

Flohria Sharp—a Relictual Genus of the Subtribe Philonthina From the Americas (Coleoptera: Staphylinidae: Staphylininae)

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ABSTRACT *Flohria subcoerulea* (LeConte), a relictual genus and species of the subtribe Philonthina (tribe Staphylinini) from the Americas, is redescribed and illustrated, its distribution documented, and lectotypes designated. The phylogenetic position of the genus within Philonthina, as well as its potential age and origin, is discussed.

RESUMEN Se redescrive e ilustra *Flohria subcoerulea* (LeConte), un género y especie relictual de la subtribu Philonthina (tribu Staphylinini) de las Américas. Se documenta su distribución y se designan lectotipos. Se discute la posición filogenética del género dentro de Philonthina, su edad potencial y origen.

KEY WORDS *Flohria*, Nearctic, Neotropical, Philonthina, Staphylinini

The genus *Flohria* belongs to the Philonthina, a very speciose subtribe of Staphylininae with 29 genera currently known in the Americas and 70 genera with >2,700 species worldwide (Herman 2001; A. F. N., unpublished data). Although *Flohria* is widely distributed in southern North America and Central America (Herman 2001; Navarrete-Heredia et al. 2002), it appears to be rare in collections and nothing is known so far about the habits of this genus. *Flohria* was erected for a single species from Mexico, *F. laticornis*, by Sharp (1884) who suggested that this genus should be “best placed between *Philonthus* and *Ocyopus*.” This assumption was probably based on the fact that *Flohria* shows characters that are found in either one or the other of these two genera, such as the emarginate ligula and the enlarged apical labial palpomere (*Ocyopus* Leach) or the lateral puncture of pronotum bearing long macroseta close to the superior line of pronotal hypomeron (*Philonthus* Stephens). The taxonomy of *Flohria* remained unchanged and without subtribal assignment until Newton et al. (2000) transferred another species to this genus (*Gastrisus subcoeruleus* (LeConte 1863)) and suggested it might be conspecific with *F. laticornis*; this synonymy was confirmed by Navarrete-Heredia et al. (2002). *Flohria subcoerulea* had been originally described by LeConte as belonging to *Trigonophorus* Nordmann, which was later replaced by *Trigonopselaphus* Gemminger and Harold by these

authors (see Herman, 2001: 3599). *Trigonopselaphus subcoeruleus* as well as a few other species belonging to this genus were subsequently transferred to *Gastrisus* Sharp by Scheerpeltz (1972). Based on the glabrous tarsal empodium, Newton et al. (2000) suggested the placement of *Flohria* in Philonthina as defined by Smetana and Davies (2000). *Flohria* has been considered as belonging to Philonthina since then (e.g., Herman 2001, Navarrete-Heredia et al. 2002, Chani-Posse 2014). Such assignment has also been supported by a recent phylogeny including all but one of the so-called New World genera of Philonthina (Chani-Posse 2013). The resulting phylogenetic hypothesis proposes that *Flohria* is the lineage sister to the clade that forms the rest of the subtribe. However, this study targeted resolution on the phylogenetic relationships of only the Neotropical endemic genera of Philonthina, and therefore, the basal relationships recovered within the subtribe should be taken with caution.

The objectives of this study are to redescribe *Flohria* and its current single species using characters from external morphology and genitalia, to detail its distribution and morphological affinities with other taxa within and outside of Philonthina, and to discuss current evidence about its phylogenetic position, age and origin within the subtribe.

Materials and Methods

Type material relevant to this review is deposited in the following institutions:

BMNH: The Natural History Museum, London, UK.
 FMNH: Field Museum of Natural History, Chicago, USA.
 MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, USA.

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Beetles were examined as pinned dry specimens, some of which were first relaxed in warm soapy water, rinsed, dissected, and examined as wet preparations in glycerin for more detailed morphological study. Dissected genitalia were macerated in 10% KOH, washed in distilled water, and placed in plastic genitalia vials with glycerin and pinned under the respective specimens. Observations were made using a Leica MZ6 dissecting microscope. Photographs were taken using a Leica DC 150 digital camera attached to the dissecting microscope. Line drawings were traced from digital photographs. Depositories of type material retain the copyright of the photographs. Scanning Electron Microscope (SEM) pictures were obtained by using a JSM-6610 system. Measurements (given in millimeters) were made with an ocular micrometer. Overall body length was measured from the apex of the labrum to the apex of the abdomen. Other measurements were taken and abbreviated as follows: HW, maximum head capsule width; HL, length of head capsule, from anterior margin of frontoclypeus to neck constriction (along midline); PW, pronotum maximum width; PL, pronotum length (along midline); EL, eye length (seen from above); TL, temple length (from the posterior margin of the eye to the nuchal ridge; seen from above); NW, neck width; S1, first segment of hind tarsus length; S5, last segment of hind tarsus length; EtL, elytra length at sides (from humerus to apex; seen from above); Etl, elytra length along suture; S9b/d, sternum IX basal or distal portion length (measured along the longitudinal line (y) joining the most basal and distal ends of sternum IX, the limit between the two portions given by a transverse line (x) at the maximum width of sternum IX). Terminology mainly follows Blackwelder (1936), Smetana (1995), Smetana and Davies (2000), Schilhammer (2000), and Solodovnikov and Newton (2005).

Lectotypes are designated to fix the identity of each specific name, as holotypes were not established at the time of original publication. Exact label data are cited below only for the type material, with separate labels indicated in brackets. Data for all nontype material examined are given in minimally edited form in the [Supp Table 1](#) (online only), and deposition codens for those records explained in [Supp Table 2](#) (online only), following Evenhuis (2014) for public collections. All sufficiently detailed localities were georeferenced, if coordinates were not already provided, using Selander and Vaurie (1962), Google Earth (<http://www.google.com/earth/>), or (Mexico only) 1:250,000 scale topographic maps. Data for a few unexamined specimens (indicated as such in the Comments field in [Supp Table 1](#) [online only]) are included based on photos and associated data available on the online resource BugGuide (<http://bugguide.net/node/view/15740>) and on the data and figure in Dugès and Villada (1901). Data were mapped onto a satellite-derived and shaded relief map (naturalearthdata.com) including administrative areas (boundaries) using DIVA-GIS version 7.5.0.0 (Hijmans et al. 2012).

Taxonomy

Genus *Flohria* Sharp, 1884

(Figs. 1–5)

Flohria Sharp, 1884: 391 (species included: *laticornis*); Bernhauer and Schubert 1914: 366 (catalog); Blackwelder 1944: 136 (checklist); Blackwelder 1952: 166 (type species: *laticornis*); Newton et al. 2000: 332, 396 (key); Herman 2001: 2605 (catalog); Navarrete-Heredia et al. 2002: 310, 338 (key, catalog); Newton et al. 2005: 19 (checklist, as “probable” for Colombia); Chani-Posse and Couturier, 2012: 83; Chani-Posse 2013: 4, 7, 8, 11 (phylogenetic placement); Chani-Posse 2014: 62, 68, 69, 71, 72, 75, 78, 80 (key).

Type Species. *Flohria laticornis* Sharp (subjective junior synonym of *F. subcoerulea* (LeConte)), fixed by monotypy.

Diagnosis. *Flohria* differs from all other genera of Philonthina by its elongate and cylindrical body with the abdomen (when fully exposed) distinctly longer than the head, pronotum, and elytra combined, as well as the following combination of characters: labial palpi with apical palpomere distinctly wider than that of the maxillary palpi, antennae with antennomere I about twice as wide as II, pubescence starting on V, antennomeres I–IV with only long sparse setae.

Redescription. Length 13.2–15.2 mm. Coloration. Head, thorax, and abdomen black; elytra metallic blue; antennae, palpi, and legs black to piceous-black (Fig. 4).

Head. Rounded-quadrate shape, slightly narrowed at basal third, with obliterated hind angles, widest behind eyes, gradually narrowed anteriorly; moderately wider than long, slightly to moderately narrower than pronotum at widest point; nuchal constriction and nuchal ridge developed laterally and dorsally; infraorbital ridge present, extending some distance in front of the lateral bend of the postgenal ridge and continuing (or not) anteriorly to near the base of the mandible; ventral basal ridge well developed (Fig. 2A and B); postmandibular ridge and dorsal basal ridge present (Fig. 2A); dorsal and ventral surface of head with coarse punctation, microsculpture indistinct. Eyes moderately convex but not prominent, distinctly shorter than temples seen from above. Antennae inserted closer to anterior margin of frontoclypeus than to eyes, separated from each other by no more than 2.5× the distance to eye, antennomere I not longer than half of the head length and 1.8–2× as wide as II, II distinctly shorter than III, I–IV with only long sparse setae, pubescence starting on V and more dense on VI–XI (Fig. 2C). Labrum strongly transverse, broadly bilobed (Chani-Posse, 2013: Fig. 1G). Mandibles moderately prominent and stout, each with setose prosthema well-developed on medial margin and 2–3 teeth near middle of inner edge in addition to the apex. Maxillary palpus with palpomere II about as long as III (subapical), IV longer but slightly narrower than III (Fig. 2A). Gular sutures narrowly separated near middle, running close to the base of head (Fig. 2A and B, and Chani-Posse, 2013: Fig. 3C). Mentum with anterior margin straight to slightly emarginated and about as long as submentum,

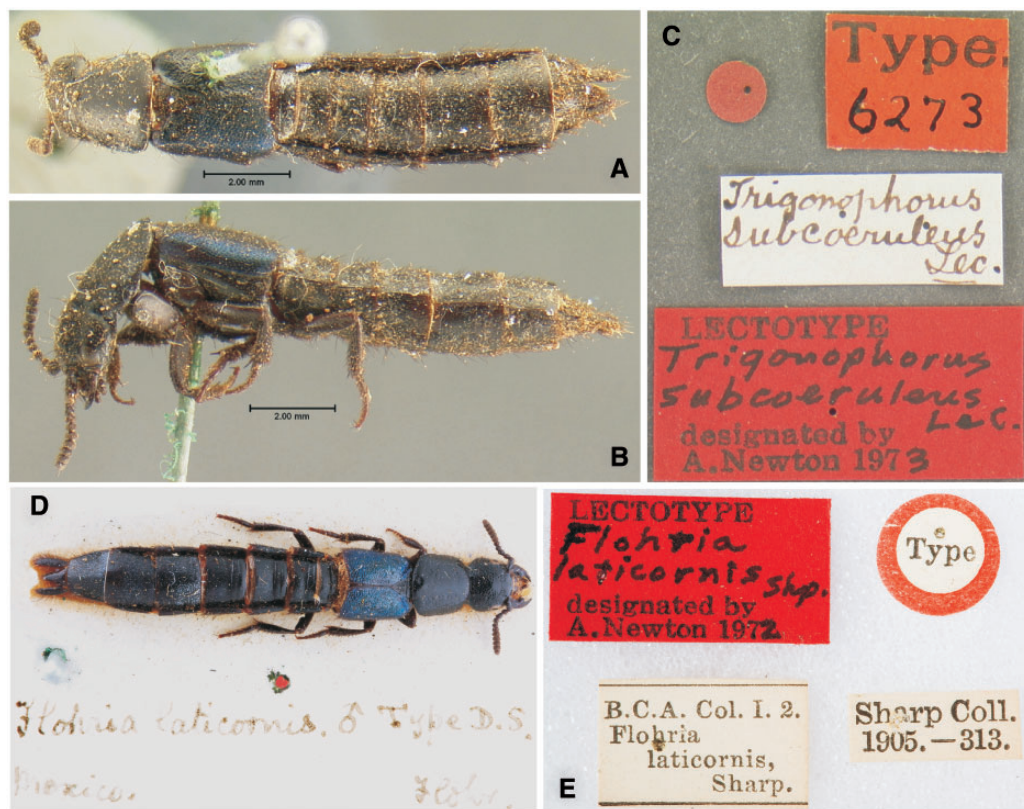


Fig. 1. *Trigonophorus subcoeruleus* LeConte, lectotype (A) habitus, dorsal view; (B) habitus, lateral view; (C) labels. Photographs by Whit Farnum © Copyright 2013 President and Fellows of Harvard College, Museum of Comparative Zoology, Harvard University. *Flohria laticornis* Sharp, lectotype (D) habitus, dorsal view; (E) labels. © Copyright 2014 The Natural History Museum, London, UK, and Stylianos Chatzimanolis.

with two pairs of long setae (Fig. 2B). Labial palpus moderately long, palpomere I 1.5–2× as long as II, III (apical) distally inflated and distinctly longer than II (Fig. 2C).

Prothorax. Pronotum slightly to moderately longer than wide, slightly narrowed anterior to parallel-sided; front margin subtruncate, hind margin broadly arcuate, anterior angles distinctly angulate, posterior angles rounded; disc more or less densely and finely punctate, with a rather smooth, impunctate longitudinal area of variable width along midline that is usually delimited by two rows of coarse punctures, each with 4–9 or more punctures; superior marginal line of pronotal hypomeron slightly deflexed under anterior angle, inferior marginal line subcontiguous to superior line behind anterior angles (Fig. 2D); lateral puncture with long macroseta seta at a distance from superior marginal line of hypomeron no more than diameter of puncture. Prosternum short and transverse, triangular, with only a medial prominence, not carinate, not longitudinal along basisternum, basisternum longer than furcasternum, with two medio-apical macrosetae. Mesoscutellum with two transverse carinae. Mesoventrite with sternacostal carina and sternopleural (anapleural) suture more or less curved so that medial part of suture is more

longitudinal and lateral part more transverse; mesoventral intercoxal process narrow and pointed; disc of mesoventrite situated more or less in one plane with the mesoventral part of mesocoxal acetabula.

Legs. Procoxae distinctly enlarged basally, contiguous. Profemora distinctly broadened at basal half and narrowed apically; protibiae stout and spinose, with ventral setae denser than on meso- and metatibiae; protarsi with first four segments flattened dorsoventrally and slightly widened distally, more distinct in males, with long, straight, and pale (adhesive) setae underneath; meso- and metacoxae subcontiguous; meso- and metatibiae dorsoventrally flattened and spinose; metatarsomere I as long as to slightly longer than metatarsomere V (last) ($S1/S5 = 1.0-1.1$).

Elytra. At suture moderately to slightly shorter than pronotum at midline.

Hind Wings. Fully developed, venation with MP3 free and MP4 fused to CuA, similar to wing of *Belonuchus mordens* Erichson (Chani-Posse, 2013: Fig. 4A).

Abdomen. Tergum I with pair of large deep prototergal glands similar in placement and external appearance to those of *Philonthus varians* (Paykull) described by Quenstedt et al. (2002); abdominal terga III–V (rarely also VI) with anterior and posterior transverse basal carinae, area between both carinae densely and

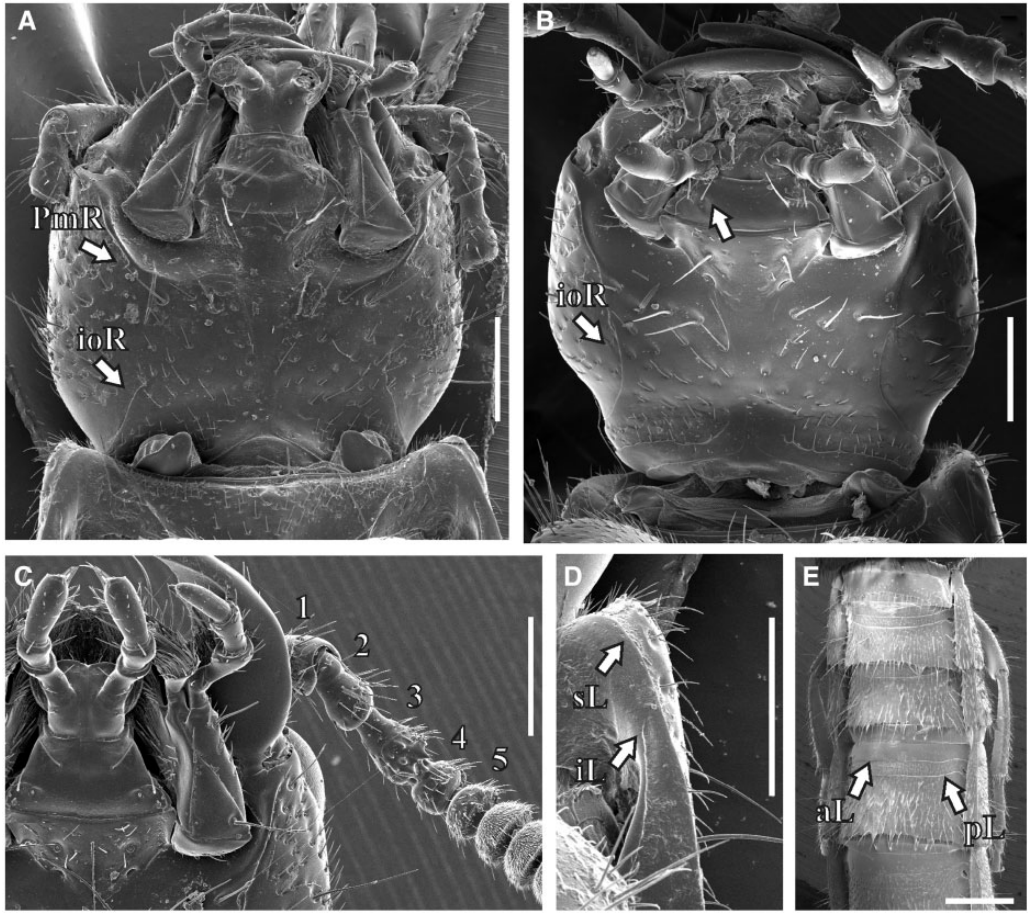


Fig. 2. *Flohria subcoerulea* (A, B) head, ventral view; (C) mouthparts and right antenna, ventral view; (D) pronotal hypomeron; (E) abdominal tergites. Scale bar = 500 μ m. Abbreviations: aL, anterior line; iL, inferior line; ioR, infraorbital ridge; pL, posterior line; pmR, postmandibular ridge; sL, superior line.

finely punctate (Fig. 2E); terga VI–VIII with anterior carina only; apices of terga III–VI and sterna III–VIII finely crenulate (with minute rounded teeth); sterna III–VII with single transverse carina that is medially angulate (III) or broadly posteriorly rounded. Intersegmental membranes between segments III–VI preapically attached to preceding segment, with pattern of minute triangular or irregular microsclerites. Hind margin of both sternum VII and tergum VIII truncate in both sexes.

Male Genitalia. Sternum VIII emarginate medioapically (Fig. 3A). Genital segment with lateral tergal sclerites IX (styli) stout; tergum X truncate at apex with several apical setae (Fig. 3E); sternum IX with basal portion moderately asymmetrical, distinctly shorter than the distal portion ($S9b/S9d=0.5$), moderately emarginate apically, with several fine and short setae at each side of emargination (Fig. 3B). Aedeagus with paramere elongate and entire with two lateral rows of sensory peg setae joined at apex; median lobe elongate, with apical part narrowed into a rounded apex (Fig. 3C and D).

Female Genitalia. Sternum VIII hind margin truncate. Genital segment with lateral tergal sclerites IX and tergum X similar to that of male, but X narrower apically (Fig. 3G); second gonocoxites each with 1–2 long macroseta basally, with a minute stylus (Fig. 3F) bearing two long apical macrosetae.

Immature Stages. Unknown.

Distribution and Diversity. The genus *Flohria*, with only one species known at present, is widely distributed from southern USA (Texas) to Costa Rica (Herman 2001, Navarrete-Heredia et al. 2002, Supp Table 1 [online only] and Fig. 5).

Note. The gender of *Flohria* was not expressly stated by Sharp (1884) when he established it. The taxonomic epithet used for naming the single species for which the genus was originally described (“*laticornis*”) has identical masculine and feminine spellings. Following the ICZN (1999, Article 30.2.4), Newton et al. (2000) and Navarrete-Heredia et al. (2002) assumed a feminine gender for *Flohria*, and accordingly adopted the feminine spelling *subcoerulea* as the valid name of this species.

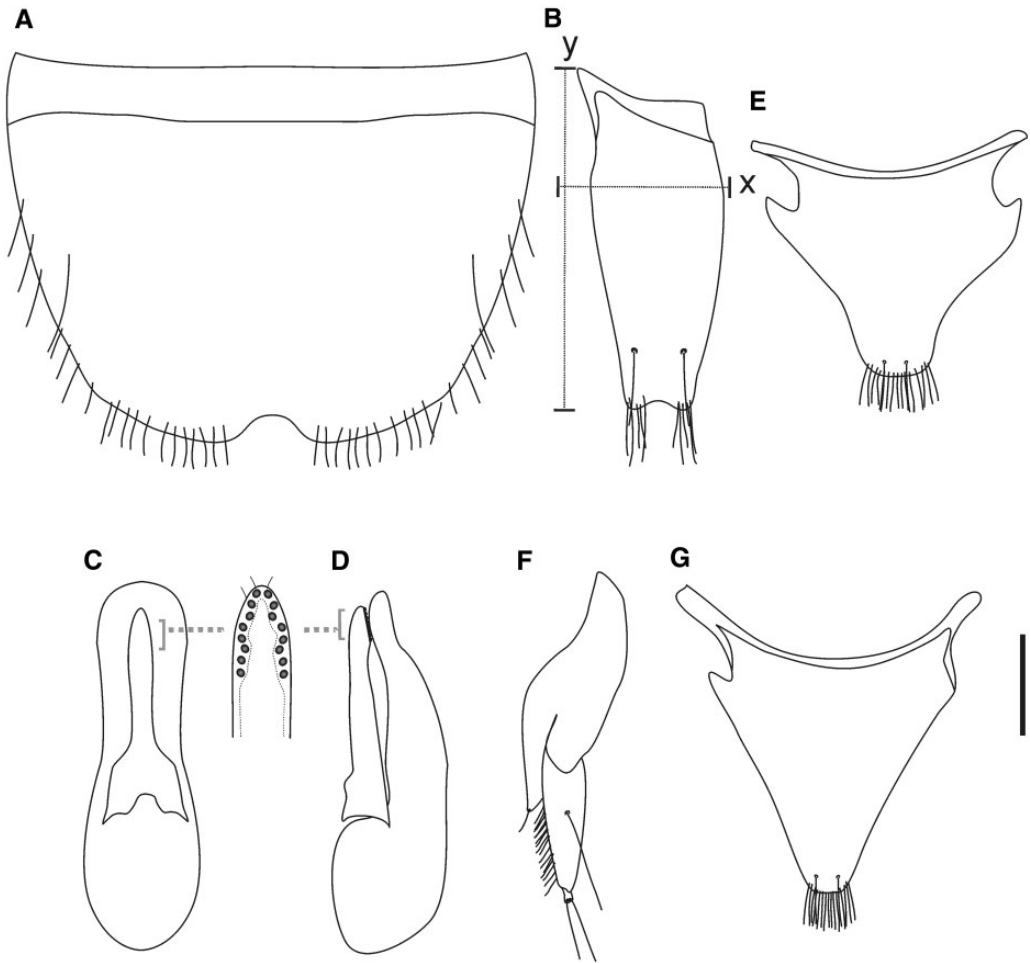


Fig. 3. *Flohria subcoerulea* (A) male sternum VIII; (B) sternum IX; (C) aedeagus, dorsal view, with detail of apex of paramere in ventral view; (D) aedeagus (lateral view); (E) male tergum X; (F) gonocoxites of female genital segment; (G) female tergum X. Scale bar = 0.4 mm.

***Flohria subcoerulea* (LeConte, 1863)
(Figs. 1–5)**

Trigonophorus subcoeruleus LeConte, 1863: 35.

Trigonopselaphus subcoeruleus; Gemminger and Harold, 1868: 597; Bernhauer and Schubert, 1914: 403 (catalog).

Gastrisus subcoeruleus; Scheerpeltz, 1972: 37.

Flohria subcoerulea; Newton et al. 2000: 296 (probably conspecific with *laticornis*); Herman, 2001: 2605 (catalog, spelled *subcoeruleus*); Navarrete-Heredia et al. 2002: 338 (catalog, synonymy); Maes, 1998: 553; Chani-Posse 2014: 62, 68, 69, 71, 72, 75, 78, 80 (key).

Flohria laticornis Sharp, 1884: 392; Bernhauer and Schubert, 1914: 366 (catalog); Dugès and Villada, 1901: 29, Fig. 51; Lucas, 1920: 245; Blackwelder, 1944: 136; Herman, 2001: 2605 (catalog); Navarrete-Heredia et al. 2002: 338 (syn. of *subcoerulea*); Chani-Posse, 2013: 4, 7, 8, 11 (phylogenetic placement).

Diagnosis. As for the genus (see above).

Redescription. Body length 13.2–15.2 mm (6.0–6.8 mm, abdomen excluded). Coloration as for the genus.

Head. Moderately wider than long ($HW/HL = 1.2$), slightly to moderately narrower than pronotum ($HW/PW = 0.8–0.9$); postmandibular ridge bordering almost completely mandibular base (Fig. 2A). Eyes distinctly shorter than temples ($EL/TL = 0.70–0.75$) seen from above. Antennae with antennomere I about as long as II and III combined, III about $1.3\times$ as long as II. Labial palpus with palpomere III about twice as long as II. Maxillary palpus with palpomere IV (apical) $1.3\times$ as long as III. Neck about $0.7–0.8\times$ as wide as head at widest point.

Prothorax. Pronotum slightly to moderately longer than wide ($PW/PL = 0.8–0.9$), dorsal rows of punctures (if distinct) each with 7–9 punctures.



Fig. 4. Habitus of *Flohria subcoerulea*. © Copyright 2008 Mike Quimm. Scale bar = 1 mm.

Legs. Metatarsomere I as long as to slightly longer than metatarsomere V (last) ($S1/S5 = 1.0-1.1$).

Elytra. At sides about $1.5\times$ as long as elytra along suture ($EtL/EtI = 1.4-1.6$); at suture distinctly shorter than pronotum at midline ($EtI/PL = 0.6-0.7$); punctuation fine and dense.

Abdomen. Abdominal terga III–V with posterior transverse basal carina straight.

Male Genitalia. Sternum VIII distinctly emarginate medioapically (Fig. 3A). Sternum IX with longest apex of basal portion acute and two long subapical setae (Fig. 3B). Tergum X truncate at apex with two long subapical setae and >10 apical setae (Fig. 3E). Aedeagus with median lobe slightly narrowed at apical fourth (Fig. 3C and D); paramere reaching four fifths of median lobe length, with two lateral rows of sensory peg setae joined at apex, each with about eight setae.

Female Genitalia. As for the genus (see above).

Geographical Distribution. As for the genus (see above).

Bionomics. *Flohria subcoerulea* is a rare species; although about 60 independent captures of it are known (see Supp Table 1 [online only]), all except five captures were of only a single specimen, and the largest known series collected at one time is four specimens. Nevertheless, the known distribution is not only quite broad (Fig. 5), but covers an exceptionally wide range of elevations, climates, and habitats, from subtropical or tropical forests near sea level in southern Texas and Costa Rica to temperate forests of Mexican volcanic peaks at nearly 3000 m; it has also been found in drier regions that lack natural forest, and even in very disturbed habitats such as former farmland and in city suburbs. It has been collected in all months except January through March, but mostly in the summer (June–September). It has been found in forest leaf litter, in pitfall and Malaise traps, in the entrance room of a cave, and in a suburban garden, but most collections lack such details. The peculiar morphology that makes this species distinctive within Philonthina and other Staphylinini (e.g., extremely elongate body form and especially long abdomen, short thick antennae, unusual head shape) suggests that this species inhabits some odd microhabitat or has an unusual natural history (Newton et al. 2000; Navarrete-Heredia et al. 2002). Short thick antennae and legs (but not a slender body form) are observed in the myrmecophilous genera *Cordylaspis* Nordmann and *Weiserianum* Bernhauer (Scheerpeltz 1937a, Chatzimanolis 2014), while the slender body form is more reminiscent of Xantholinini and other staphylinids that are considered well-adapted to maneuvering through small interstitial spaces in litter and soil (e.g., Hammond 1979, Pace 1996). So far, however, the habits of *Flohria* remain enigmatic. The immature stages are unknown.

Type Material. *Trigonophorus subcoeruleus* LeConte: LECTOTYPE (designated here) (Fig. 1A–C), ♂, specimen mounted on pin: '[solid dark red circle, =Texas]', 'Type 6273' [printed text and handwritten number on red label], '*Trigonophorus subcoeruleus* LeC.' [handwritten white label], Lectotype



Fig. 5. Distribution of *Flohria subcoerulea* in North and Central America.

Trigonophorus subcoeruleus LeConte des. | Chani-Posse & Newton 2014 [printed red label] (MCZ). PARALECTOTYPE, ♀, specimen mounted on pin: [solid dark red circle, =Texas], Paralectotype *Trigonophorus subcoeruleus* LeConte des. | Chani-Posse & Newton 2014 [printed red label] (MCZ). Note: LeConte (1863) did not mention how many specimens he saw, but fixed the type locality as Texas (indicated only by a color coded round label on each specimen). Although lectotype and paralectotype labels were attached by A.F.N. in 1973 (Fig. 1C, lectotype), these designations were never formally published, and those labels have now been replaced with the current ones cited above.

Flohria laticornis Sharp: LECTOTYPE (designated here) (Fig. 1D and E), mounted on card: 'Flohria laticornis. ♂ Type D. S. | Mexico. Flohr.' [handwritten by Sharp on card with specimen], 'Type' [round printed label with red border], 'B. C. A. Col. I. 2. | Flohria | laticornis, | Sharp.' [printed white label], 'Sharp Coll. | 1905 - 313' [printed white label], Lectotype *Flohria laticornis* Sharp des. | Chani-Posse & Newton 2014 [printed red label] (BMNH). PARALECTOTYPE, mounted on card with head and left antenna propped up on smaller cards: 'Flohria laticornis. ♀ Type D. S. | Uruapan. Mexico. Flohr.', 'Type' [round printed label with red border], 'B. C. A. Col. I. 2. | Flohria | laticornis, | Sharp.' [printed white label], 'Sharp Coll. | 1905 - 313' [printed white label], Paralectotype *Flohria laticornis* Sharp des. | Chani-Posse & Newton 2014 [printed red label] (BMNH). PARALECTOTYPE, mounted on small card supporting abdomen: 'Flohria laticornis. D. S. | Mexico City. Forrer.' [handwritten by Sharp on large card], 'Cuidad [sic] | Mexico | Forrer' [small handwritten label not in Sharp's writing], 'Syn-type' [round printed label with blue border], 'B. C. A. Col. I. 2. | Flohria | laticornis, | Sharp.' [printed white label], 'Paralectotype *Flohria laticornis* Sharp des. |

Chani-Posse & Newton 2014' [printed red label] (BMNH). PARALECTOTYPE, ♂, mounted on card [aedeagus partly extruded from abdomen]: '♂ | Flohria laticornis. D. S. | Mexico. Flohr.' [handwritten by Sharp on card with specimen], 'B. C. A. Col. I. 2. | Flohria | laticornis, | Sharp.' [printed white label], 'Sharp Coll. | 1905 - 313' [printed white label, inverted on pin], 'Chicago Nat. Hist. Mus. | (ex D. Sharp Colln. | by exchange with | Brit. Mus. Nat. Hist.)', Paralectotype *Flohria laticornis* Sharp des. | Chani-Posse & Newton 2014 [printed red label] (FMNH).

Note. Sharp (1884) indicated that he had seen four specimens, from "Almolonga, Jalcomulco, Uruapan (Flohr), and Ciudad in Durango (Forrer)," and that one of these was a male. We believe we have identified these four specimens, all labeled and named by Sharp in his handwriting on the card with the specimen (3) or below a pointed specimen (1), and have designated them as lectotype and paralectotypes above. Two additional specimens at BMNH were collected by another collector (Höge) and have printed B. C. A. name labels as above but do not have Sharp's own handwritten labels; one is from a different locality ("Colima city, Mexico") and the other from "Ciudad, Durango"; these specimens lack circular BMNH type labels and we agree with Roger Booth of BMNH that they were not part of the original type series. However, there are some discrepancies between the designated type specimens and Sharp's (1884) published statements that should be noted: (a) The published localities Almolonga and Jalcomulco do not appear on any of the specimens, instead the lectotype at BMNH and paralectotype at FMNH say simply "Mexico. Flohr." on their cards and have no original locality labels attached; we think the original labels were probably removed or lost. Thus, there is no way now to know which locality corresponds to which of these specimens; the type locality (locality of the lectotype) could therefore be either of these

towns, but they are both in the state of Veracruz within 27 km of Jalapa (Selander and Vaurie 1962), so the type locality can be stated as Veracruz state, Mexico. (b) The second paralectotype at BMNH was labeled on the card by Sharp as “Mexico City” [= Ciudad de México, in Distrito Federal within México state], but this is almost certainly a temporary misinterpretation by Sharp of the original locality label, “Ciudad [sic, = Ciudad] Mexico Forrer” which could be interpreted as either “Ciudad, Mexico” [town in Durango state] or “Ciudad México” [as above]. According to Selander and Vaurie (1962), “Ciudad” is a “... Forrer locality, cited in the Biologia as Ciudad in Durango or Ciudad, province of Durango”; we think this specimen represents the original specimen cited correctly by Sharp (1884) as “Ciudad in Durango (Forrer)”. (c) Sharp (1884) indicated having seen only one male, but two of the Sharp-labeled cards indicate “♂” and at least one of these is correct (male at FMNH with aedeagus partly extracted); we did not confirm the sex of the others at BMNH. Although lectotype and two paralectotype labels were attached by A.F.N. in 1972 (Fig. 1E, lectotype), these designations were never formally published, and those labels have now been replaced with the current ones cited above.

Other Material Examined. A total of 57 nontype specimens from 24 collections have been seen and identified by one or both of us, and six additional specimen records were taken from other sources, including Dugès and Villada (1901). Full data on all these specimens and their depositories (if known) are provided in Supp Tables 1 and 2 (online only), respectively, and the distribution of all sufficiently detailed capture records (including types) is mapped in Figure 5.

Age and origin of *Flohria*

The most comprehensive basis for a modern taxonomic study of the Nearctic genera and species of Philonthina belongs to Smetana (1995). However, the assignment of *Flohria* to the subtribe Philonthina (Newton et al. 2000) was posterior to Smetana (1995) who did not include *Flohria* among the eight genera treated in his study. A formal morphology-based phylogenetic analysis of the primarily Neotropical Philonthina lineages that included *Flohria* along with a number of non-Philonthina outgroups (Chani-Posse 2013), confirmed its relation with Philonthina. Therefore, *Flohria* has been recently included in Chani-Posse's (2014) key to New World genera of Philonthina, where it is keyed out early (couplet 7) after the following combination of characters: antennae with pubescence starting on 5th antennomere, lacking on antennomeres 1–4 (with only longer sparse setae), and 1st antennomere distinctly more than 1.5 times as wide as 2nd, sternopleural (anapleural) suture more or less curved so that medial part of suture is more longitudinal and lateral part more transverse, and abdomen subcylindrical in lateral view. While the last two characters appear as unique in *Flohria* and within Philonthina according to Chani-Posse (2013), the antennal condition is also shown by the Old World genera *Agacerus*

Fauvel and *Moeocerus* Fauvel. These two genera have been shown to form a natural group together with the Afrotropical genus *Glyphesthus* Kraatz (Li and Zhou 2011). Additionally, *Glyphesthus*, *Moeocerus*, *Agacerus*, and *Flohria* share the last labial palpomere distinctly broadened apically (Li and Zhou 2011, Chani-Posse 2013) and have certain similarity in habitus, especially *Flohria* and *Agacerus*. On the other hand, characters that are unique for *Flohria* within Philonthina, such as mentum with two pairs of macrosetae and the front femur densely spinose on lateroventral side, are common across Staphylinini. Furthermore, the condition shown by *Flohria* for the superior and inferior lines of the pronotal hypomeron rarely occurs in Philonthina (e.g., *Philonthus caeruleipennis* (Mannerheim)), appearing as intermediate between those that distinguish Xanthopygina and Philonthina as they were defined by Smetana and Davies (2000). All these presumably plesiomorphic characters seem to support a rather basal position for *Flohria* within the subtribe Philonthina in general, as it was inferred in the mentioned morphology-based phylogenetic analysis of Chani-Posse (2013). The present study also shows evidence favoring this hypothesis as suggested by the development of the infraorbital ridge (see Chani-Posse 2014) and the punctuation pattern of the pronotum, both presumed plesiomorphic character conditions for Philonthina. Furthermore, short thick antennae and legs are observed in a few genera of Xanthopygina (i.e., *Cordylaspis*, *Darwinilus* Chazimanolis, *Haematodes* Nordmann, *Weiserianum*), whose phylogenetic affinities have been hypothesized by various authors (e.g., Lynch-Arribáizaga 1884; Bernhauer 1927; Scheerpeltz 1937a,b; Chazimanolis 2014) but so far not resolved.

While the cladistic analyses in Li and Zhou (2011, including *Agacerus* but not *Flohria*) and Chani-Posse (2013, including *Flohria* but not *Agacerus*) are differently limited in their taxon sampling and biogeographic scope, both did include *Glyphesthus* and *Moeocerus* and recovered these as closely related members of a well-supported clade in a distant nodal position to the root of Philonthina. Additionally, Neotropical Philonthina other than *Flohria* also appear to be in a rather terminal nodal position compared with most of the currently known Holarctic genera in both studies, suggesting their younger age. Within this context, a rather basal position of *Flohria* as a sister taxon to the rest of Philonthina in Chani-Posse (2013) casts doubt on the potential affinity of *Flohria* to a compact and rather terminal philonthine clade (*Glyphesthus* (*Moeocerus* + *Agacerus*)). Besides, the latter possibility seems to be rather unlikely, as synapomorphies supporting at present the monophyly of a group including those genera are not shown by *Flohria* (Li and Zhou 2011, Chani-Posse 2013). Nevertheless, as neither Li and Zhou (2011) nor Chani-Posse (2013) aimed at a detailed study of the sister relationships of *Flohria* but have rather addressed other taxonomically and biogeographically restricted questions, the position of this genus within the “Staphylinini propria” (a clade that includes Anisolinina, Staphylinina, Xanthopygina, and Philonthina) remains uncertain. This uncertainty can

be restricted to two hypotheses: 1) either this genus is sister to the rest of Philonthina, or at least closely related to this subtribe, bearing intermediate characters between those that distinguish Xanthopygina and Philonthina; 2) or it is deeply nested within the latter subtribe assuming its affinity to the abovementioned derived clade (*Glyphesthus* (*Moocerus* + *Agacerus*)). Because of the considerable nodal distance between these competing hypotheses, they imply different age estimates for this genus.

Based on the pattern of the Staphylinini phylogenetic tree and modern distributions of its main clades, Solodovnikov et al. (2013) suggested that the ancestor of “Staphylinini propria” originated in Laurasia sometime when it was already well separated from Gondwana and that, based on the fossil data, the basal diversification of that lineage could have taken place later than the Early Cretaceous. Consistently with that study, Chatzimanolis (2013) suggested that Xanthopygina, one of the internal groups of “Staphylinini propria” originated in the Late Cretaceous or even later. Given that Xanthopygina and Philonthina have been broadly recognized as sister groups (e.g., Solodovnikov and Schömann 2009, Chatzimanolis et al. 2010, Solodovnikov and Newton 2010), it seems reasonable to hypothesize the same age for Philonthina. Such estimate is consistent with the fact that Philonthina were already represented by some modern genera by the early Miocene, as shown by the available fossils of *Philonthus* from the Dominican Amber (Chatzimanolis and Engel 2013).

During much of the Late Cretaceous North America was divided into eastern and western landmasses by the transgression of an epicontinental seaway, the “Western Interior Seaway” (e.g., Schröder-Adams et al. 2001, Sampson et al. 2010). While western North America kept in connection with eastern Asia through Beringia for the most part of the Cretaceous, the eastern unit remained closer to Europe until the end of the Late Cretaceous when the ongoing opening of the North Atlantic led to the complete severing of the connections between America and Europe (Weishampel et al. 2010). In the southern Hemisphere, South America was already separated from Africa and India from Madagascar while connections between southern South America, Antarctica, and Australia were still kept (Scotese 2001). Potential exchange routes between the different landmasses during the Late Cretaceous have been documented by several authors and summarized by Weishampel et al. (2010), none of them showing a connection between eastern and western North America during this period. This paleogeographic evidence is very interesting for the hypothesis about a basal position of *Flohria* that implies this genus to be separated from other Neotropical Philonthina by several nodes of non-Neotropical philonthine lineages. These two facts together allows one to suspect that the “Western Interior Seaway” could have triggered a divergence of *Flohria* from other Philonthina (Chani-Posse 2013), suggesting, therefore, a Late Cretaceous origin for this genus and its isolated evolution in western North America, while the remaining stock of Philonthina was undergoing initial diversification in the landmass,

uniting today’s eastern North America, Europe, and Asia (Russell 1993). The first cladogenetic events within the main Philonthina lineage could have been promoted by both vicariance and dispersal in a global dynamic environment at the end of the Late Cretaceous and the Paleogene (Grimaldi and Engel 2005). Whether *Flohria* is indeed a basal branch of Philonthina, sister to the remaining genera of the subtribe, and its origin can be dated back to the Late Cretaceous, remains to be explored by further studies based on morphological and molecular data of a more representative taxon sampling and including time-calibration of the obtained phylogeny. But, at the present state of knowledge at least, a hypothesis about basal position of *Flohria* within Philonthina and its Late Cretaceous age has some paleobiogeographic plausibility. Some resemblance of *Flohria* with the African- and Asian-derived Philonthina possibly can be convergent, related to some special adaptations, possibly caused by independently acquired myrmecophily or some other specialized but yet unknown life history.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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