex: male strobile *Dioon spinulosum*; 3) [rectangular; red; printed in black ink] “HOLOTYPE ♂ *Pharaxonotha woodruffi* Skelley, Tang and Pérez-Farrera 2022”. Deposited in the FSCA.

Paratypes (total 4). Allotype and 3 paratypes with same data as holotype deposited at the FSCA.

Etymology. The species is dedicated to Robert E. “Bob” Woodruff, mentor and advisor of author PES. Unlike most graduate advisors, he allowed PES freedom to work on whatever beetles were of interest. This freedom allowed PES to explore the Erotylidae, which eventually lead to all of the recent work on *Pharaxonotha*.

Remarks. *Pharaxonotha woodruffi* has been found together on male *Dioon spinulosum* cones with a species of Allocorynina weevil, *Rhopalotria (Allocorynus) vovidesi* O’Brien and Tang (O’Brien and Tang 2015). These or related beetles may also be present on the closely related *Dioon rzedowskii*, also found in wet forests of northeastern Oaxaca, but at higher altitudes on steep limestone slopes.

**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. Like species inhabiting other cycad genera, *Ceratozamia, Microcycas* and *Zamia*, this group has relatively short indistinct dorsal body hairs emerging from punctures at 30× magnification. Other species groups found on *Dioon* are generally characterized by having setae longer than species found on these other cycad genera. Excluding the elytra, the dark brown body is the darkest of all known *Pharaxonotha*. Only the elytra of the bicolor species group are darker.

Remarks. This species group is proposed 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). Materials of the kirschii group analyzed by Tang et al. (2018b: 8, fig.4; 2020: 18, fig. 3) are presented in their trees labeled as follows: “D0057 Veracruz – Z. inermis” and “D0068 C. Amer. – not on cycads – *Pharaxonotha kirschii*”. These two are widely separated from the majority of other lineages but also shows a cycad-inhabiting species to be more divergent from a free-living *P. kirschii* than many species are from each other. Members of this group are known from other genera of cycads and likely represents a complex of species. Further work is needed on both the cycad associated and the free-living populations. Dissected adult specimens from both new species collected with cycads usually have their guts packed with the distinctive monosulcate pollen grains of cycads, indicating that this is a major food source.

**Pharaxonotha dimorpha** Skelley, Tang and Pérez-Farrera, new species

Figure 10A–L

Diagnosis. A member of the kirschii group; this species has the most striking sexual color dimorphism of any known *Pharaxonotha*, with the dorsal color of the male a uniform medium brown, while the pronotum and elytra of the female is almost completely dark brown to black, except for edges of the pronotum and the apex of the elytra. Additional diagnostic characters include small antennomere XI, the female spermathecal apex abruptly
curving to a truncated point, and the male paramere width in lateral view < 3.4× own length. It has been found at El Farallón, Veracruz, Mexico on Dioon edule.

**Description.** Length 3.44–4.35 mm, width 1.22–1.62 mm. General body color (Fig. 10A–D) with the dorsal color of the male a uniform medium brown, while the pronotum and elytra of the female is almost completely dark brown to black, except for edges of the pronotum and the apex of the elytra. Dorsal surface glossy, with very short setae in punctures.

**Head.** Not broad, width = 0.62–0.67× pronotal width (Fig. 10E–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 0.70–0.88 mm; dorsal interocular distance 0.46–0.60 mm, head width/dorsal interocular distance ratio 1.45–1.56, ventral interocular distance 0.40–0.53 mm, head width/ventral interocular distance ratio 1.45–1.75. 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, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV small, circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI small, 1.1× 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, ½–⅔× diameter of facet, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation.

**Thorax.** With pronotum transversely rectangular in dorsal view, length/width ratio 0.70–0.75; 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 ½ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few punctures. Scutellar shield distinctly transverse, posterior margin weakly roundly pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.83–1.87, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striae extending ½ elytral length, with 7–8 punctures; punctures of elytral striae 2× larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, indistinct, shallow punctures, ½ size of stria punctures; all punctures of elytra bearing a single very short seta; seta only visible in profile, extending slightly out of puncture. Mesoventrite with strong punctuation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metaventrite glossy, with strong lateral punctuation separated by 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrmen 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 metatibiae 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 punctuation 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 small denticle at apex. Male genitalia (n = 2): not dorsoventrally flattened, tegmen in dorsal view with basal piece ring-like and narrow; parameres in dorsal view with lateral margins approximately straight to midlength, apical half with inner and outer margins curving and bulging, apex
rounded with slight curve toward one another, in lateral view length = 2.7–3.3× greatest width; elongate cylindrical median lobe with lateral margins nearly parallel; long coiled flagellum (Fig. 10G–J).

Female. Similar to male. Female differs in darker dorsal coloration with nearly completely dark elytra; female protibial and protarsus narrow, male with weakly dilated protibial and basal protarsomeres. Female lacking apical denticle on terminal abdominal ventrite. Genitalia (n = 1); gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonoxite, gonostylus length = 4.2–4.6× greatest width (Fig. 10K). Spermatheca hook-shaped, widest just apicad of rounded base, then narrowing evenly until reaching unsclerotized arc at central third, apical third narrowing evenly from junction with central third, until abrupt bend to a truncated apex, length = 5.4× greatest width (Fig. 10L).

Distribution. This species is known only from El Farallón, Veracruz, Mexico on Dioon edule. This is a stabilized dune, beach habitat. The plants are exposed to nearly full sun, with only scattered low tree cover, and are likely subject to salt spray during storms.

Material examined. Holotype (by designation) male of Pharaxonotha dimorpha with the following labels: 1) [rectangular; white; printed in black ink] “MEXICO, V.C., Farallón, [GPS omitted] ex ♂ cone Dioon edule, 16-XI-2012, W. Tang”; 2) [rectangular; red; printed in black ink] “HOLOTYPE ♂ Pharaxonotha dimorpha Skelley, Tang and Pérez-Farrera 2022”. Deposited in the FSCA.

Paratypes (total 3). Allotype and 2 paratypes with same data as holotype deposited at the FSCA.

Etymology. The species is named for its striking sexual color dimorphism.

Remarks. Only four specimens of Pharaxonotha dimorpha were found together with over 120 individuals of P. vovidesi on a male cone of D. edule that was at the end stage of pollen shedding. The difference in numbers bring up the possibility that these two species of Pharaxonotha, while sharing the same spatial niche, may have differing temporal niches, with preferences to feed and/or reproduce in the cone at different stages of cone development. See remarks under P. sclerotiza. In D. edule cones at this site, P. dimorpha also occurs with the weevils Parallocoxyrnis (P.) perezfarrerai and P. (Neocorynus) iglesiasi (O’Brien and Tang 2015).

Pharaxonotha sclerotiza Skelley, Tang and Pérez-Farrera, new species
Figures 2F, 11A–K

Diagnosis. A member of the kirschii group this species has a striking sexual color dimorphism with the dorsal color of the male a uniform medium brown, while the pronotum and elytra of the female with only the medial half darkened into a fuscous spot. Other diagnostic characters include small antennomere XI, the female spermathecal apex gradually curving to a rounded point, and male paramere width in lateral view > 3.4× own length. It has been found at Gómez Farias, Tamaulipas, Mexico on Dioon angustifolium.

Description. Length 4.14–4.39 mm, width 1.58–1.60 mm. General body color (Fig. 11A–D) dark brown. General body (Fig. 10A–F) with the dorsal color of the male a uniform medium brown, while the pronotum and medial half of female elytra are dark brown to black. Dorsal surface glossy, with very short setae in puncture.

Head. Not broad, width = 0.67–0.68× pronotal width (Fig. 11E–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 0.88–0.90 mm; dorsal interocular distance 0.59 mm, head width/dorsal interocular distance ratio 1.49–1.53, ventral interocular distance 0.50–0.54 mm, head width/ventral interocular distance ratio 1.63–1.80. 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, 1.5× head width; antennomere I (scape) fairly large, slightly elongate; antennomere II slightly shorter than III; IV small, circular; V–VII same length as IV, gradually becoming wider with VIII transverse and flattened apically; club fairly large, IX and X similar in length; XI small, 1.1× 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, ¼–⅓× diameter of facet, distance between nearest punctures approximately 1× own diameter, each puncture with a short seta. Gular area smooth, without punctuation or setae, border with submentum marked by change in punctuation.
Thorax. With pronotum transversely rectangular in dorsal view, length/width ratio 0.73–0.74; 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 arched 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, with few scattered punctures; anterior margin slightly emarginate, finely denticulate with row of long, anteriorly directed setae, longest setae approximately ½ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few punctures. Scutellar shield distinctly transverse, posterior margin weakly roundedly pentagonal. Elytra in dorsal view elongate, flattened dorsally; length/width 1.83–1.84, greatest width near midlength; with distinct marginal line basally; 10 complete striae of moderate puncture size; scutellary striae extending ½ elytral length, with 9–10 punctures; punctures of elytral striae 2× larger than pronotal punctures, striae weakly impressed; intervals of striae with fine, indistinct shallow punctures, ½ size of strial punctures; all punctures of elytral bearing a single very short seta; setae obviously 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 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrinen 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 tooth small, with complete apical fringe of very short stout spines on straight ventral apical margin; meso- and metatibia with apical fringe of short stout spinules on straight ventral apical margin; femora and tibiae shorter than elytra.

Abdomen. Ventrite apical margin bearing short, sparse setae; all ventrites bearing moderate, shallow punctuation 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 small denticle at apex. Male genitalia (n = 1): not distinctly dorsoventrally flattened, tegmen in dorsal view with basal piece ring-like and wide; parameres in dorsal view with lateral margins approximately straight to midlength, apical half with inner margin straight and outer margin curved slightly and bulging, in lateral view length = 3.5× greatest width; elongate cylindrical median lobe with lateral margins tapering strongly apically; long coiled flagellum (Fig. 11G–I).

Female. Similar to male. Female differs in having dark central markings on elytra; female protibial and protarsus narrow, male with weakly dilated protibial and basal protarsomeres. Female lacking apical denticle on terminal abdominal ventrite. Genitalia (n = 1); gonostylus cylindrical, widest at apex, tapering slightly and gradually to base, set apically on gonocoxite, gonostylus length = 4.2–4.6× greatest width (Fig. 11I). Spermatheca hook-shaped, base rounded on dorsal side, angulate on ventral side, width greatest just apicad of base, then narrowing evenly until reaching unsclerotized arc at central third, apical third narrowing and curving evenly from junction with central third until rounded apex, length = 5.4× greatest width (Fig. 11K).

Distribution. This species is known from the Mexican states of Nuevo León, Querétaro and Tamaulipas. At the type locality at Gómez Farías, Tamaulipas the host plant Dioon angustifolium grows in fissures on limestone and except for scattered low trees are exposed to full sun.

Material examined. Holotype (by designation) male of Pharaxonotha sclerotiza with the following labels: 1) [rectangular; white; printed in black ink] “MEXICO, Tamp., Gómez Farías, tsinge limestone, [GPS omitted], cone of Dioon angustifolium, 12-XI-2014, W. Tang” 2) [rectangular; red; printed in black ink] “HOLOTYPE of Pharaxonotha sclerotiza Skelley, Tang and Pérez-Farrera 2022”. Deposited in the FSCA.

Paratypes (total 1). Allotype with same data as holotype, deposited in FSCA.

Flores, [GPS coord. omitted], 6–VII-2003, J. A. Peréz de la Rosa y G. Vargas Coll. Ex *Dioon edule* (cono femenino) (3 CZUG, FSCA)

**Etymology.** While not as heavily sclerotized as *P. kirschi*, this species is more sclerotized than other cycad dwelling species. It is named for this more heavily sclerotized body.

**Remarks.** The specimens from Querétararo show some variation in coloration, different from those described from Tamaulipas. The single female has entirely fuscous elytra, lacking dark maculations, while one male is entirely dark brown and the other entirely fuscous. No morphological character was found to separate these from the type series. Based on the paucity of specimens we prefer to consider this population as *P. sclerotiza* until series of specimens and potential molecular analyses are available.

At the type locality only two specimens of *Pharaxonotha sclerotiza* were found together with 28 individuals of *P. vovidesi* on a male cone of *D. angustifolium* that was at the end stage of pollen shedding. The difference in numbers bring up the possibility that these two species of *Pharaxonotha*, while sharing the same spatial niche, may have differing temporal niches, with preferences to feed and/or reproduce in the cone at different stages of cone development. The non-paratype specimens from Querétararo, however, were collected on a female cone. While adults of the kirschii group have been found feeding on pollen, it is possible they may breed in decaying female cones also. Thus, species of *Pharaxonotha* may stratify the niches based on cone gender. To our knowledge, no efforts have been made to sample beetles from mature female cones. There is no indication if the female cone the non-paratypes were found on was young or mature. In *D. angustifolium* at the type locality *P. sclerotiza* also occurred with the Allocorynina weevil *Parallocorynus* (*P.* norstogi) (O’Brien and Tang 2015).

*Pharaxonotha kirschi* Reitter

**Figures 1A, 2A, 2D–E, 12A–K**


*Thallisella condradti* Gorham 1898: 249 ~ Champion 1904: 36 [syonymy].

**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 kirschi* is widespread from the southern US to Panama, is not associated with cycads. It is known as the “Mexican grain beetle”, a pest in stored plant products which has been intercepted in many countries.

**Description.** 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. 12E–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 punctuation or setae, border with submentum marked by change in punctuation.

**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 denticule 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 ½ length of eye; prosternal process flattened apically, expanded and truncate at apex. Hypomeron smooth, with few punctures. Scutellar shield distinctly transverse, posterior margin weakly rounded pentagonal. 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; scutellar striaole extending ½ 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, ½ size of strial punctures; all punctures of elytra bearing a single very short seta; seta only visible in profile, extending slightly out of puncture. Mesoscutellum with strong punctuation, distance between nearest punctures approximately equal to diameter of punctures, puncture depth moderate. Metascutellum glossy, with strong lateral punctuation separated by 1–2× own diameter; medial surface finely distinctly punctured, separated by 3–4× own diameter; surface medially flattened, metathoracic discrern extending approximately ½ metascutellum 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 punctuation 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 = 2) similar to all others in the genus with widened tegmen, elongate cylindrical median lobe, and long coiled flagellum (Fig. 12G–I).

**Female.** Similar to male. Female differs with narrow protibia and protarsus, male have weakly dilated protibial and basal protarsomers. Female lacking apical denticle on terminal abdominal ventrite. Genital tube shortened, length past abdominal segment VIII = 1.5× width (n = 2); gonostylus set apically on gonocoxite, gonostylus length = 4–5× width (Fig. 12J). Spermatheca base rounded on dorsal side, angulate on ventral side, basal third broadest at basal end, narrowing until unscerotized arc at central third, apical third narrowing and curving gradually to a rounded apex (Fig. 12K).

**Type specimens.** The type specimen(s) of *Pharaxonotha kirschii* were collected in Silesia on plant materials from Mexico (Reitter 1985; Pakaluk 1988), present location of the type(s) is unknown (not examined). The type of *Thallisella condradti* were collected in Vera Paz, Guatemala (Gorham 1898), present location of type material is the NHMUK (examined).

**Distribution.** As considered here, *Paraxonotha kirschii* is not associated with cycads and occurs naturally in the wild from the southern US to Panama.

**Material examined (total 641).** Data presented below were collected over many years of study and specimens returned to the stated repository. Considering the newly recognized cycad species in the kirschii group, most of the following materials need to have their identity confirmed. The only materials confirmed at present are those in the FSCA where all materials not associated with cycads were *P. kirschii*. Data for materials here considered to be *P. kirschii* include: **BELIZE:** Cayo, 0.5 mi. W. Augustine, 30-VII-1976, T. McCarthy, Berlese litter broad-leaf seasonal forest, FM(HD)#76-207 (1 FMNH); Orange Walk, Rio Bravo Cons. Area, vic. LaMilpa Archeol. Site, Site#9, 10–16-IV-1995, P. Kovarik, rotting mushroom baited pitfall (1 FSCA); same data except, Site#12, 11–18-IV-1995, P. Kovarik, rotting mushroom baited pitfall (1 FSCA); **COSTA RICA: Cartago:** Turrialba, 16–20-V-1979, J.M. & B.A. Campbell (1 CNCI); Guanacaste: 3 km N. Cañas, Hac. La Pacifica, 5–6-VI-1979, H. & A. Howden (2 CNCI); same data except, 9–11-VIII-1987 (1 CMNC); 4 km NW Cañas, La Pacifica, 5–VI-1979, JM & BA Campbell (4 CNCI); Comelco, Palo Verde, OTS, 9 km W. Bagaces, 103°32’N, 85°18’W, 9-IV-1972, J. Wagner, J. Kethley, Berlese, 4 liters conc. organic debris on rocks below falls, drip zone, FM(HD)#73-388, 73CRIV-9a (1 FMNH); Liberia, 20-V-1993, J. & A. Ashe, #047 ex rotting mangos (2 SEMC); Liberia, ca. 32.2 km. N., 23-V-1993, J. & A. Ashe, #046 ex fruit fall litter (40 SEMC, 6 FSCA); Maritza Biol. Sta., 22-V-1993, J. & A. Ashe, #036 ex flight intercept (4 SEMC); same data except,
22-V-1993, #040 ex bracket mushroom (1 SEMC); same data except, 22-V-1993, #039 ex treefall litter (1 SEMC); same data except, 22-V-1993, #038 ex flower fall litter (3 SEMC); Rincon de la Vieja N.P., Las Pailas, 4-IX-1998, C. W. & L. O’Brien (1 FSCA); La Pacifica: Rio Corbili, V-VI-1992, B. Ratcliffe, M. Jameson, C. Dwyer, ex sifting (3 SEMC); Puntarenas: Monteverde, 25-V-1994, J. Ashe, R. Brooks, R. Leschen, Costa Rican Expedition #480 ex black light (1 SEMC); Monteverde, Areas, 6-VI-1973, Erwin & Hevel Central American Expedition, 1973 (1 USNM); Monteverde, Pension Quetzal, 14–17-VI-1987, B&B Valentine (1 FSCA); Reserva de Monteverde, 1–4-VI-1979, JM & BA Campbell (1 CNCI); San José: La Caja, III-1929, H. Schmidt leg; F. Nevermann, auf Sandbank (4 USNM); same data except, II-1932 (2 USNM); San Pedro de Montes de Oca, 12-11-1932, C. H. Ballou, C.R.888, reared in raisons (2 USNM); same data except, Rec. Jan 1947, Luis Salas-2, 47-982, corn & beans (14 USNM). EL SALVADOR: Ahuachapán: Parque Nacional el Imposible, Centro de Interpretacion Mixtpec, 13°49′39″N, 89°56′51″W, V-14-2000, Smith, Ocampo, Cave, Cordero, m.v. light (1 UNSM, 1 MTEC); San Marcos: Los Planes, 25-VI-1959, P. A. Berry (1 USNM); San Salvador, 29-V-5-VI-1958, C. L. Cartwright, at light (1 USNM); Santa Ana: 6.0 km. W. Hwy CA1 above Lago de Coatepeque, 1-VI-1973, Erwin & Hevel Central American Expedition, 1973 (2 USNM). GUATEMALA: [unknown locality], Sallé coll., 1911-403 (1 NHMUK); Alta Verapaz: Cobán, Condradt, Thallisella condradti Gorham, [red ringed circle] TYPE, B.C.A., Col., VII (1 NHMUK); San Juan, Champion, 1911-403, Tr. Ent. Soc. L., 1913, det. Champion, Pharaxonotha kirshi R. (see Champion 1913; 1 NHMUK); Senahu, Champion, 1911-403 (1 NHMUK); 22-4, Schwarz & Barber, Cacao Trece Aguas (1 USNM); 17-4, Schwarz & Barber, Cacao Trece Aguas (1 USNM); Baja Verapaz: San Jerónimo, Champion, 1911-403, B.C.A., Col., II(1). Pharaonotha kirshi Reitt. (1 NHMUK); Guatemala: Capetillo, Champion, 1911-403 (1 NHMUK); Catarina Pinula, Puerta Parada, N145572, W90.4653, 23-II-1-III-2008, J. Schuster (1 FSCA); Jalpa: Mataquesuintila, Finca Concepcion, 2-VII-1986, J. M. Campbell, beating roadside vegetation (1 CNCI); Quiché: Panimá, Champion, 1911-403 (1 SEMC); Suchitepequez: Finca Chitalon Mazatenango, 8-III-1965, J. M. Campbell (1 CNCI); Finca San Rafael Olimpo, Cuyotenango, 22-1-I-1966, J. M. Campbell (1 CNCI); same data except, 20-1-I-1966, ex fungal gardens of Atta nest, 3 ft. below ground level (1 CNCI). HONDURAS: Francisco Morazán: Monte Uycau, 24-V-2993, F. E. Skillman JR, UV & MV light (1 FSCA); Tegucigalpa, El Loarque, 30-VII-1968, B. K. Dozier (2 FSCA); Zamorano, XI-XIII-1970, G. F. Freytag (1 MTEC); Zamorano, 13-X-1993, R. Turnbow (5 RHTC); Zamorano, 24-V-1993, R. Turnbow (1 RHTC); Zamorano, 6-VI-1993, R. Turnbow (1 RHTC); Zamorano, 14°N 87°W, 6-VI-1994, J. Ashe, R. Brooks, #014 ex rotting breadfruit (10 SEMC, 2 FSCA); same data except, 7-VI-1994, J. Ashe, R. Brooks, #028 ex breadfruit fall (1 SEMC); same data except, 7-VI-1994, #056 ex rotting vegetation (1 SEMC); same data except, 9-VI-1994, #055 ex rotting mangos (1 SEMC); same data except, 12-VI-1994, #091 ex leaf litter/rotting fruit (1 SEMC); same data except, 12-VI-1994, #093 ex leaf litter/rotting fruit (1 SEMC); same data except, 7-VI-1994, #028 ex breadfruit (1 SEMC); same data except, 7-VI-1994, #056 ex rotting vegetation (1 SEMC); same data except, 9-VI-1994, #055 ex rotting mangos (1 SEMC); same data except, 12-VI-1994, #091 ex rotting flowers (1 SEMC); same data except, 12-VI-1994, #093 ex leaf litter/rotting fruit (1 SEMC); same data except, 12-VI-1994, #094 ex leaf litter along stream (1 SEMC); same data except, 30-VI-1994, #258 ex rotting breadfruit (1 SEMC); Zamorano, along Rio Yeguare, 6-VI-1996, F. G. Andrews & A. J. Gilbert (58 CSCA). MEXICO: Chiapas: 12 mi. E. Santa Isabel at Rio Zoyoltenco, 9-VI-1991, J. Ashe, #81 ex fig-fall and litter (27 SEMC, 2 FSCA); 2 mi. S. Simojovel, 9-VI-1969, J. M. Campbell (1 CNCI); 22 km. N. Ocozocuatla, 1-VI-1979, JM & BA Campbell (1 CNCI); same data except, 2-VII-1969 (1 CNCI); 76 km. N. Ocosingo, 1-X-1986, R. Turnbow (1 RHTC); 8 km. S. Chicoasen, 1-VI-1991, J. Ashe, #42, ex leaf litter, sifted (4 SEMC); Barriozabal, VII-1966, ex maiz (4 CSCA); El Chorreadero, 26-VI-1990, R. Turnbow, mv + bl (1 RHTC); Tapachula, 28-II-1990, K. Hibbard, light trap (1 FSCA); Colima: Volcán de Colima, L. Conrad (3 USNM); Volcán de Colima, Conradt (1 USNM); Distrito Federal: Mexico City, Feb-76, F. L. Walters, ex irradiated maize (6 CNCI); Guanajuato: Tupátaro, Hög, B.C.A., Col., II(1). Pharaonotha kirshi Reitt. (3 NHMUK); Sallé coll., 1911-403 (1 NHMUK); Hidalgo: Jacala, 31-VIII-1960, Howden, at light (1 CNCI); Jalapa: Flohr, 1911-403 (1 NHMUK); Jalisco: 20 mi. SW. Autlan, 13-VII-1982, F. G. Andrews, blacklight (39 CSCA); Nuevo Leon: 10 km. N. Linares, 22-III-1991, R. Brooks, R. Leschen, #57, ex mercury vapor light (3 SEMC); 17 mi. W. Linares, 11-V-1994, J. E. Wappes, 2 FSCA); 29 km. W. Linares, S. Rosa Can., 3-VI-1983, S. & J. Peck, ravine oak forest litter Berlese (1 CNCI); 31.5 km. SW. Linares, 24-III-1991, R. Brooks, R. Leschen, #64, under leaves (1 SEMC); 32 km. SW. Linares, 17-24-III-1991, R. Brooks, R. Leschen, #44 ex flight intercept (10 SEMC); 5 mi. S. Monterrey, 21-VII-1963, H. F. Howden (1 CNCI); same data except, 6-VI-1963 (1 CNCI); same data except, 31-VI-1963 (1 CNCI); same data except, 20-VI-1963 (1 CNCI); Monterrey, 27-IV-1969, H. F. Howden (1 CNCI); Monterrey, Chipinque Mesa, 21-25-VI-1969, S. & J. Peck, forest (1 CNCI); Oaxaca: Tlaxiaco, 3-XII-1902, A. L. Herrara, in corn (7 USNM); Mitla, 27-VI-1900, C. C. Dean (1 USNM); Chittenden coll [likely an interception] (4 USNM); Querétaro: Arroyo
Review of Pharaxonotha inhabiting the cycad genus Dioon

Seco, San José de la Flores, 21°22′52″, N 99°30′12″, W, 6-7-VII-2003, J. A. Peréz de la Rosa y G. Vargas, ex Dioon edule (cono femenino) (1 CZUG); Mpío.Jalpan, RT-190, 4.9 km. NW. Zoyapica, 21°20′58″N, 99°18′38″W, 11-XII-2013, Kovarik, Skelly, Jones, ex oak leaf litter Berlese (4 FSCA, 2 UAQM); Tamaulipas: Bocotama w.s., 7 km. SSE Gomez Farias, 15-X-1985, R. Turnbow (1 RHTC); Cd. Mante, 27-VII-1960, H. Howden, light (1 CNCI); Guemes, 15 km. N. Ciudad Victoria, 6-6-1961, Univ. Kans. Mex. Exp. (14 SEMC); 12 miles south of El Mante, 17-VI-1941, H. Dybas (1 FMNH); Veracruz: 2.5 km. S. Jalapa, 28-V-1991, J. Ashe, #26 ex fungusy log (1 SEMC); Córdoba, 21-VII-1941, H. Dybas, at light (1 FMNH); Córdoba, Höge, B.C.A., Col., II(1). Pharaxonotha kirshi Reitter (2 NHMUK); Córdoba, Sallé coll. (3 NHMUK); Rd 185, 2 mi. S. Acayucan, 10-VII-1962, Campbell & Hill (2 CNCI); Tuxtla, Sallé coll., 1911-403 (1 NHMUK). NICARAGUA: Granada: Reserva Silv. Priv. Domitila, 11°42′50″N, 85°57′20″W, 6-9-VI-2002, R. Brooks, Z. Falin, S. Chatizimanolis, ex flight intercept trap NIC1BFC02_255 (1 CMNC); Reserva Silv. Priv. Domitila, 11°2.322′N, 85°6.88′W, 31-V-6-VI-2005, Fred. G. Andrews, mercury vapor light (3 CSCA); Reserva Silv. Priv. Domitila, 11°70830″, −85.95330″, 31-V-2011, C. W. Shin, NIC-CWS-2011 001 (43 SEMC, 8 FSCA); some data except, 1-VI-2011, at light, NIC-CWS-2011 007 (12 SEMC); some data except, 2-VI-2011, at light, NIC-CWS-2011 016 (22 SEMC); some data except, 4-6-VI-2011, Malaise trap, NIC-CWS-2011 Mal03 (1 SEMC); some data except, 6-VI-2011, Mercury vapor light on hill, NIC-CWS-2011 021 (13 SEMC); some data except, 8-10-VI-2011, flight intercept trap near stream, NIC-CWS-2011 FIT05 (2 SEMC); some data except, 9-VI-2011, Mercury vapor light, NIC-CWS-2011 066 (87 SEMC); some data except, 13-VI-2011, Mercury vapor light, NIC-CWS-2011 090 (1 SEMC); some data except, 14-VI-2011, Mercury vapor light, NIC-CWS-2011 092 (1 SEMC); Managua: Managua, 4-VI-2018, R. Turnbow (1 RHTC); Rio San Juan: 60 km. SE. San Carlos, Refugio Bartola, 10°58′40″N, 84°20′30″W, 26-V-2002, R. Brooks, Z. Falin, S. Chatizimanolis, ex ginger fruits, NIC 1BFC02 077 (SEMCA). PANA MA: Canal Zone, 12-V-1952, F. S. Blanton, at light (1 USNM); Chiriqui: Chiriquiquito, 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-VII-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, 21–25-IV-2015 (12 FSCA); Bexar Co., Leon Valley, 14-VI-1971, G. H. Nelson, black-light (2 FSCA); same data except, 3-VII-2012, J. E. Wappes, UV light trap (1 FSCA); same data except, 1-IV-2012 (1 FSCA); same data except, 30-IV-2012 (3 FSCA); same data except, 21–25-IV-2015 (12 FSCA); Bexar Co., Leon Valley, 14-VI-1971, G. H. Nelson, black-light (2 FSCA); same data except, 3-VII-1971 (1 FSCA); Caldwell Co., 4.5 mi. E. McMahan, 1-IV-1998, Wappes & Turnbow, MV/UL (1 FSCA); Comal Co., vic. Bulverde, 9-7-VII-1967, A. & M. E. Blanchard (1 USNM); Bastrop Co., Bastrop State Park, 14-IV-1959, Baker & Howden (2 CNCI); Bee Co., Beeville, 5-11-53, Univ. Kans. Mex. Exp. (1 SEMC); Bexar Co., 3 mi. N. Leon Springs, Scenic Oaks, 29°41′21″N, 98°39′40″W, 31-III-2012, J. E. Wappes, UV light trap (1 FSCA); same data except, 1-IV-2012 (1 FSCA); same data except, 30-IV-2012 (3 FSCA); same data except, 21–25-IV-2015 (12 FSCA); Bexar Co., Leon Valley, 14-VI-1971, G. H. Nelson, black-light (2 FSCA); same data except, 3-VII-1971 (1 FSCA); Caldwell Co., 4.5 mi. E. McMahan, 1-IV-1998, Wappes & Turnbow, MV/UL (1 FSCA); Comal Co., vic. Bulverde, 31-1-V-1998, J. E. Wappes (1 FSCA); Cottle Co., Paducah, 9-7-VII-1967, A. & M. E. Blanchard (1 USNM); Guadalupe Co., 10 mi. SE. Seguin, 1187 Kolman Rd., 29°29′N, 97°51′W, 17-21-V-2014, J. E. Wappes, MV/UV (1 FSCA); same data except, 23-IV-2015 (1 FSCA); Kerr Co., Kerrville, 5-VI-1956, H. & A. Howden, light (2 CMNC); same data except, 22-VII-1956 (2 CMNC); Kerr Co., Kerrville, 1-IV-1959, Becker & Howden, in malt trap (12 CNCI); same data except, 4-IV-1959 (1 CNCI); same data except, 5-IV-1959 (1 CNCI); same data except, 6-IV-1959 (2 CNCI); same data except, 10-IV-1959 (2 CNCI); same data except, 13-IV-1959 (6 CNCI); Kimble Co., Junction, 29-30-1967, A. & M. E. Blanchard (1 USNM).

**Intercepted materials (total 33).** These data represent specimens collected in commercial transport into Canada and the USA. They are deposited in the California (CSCA), Canada (CNCI), and United States (USNM) institutions with identification services for their official agricultural inspectors. There are no associated data that indicates where in US or Canada these were intercepted. Label data with host information include specimens originating: From Guatemala: 19-VI-1935, H. Y. Gouldman, E.Q.A31625, with corn (1 USNM). From Mexico: VI-1925, #277, on pke of cotton seed meal (1 USNM); VIII-1929, S.F.2236, corn (1-CSCA); 6-IX-1933, L.J. Ray, #1401, in cotton bolls (1-USNM); 17-VII-1934, H. Y. Gouldman, B.P.Q. A29060, on tree seeds (3 USNM); 22-VI-1935, G. F. Callingham, #158, on pineapple (1 USNM); 7-VII-1935, L. R. Dorland Thayer, 209, on sugar cane (1 USNM); 30-III-1936, 2881, on beans (1 USNM); 23-IX-1936, H. A. Carey, #7078, 36-32095, on cacti (6 USNM); 2-X-1936, B. C. House, #7097, 36-32096, on cactus plants (5 USNM); 8-X-1936, #7168, on cactus (1 USNM); 8-IX-1942, No. 29673, orchids (1 USNM); 12-VII-1944, 44-19882, on lilies (1 USNM); 7-XII-1950, Zuck...
colr. #72490, lot 52-13872, with dry banana fruit (2-USNM); 22-V-1952, H. Y. Gouldman, X28238, lot-52-6282, Cucurbita moschata seed (1 USNM); 4-XI-1955, D. Brock, Cal. Dept. Agr. No. 55K55, on corn (2 CSAC); 1957, E. de las Casas, en granos almacenados (2 USNM); 8-VIII-1966, ex corn (4 CNCI). From southern USA: XII-1943, ex peanuts from El Paso, Texas (1 CNCI).

Remarks. Based on the volume of data for *P. kirschii* listed above, 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. All specimens intercepted on plant products as a pest were associated with various grains or tubers. Even with the recognition of cycad associated species in the kirschii group, it is possible that cryptic species reside within the materials here considered *P. kirschii*. We prefer to 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. Many references cite the genus and species names with different spellings (see Leschen and Węgrzynowicz 1998). An effort was made to find every reference listing the species which might present additional information. Most only list the name or repeat previous information and are too numerous to present here in a comprehensive accounting. In the following paragraphs, we review some of the important literature.

In the original description, Reitter (1875) stated *P. kirschii* was collected in Opava [Troppau], Czecho- slovakia, in a plant product [depending on the translation it could be drugs, grain, or spelt] from Mexico. That was followed by the accounts of Riley (1894) and Chittenden (1895) discussing damage to grains at the World's Fair, Columbian Exposition in 1893, Chicago, Illinois, USA. Chittenden (1911), who possessed a captive colony, described and illustrated the life stages and made observations on the life history of *P. kirschii*. Larvae were illustrated again by Böving and Craighead (1931), and are only mentioned in other references (e.g., Roberts 1939; Sen Gupta and Crowson 1967, 1971; Lawrence 1991). With one exception, all literature with life history information simply repeats Chittenden (1911), this includes Hinton (1945) and Booth et al. (1990). More recent original work on their life history was published by Konoike et al. (1987).

The description of *P. kirschii* was soon followed by the description of *Pharaxonotha zamiae* Blake, 1928 [now a synonym of *P. floridana* (Casey, 1890) by Kingsolver 1973], that was reared from the “flowers of *Zamia floridana*”. After 60 years with no new species described in *Pharaxonotha*, Pakaluk (1988) offers a short redescrip-
tion of *P. kirschii* while describing two new cycad associated species in the genus. With several species in the genus being associated with cycads, there has been a misconception that *P. kirschii* could also be a cycad associate in the wild. We now know this is not the case.

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), Lawrence (1991) and many others. They report it feeding on stored plant products such as corn, corn meal, wheat, flour, beans, and edible tubers. Based on label data in this study, we can add that it has also been associated with imported cactus, orchids, fungus logs, lilies, pineapples, cotton, cotton seed meal, sugar cane, peanuts, squash (*Cucurbita moschata* Duchesne ex Poir) seeds, and tree seeds. Wild collections indicate associations with fruit, flower and treefall litter, leaf litter, various rotting fruits, rotting mushrooms, bracket fungus, fungusy log, leaf cutter ant fungal gardens, and general organic debris.

With the recognition of the cycad associated species in the kirschii group, we know of only one specimen of true *P. kirschii* associated with a cycad. This specimen was collected with the three specimens of *P. sclerotiza* on *D. angustifolium* in Querétaro. Our concept of *P. kirschii* is based on the type of *P. condradii* and specimens collected with stored products or collected in the wild without any cycad association. It is also possible that these non-cycad associated materials harbor cryptic species.

*Pharaxonotha kirschii* superficially resembles some species of *Cycadophila* Xu et al. in Asia, a genus that also has members associated with cycad pollination and others that are not (Xu et al. 2015; Skelley et al. 2017). We speculate that there is convergence in body characters for *Pharaxonotha* species that occur in early vs. late cone stages of development or are free living. This would allow for a stratification of niches. Species of *Cycadophila* associated with later cone development or not associated with cycads are similar externally to the kirschii group.
While those occurring on early cone development and possibly acting as primary pollinators are superficially more similar to other *Pharaxonotha* with similar habits. Diet shifts within in the Erotylidae were studied by Leschen and Buckley (2007), who briefly mention *Pharaxonotha* as cycad feeders.

**Discussion**

In recent phylogenetic analyses of beetle diversity based on a large nuclear data set (McKenna et al. 2019) and on nuclear and mitochondrial legacy loci (G. Powell, pers. comm. 2021), *Pharaxonotha* was shown to be sister to all remaining Erotylidae in a clade comprised of the Erotylidae+Phytophaga, which includes Cucujoidea. It is probable that these ancient plant and beetle lineages have coevolved at some level for many millions of years.

Within the Erotylidae, Leschen and Buckley (2007) hypothesize that fungivory may be the ancestral state in the Erotylidae, likely based on other habits of other subfamilies. However, adult and early instar larvae of *Pharaxonotha floridana* (Casey) inhabiting cycad cones appear to be pollen feeders, while late instar larvae feed on cone sporophyll and axis tissue (Norstog et al. 1992). *Pharaxonotha* may inhabit cycad cones in the New World with other beetle genera, including *Ceratophila* Tang, Skelley and Perez-Farrera (Erotylidae: Pharaxonothinae) in the cycad host *Ceratozamia* Brongn., and primitive weevils of the subtribe Allocorynina (Belidae) in the host cycads *Dioon* Lindl. and *Zamia* (O’Brien and Tang 2015; Tang et al. 2018a, 2018b, 2020).

Tang et al. (2018b, 2020) presented preliminary relationships of populations within *Pharaxonotha*, based on analysis of the 16S rRNA gene, recognizing three distinct radiations: early-diverging lineages, a Caribbean radiation, and a recent radiation. For *Pharaxonotha*, there are currently 11 previously described species: 7 associated with *Zamia*, 2 associated with *Ceratozamia*, one with *Microcycas*, and one free living. Adding 9 with *Dioon* described here, the total described is 20. Evaluating morphological characters of *Pharaxonotha* populations that lack molecular data and the trees in Tang et al. (2018b, 2020), we estimate at least 30 species are present in the available materials. However, many species and populations of cycads remained to be sampled and this number will surely increase in the future.

Genetic analysis indicates that *Pharaxonotha* has radiated at least twice in the genus *Dioon*, as exhibited in the distant placement of species groups recognized in this paper in the trees of Tang et al. (2018b, 2020). These species groups include older, early-diverging lineages as well as a recent radiation which does not precisely match current divergence patterns in *Dioon* (Gutiérrez-Ortega et al. 2018). Radiations in insects and hosts may have responded differently to episodes of orogeny or climatic shifts due to glacial cycles (Gregory and Chemnick 2004; Gutiérrez-Ortega et al. 2018) or beetle diversity patterns were altered by host shifts of beetle lineages from other cycad genera (Tang et al. 2018b, 2020). While some species lineages may have coevolved, these patterns indicate that *Pharaxonotha* and *Dioon* do not exhibit exact parallel evolution and that radiations in *Pharaxonotha* have been to some extent independent from the evolution of their host cycads.

**Acknowledgments**

We thank Michael Calonje, Jeff Chemnick, Wes Field, Hector Gómez Dominguez, Tim Gregory, Chip Jones, Robert Jones, Pete Kovarik, Anders Lindström, Silvia Salas Morales, Oscar Moreno and Andrew Vovides for assistance in the field and Jeff Chemnick and Tim Gregory for financial support. Thanks also to Ítalo Salvatore de Castro Pecci-Maddalena (Departamento de Zoologia, Universidade Federal do Paraná (UFPR), Curitiba, PR, Brazil) and Héctor Jaime Gasca-Álvarez (Programa de Biología, Universidad Pedagógica y Tecnológica de Colombia) Sede Central – Tunja, Boyacá, Colombia) for helpful comments in presubmission reviews. We thank the Florida Department of Agriculture and Consumer Services, Division of Plant Industry for support of this work.

**Literature Cited**


Roberts AWR. 1939. On the taxonomy of Erotylidae (Coleoptera), with special reference to the morphological characters of the larvae. Transactions of the Royal Entomological Society of London 88: 89–118.


Received January 10, 2022; accepted January 25, 2022.

Review editor Erin Powell.