

Journal of Melittology

Bee Biology, Ecology, Evolution, & Systematics

The latest buzz in bee biology

No. 52, pp. 1–18

18 September 2015

A review of the genera and subgenera of Oxaeinae (Hymenoptera: Andrenidae)

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Abstract. The supraspecific groups of the bee subfamily Oxaeinae are briefly reviewed and a revised classification proposed. The following new groups are established: *Mesoxaea* (*Heteroxaea*) Engel, new subgenus; *Oxaea* (*Rhodoxaea*) Engel, new subgenus; and *Oxaea* (*Percnoxaea*) Engel, new subgenus. A key to the genera and subgenera of Oxaeinae is provided.

INTRODUCTION

The subfamily Oxaeinae is perhaps one of the more distinctive groups of bees in Andrenidae, comprising 22 robust species distributed from the United States south to northern Argentina (Michener, 2007). The considerable differences between oxaeines and other andrenids have seemed at times so dramatic that some previous authors accorded them familial rank (*e.g.*, Popov, 1941, 1945; Rozen, 1964, 1965, 1993; Hurd & Linsley, 1976), but their placement as nested within Andrenidae and even close to Panurginae is well established (*e.g.*, Michener, 1944; Graf, 1966, 1972; Alexander & Michener, 1995; Engel, 2001; Ascher, 2003), although the precise positions of *Euherbstia* Friese and *Orphana* Vachal in relation to Oxaeinae (*e.g.*, Rozen, 1993) and the monophyly of Andreninae or recognition of Euherbstiinae remains to be resolved. There is a general homogeneity to oxaeine species, yet where differences are present they are significant (*e.g.*, structure of the genitalia, maxillary palpi, mandibles, pubescence). Hurd & Linsley (1976) classified the various species known at that time into four genera — *Oxaea* Klug, *Protoxaea* Cockerell & Porter, *Notoxaea* Hurd & Linsley, and *Mesox-*

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doi: <http://dx.doi.org/10.17161/jom.v0i52.4902>

aea Hurd & Linsley. A fifth genus, *Alloxaea* Ascher, Engel, & Griswold, was recognized initially as a subgenus and for an Ecuadorian species that possessed derived features of *Oxaea* but retained maxillary palpi (Ascher *et al.*, 2006). The North American fauna is comparatively well understood thanks to the monograph of Hurd & Linsley (1976), although much about the biology of these species remains to be studied in depth. By contrast, the South American fauna is in need of revision, although before such a work is undertaken further surveys are needed as the isolated collecting events at present highlight only how little is available for comprehensive studies. There are undoubtedly undescribed species awaiting further attention and the circumscriptions of even seemingly well-known taxa require testing, as well as the geographic distribution of those species. The discovery of *Alloxaea*, known still from only a single locality at the transition from the mesic Choco region and the xeric Tumbesian region (Ascher *et al.*, 2006), also emphasizes the need for field work throughout the Andean region so as to better document the occurrence of oxaeines. Immature stages have been described by Rozen (1964), Roberts (1973), and Rozen & Rozen (2010), while Hurd & Linsley (1976) summarized much about the biology of oxaeines, with sundry additions by Alcock (1975, 1990), Camargo *et al.* (1984), Bullock *et al.* (1991), Oliveira & Siqueira de Castro (2002), and Sarzetti *et al.* (2014).

Here is provided a brief overview of the suprageneric groupings within Oxaeinae so that these names may be made available for a forthcoming work on neotropical bees. The diagnoses are modified from those of Hurd & Linsley (1976) and Michener (2007). Although purely descriptive, such descriptions provide the foundation for hypotheses of circumscription and patterns of evolution (Grimaldi & Engel, 2007), and allow for new revisionary works at the specific level (Gonzalez *et al.*, 2013), along with the exploration of new character systems (Engel, 2011). Indeed, there are great opportunities for exploration among Oxaeinae. For example, histological studies by Guerino & Cruz-Landim (1999, 2002) and Serrão *et al.* (2004) have identified unique glandular and anatomical structures in one species of *Oxaea*, and it will be interesting to discover to what extent these are shared with other oxaeines, along with their concomitant biological and phylogenetic implications. Moreover, as mentioned above, there is considerable field and revisionary work to be undertaken and although relationships among the genera seem intuitive, a species-level phylogeny for the entire clade studies remains to be undertaken, as well as phylogeographic work on those wide-ranging taxa. It is therefore hoped that the keys provided herein will aid future work on the evolutionary history and biology of these bees, particularly those species, or species complexes, within what is here considered *Oxaea s.str.* Table 1 summarizes the current classification of the subfamily.

MATERIAL AND METHODS

Specimens of all the groups considered herein were examined from the collections of the Division of Entomology, University of Kansas Natural History Museum and the Division of Invertebrate Zoology, American Museum of Natural History. Morphological terminology generally follows that used by Hurd & Linsley (1976), Engel (2001), and Michener (2007). Photographs used in the plates were prepared using a Canon EOS 7D digital camera affixed to an Infinity K-2 long-distance microscope lens, and were then arranged in Adobe Photoshop®. As males of various species were not easily accessible and there are already existing good images of terminalic structures, references are made to those illustrations rather than reproduce them here.

Table 1. Hierarchical classification of subfamily Oxaeinae (updated from Ascher *et al.*, 2006).

Subfamily OXAEINAE Ashmead

Genus *Protoxaea* Cockerell & Porter
Protoxaea australis Hurd & Linsley
Protoxaea gloriosa (Fox)
Protoxaea micheneri Hurd & Linsley

Genus *Mesoxaea* Hurd & Linsley
 Subgenus *Mesoxaea* Hurd & Linsley *s.str.*
Mesoxaea (Mesoxaea) arizonica (Cockerell)
Mesoxaea (Mesoxaea) clypeata Hurd & Linsley
Mesoxaea (Mesoxaea) nigerrima (Friese)

Subgenus *Heteroxaea* n. subgen.
Mesoxaea (Heteroxaea) rufescens Hurd & Linsley
Mesoxaea (Heteroxaea) tachytiformis (Cameron)
Mesoxaea (Heteroxaea) texana (Friese)
Mesoxaea (Heteroxaea) vagans (Fox)

Genus *Notoxaea* Hurd & Linsley
Notoxaea ferruginea (Friese)

Genus *Alloxaea* Ascher, Engel, & Griswold
Alloxaea brevivalpis (Ascher, Engel, & Griswold)

Genus *Oxaea* Klug *s.l.*
 Subgenus *Oxaea* Klug *s.str.*
Oxaea (Oxaea) austera Gerstaecker
Oxaea (Oxaea) festiva Smith
Oxaea (Oxaea) flavescens Klug
Oxaea (Oxaea) fuscescens Sichel
Oxaea (Oxaea) stenocoryphe Moure

Subgenus *Rhodoxaea* n. subgen.
Oxaea (Rhodoxaea) rufa Friese

Subgenus *Percnoxaea* n. subgen.
Oxaea (Percnoxaea) alvarengai Moure & Urban
Oxaea (Percnoxaea) mourei Graf
Oxaea (Percnoxaea) schwarzi Moure & Seabra
Oxaea (Percnoxaea) sooretama Graf & Urban

SYSTEMATICS

Subfamily Oxaeinae Ashmead

Oxaeinae Ashmead, 1899: 70. Type genus: *Oxaea* Klug, 1807a.

DIAGNOSIS: Moderately large (13–26 mm), robust, setose bees (Figs. 1–4, 7–10, 13–15, 18–21, 25, 26, 28–32, 35–37). Head with clypeus protuberant; labrum as long as or longer than broad; lacinia composed of reduced sclerites hidden on inner side of stipes at base of galea; mentum and submentum fused into a single plate; basal labial palpomere flattened and elongate; malar area linear; facial foveae absent; ocelli low on face, near antennal toruli (Figs. 5, 6, 11, 12, 16, 17, 22, 23, 27, 33, 34, 38); orbits of compound eyes in males converging above (Figs. 5, 12, 17, 23, 27, 34); antennal toruli separated from epistomal sulcus by less than torular diameter; two subantennal sulci, outer sulcus arched; first flagellomere as long as or longer than scape (Figs. 5, 6, 11, 12, 16, 17, 22, 23, 27, 33, 34, 38); preepisternal sulcus absent below scrobal sulcus; forewing with

pterostigma virtually absent; marginal cell narrow and elongate, longer than distance from apex to wing tip, apex bent away from margin and appendiculate (resembling to some degree a narrowly truncate marginal cell analogous to Panurginae) (Figs. 2, 4, 14, 21, 24, 28, 32); three submarginal cells; distal portion of wing papillate; female meta-femoral apex enlarged and flattened to form a plate associated with metabasitibial plate (Figs. 2, 8, 19, 36); scopa abundant from metacoxa to metabasitarsus; pretarsal claws cleft, arolia reduced; female pygidial plate present; male metasomal sterna VII and VIII with large discs (refer to figures in Hurd & Linsley, 1976, and Ascher *et al.*, 2006); male genital capsule tapering basally, gonobase small; volsella elongate, digitus and cuspis fused; penis valve and aedeagus fused (refer to figures in Hurd & Linsley, 1976, and Ascher *et al.*, 2006). A complete description of the subfamily is provided by Hurd & Linsley (1976).

INCLUDED GENERA: *Oxaea* Klug, 1807a; *Protoxaea* Cockerell & Porter, 1899; *Mesoxaea* Hurd & Linsley, 1976; *Notoxaea* Hurd & Linsley, 1976; and *Alloxaea* Ascher, Engel, & Griswold, 2006.

Genus *Protoxaea* Cockerell & Porter
(Figs. 1–6)

Protoxaea Cockerell & Porter, 1899: 410. Type species: *Megacilissa gloriosa* Fox, 1893, by original designation.

DIAGNOSIS: Male without pale maculations on clypeus, labrum, mandible, and antenna (Fig. 5); mandible simple apically; maxillary palpi composed of six palpomeres; metasomal terga brownish black or black, not partly or largely reddish (Figs. 1–4); metasomal tergum VI (male) and tergum V (female) without long, conspicuous tufts of white setae at sides; apical margin of male metasomal sternum VIII entire, convex, not emarginate medially (refer to figures in Hurd & Linsley, 1976); gonobase elongate, not ringlike, much longer than wide, tapering basally; gonostylus partially differentiated from gonocoxae, with setae apically (refer to figures in Hurd & Linsley, 1976); outer lateral apex of volsella with dorsal lobed extension, outer margin from narrow ventral apex to widest point apical from apodeme shallowly concave before mediolateral process, process not protrudent (refer to figures in Hurd & Linsley, 1976); penis valve not elongate, only slightly surpassing gonostylar apices, with prominent ventral subapical ridge with apicolateral setae, not extending to thin lateral process (refer to figures in Hurd & Linsley, 1976).

INCLUDED SPECIES: *Protoxaea australis* Hurd & Linsley, 1976; *P. gloriosa* (Fox, 1893); and *P. micheneri* Hurd & Linsley, 1976. A key to species was provided by Hurd & Linsley (1976).

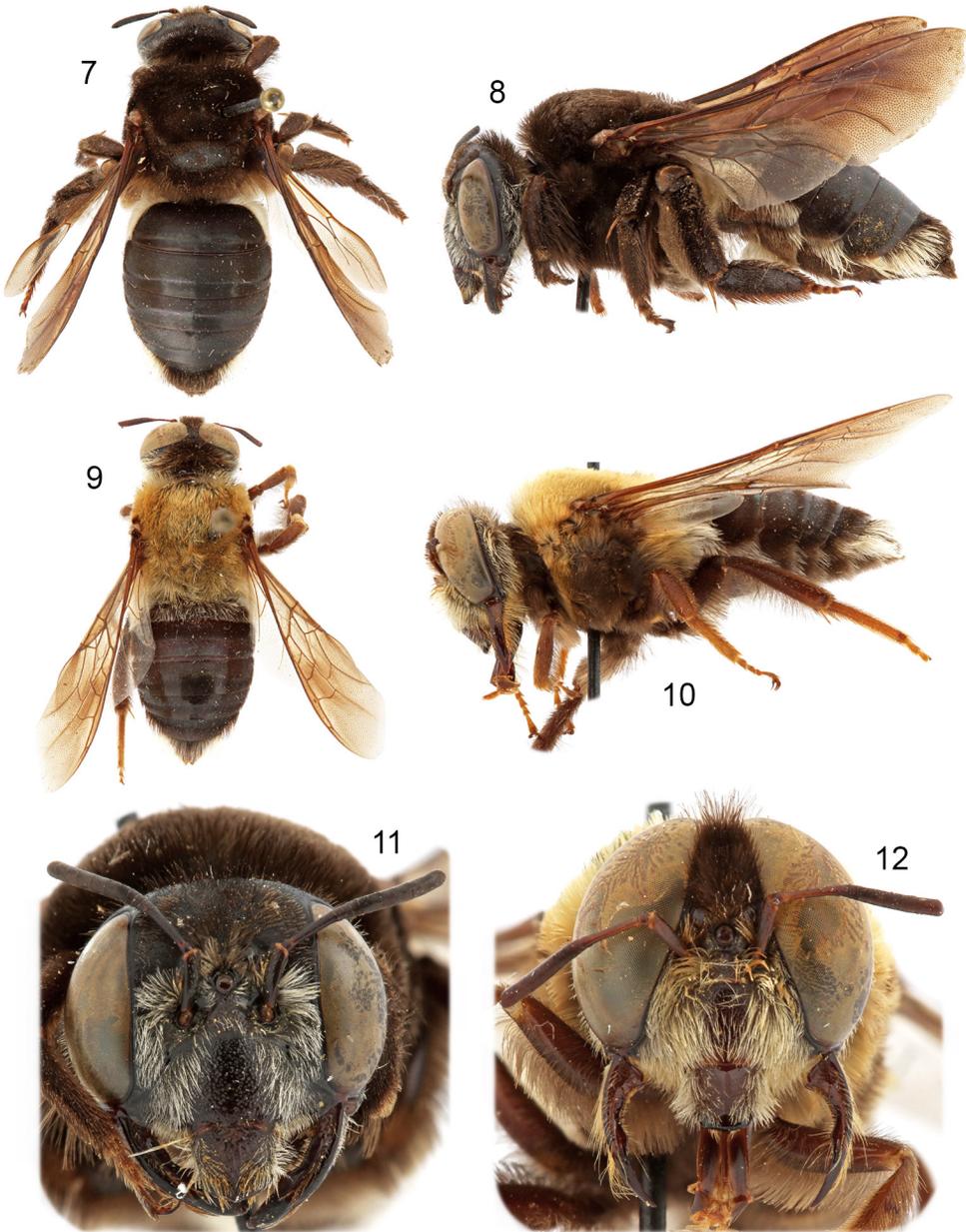
Genus *Mesoxaea* Hurd & Linsley

DIAGNOSIS: Male without pale maculations on clypeus, labrum, mandible, and antenna (Figs. 12, 17); mandible simple apically (Fig. 12); maxillary palpi composed of six palpomeres; metasomal terga brownish black or black, not partly or largely reddish (Figs. 7–10, 13–15); metasomal tergum VI (male) and tergum V (female) with long, conspicuous tufts of white setae at sides (Figs. 8, 10, 14); apical margin of male metasomal sternum VIII deeply emarginate medially (refer to figures in Hurd & Linsley, 1976); gonobase greatly reduced, ringlike, much wider than long, not tapering basally; gono-



Figures 1–6. Photographs of *Protoxaea gloriosa* (Fox). 1. Dorsal habitus of female. 2. Lateral habitus of female. 3. Dorsal habitus of male. 4. Lateral habitus of male. 5. Facial view of male. 6. Facial view of female.

stylus partially differentiated from gonocoxae, with setae apically (refer to figures in Hurd & Linsley, 1976); outer lateral apex of volsella with dorsal lobed extension, outer margin from narrow ventral apex to widest point apical from apodeme frequently deeply concave before mediolateral process, process frequently protrudent (refer to



Figures 7–12. Photographs of *Mesoxaea (Mesoxaea) nigerrima* (Friese). 7. Dorsal habitus of female. 8. Lateral habitus of female. 9. Dorsal habitus of male. 10. Lateral habitus of male. 11. Facial view of female. 12. Facial view of male.

figures in Hurd & Linsley, 1976); penis valve not elongate, only slightly surpassing gonostylar apices, with prominent ventral subapical ridge with apicolateral setae, not extending to thin lateral process (refer to figures in Hurd & Linsley, 1976).

Subgenus *Mesoxaea* Hurd & Linsley
(Figs. 7–12)

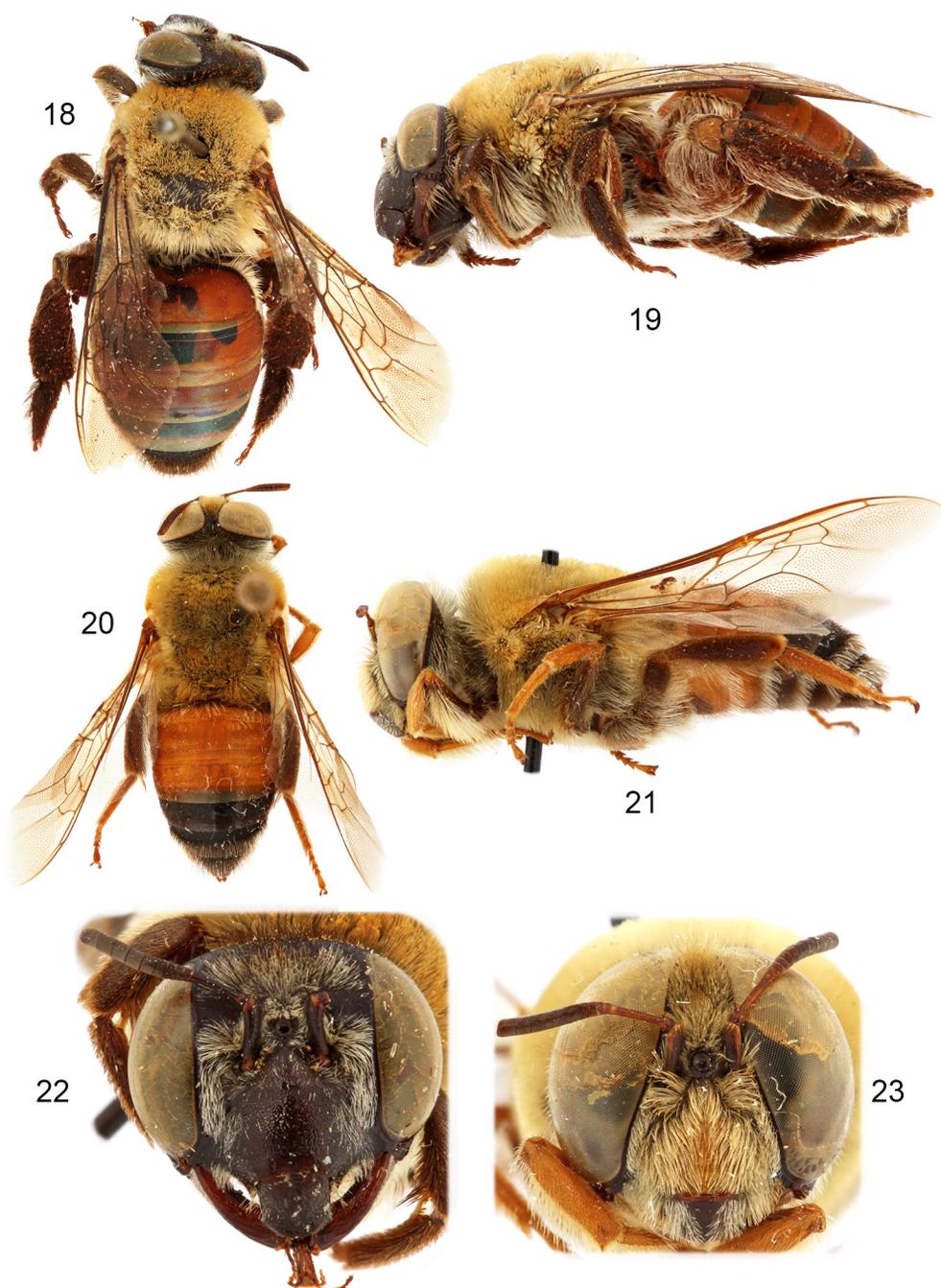


Figures 13–17. Photographs of *Mesoxaea (Heteroxaea) rufescens* Hurd & Linsley. **13.** Dorsal habitus of female. **14.** Lateral habitus of female. **15.** Dorsal habitus of male. **16.** Facial view of female. **17.** Facial view of male.

Mesoxaea Hurd & Linsley, 1976: 41. Type species: *Oxaea nigerrima* Friese, 1912, by original designation.

DIAGNOSIS: Mesosomal dorsum of female with dark brown to black pubescence (Fig. 7); metafemoral scopa brown or reddish brown to black, or largely white; forewing darkly infuscate, at most nearly hyaline basally (Fig. 6).

INCLUDED SPECIES: *Mesoxaea (Mesoxaea) arizonica* (Cockerell, 1936); *M. (M.) clypeata* Hurd & Linsley, 1976; and *M. (M.) nigerrima* (Friese, 1912). A key to species was provided by Hurd & Linsley (1976).



Figures 18–23. Photographs of *Notoxaea ferruginea* (Fries). 18. Dorsal habitus of female. 19. Lateral habitus of female. 20. Dorsal habitus of male. 21. Lateral habitus of male. 22. Facial view of female. 23. Facial view of male.

Heteroxaea Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:C34A8917-937E-4AE7-B6DC-41584A4AB39F

(Figs. 13–17)



Figure 24. Photograph of wing venation of *Notoxaea ferruginea* (Friese).

TYPE SPECIES: *Mesoxaea rufescens* Hurd & Linsley, 1976.

DIAGNOSIS: Mesosomal dorsum of female with pale pubescence (Fig. 13); metafemoral scopa largely white (Fig. 14); forewing nearly hyaline in basal half to two thirds, apically darkly infuscate (Fig. 14).

ETYMOLOGY: The new subgeneric name is a combination of *heteros* (Greek, meaning "different") and *Oxaea*, type genus of the subfamily. The gender of the name is feminine.

INCLUDED SPECIES: *Mesoxaea* (*Heteroxaea*) *rufescens* Hurd & Linsley, 1976; *M. (H.) tachytiformis* (Cameron, 1901); *M. (H.) texana* (Friese, 1898); and *M. (H.) vagans* (Fox, 1893). Hurd & Linsley (1976) provide a key to the species as part of their key to all *Mesoxaea* s.l.

Genus *Notoxaea* Hurd & Linsley

Notoxaea Hurd & Linsley, 1976: 21. Type species: *Oxaea ferruginea* Friese, 1898, by original designation.

DIAGNOSIS: Male with pale maculations on clypeus and mandible (Fig. 23); mandible with preapical tooth on inner margin; maxillary palpi composed of six palpomeres; metasomal terga I–III and sometimes IV at least partly or largely reddish (Figs. 18–21); metasomal tergum VI (male) and tergum V (female) with long, conspicuous tufts of white setae at sides; apical margin of male metasomal sternum VIII deeply emarginate medially (refer to figures in Hurd & Linsley, 1976); gonobase greatly reduced, ringlike, much wider than long, not tapering basally; gonostylus partially differentiated from gonocoxae, with setae apically; outer lateral apex of volsella without dorsal lobed extension, outer margin from narrow ventral apex to widest point apical from apodeme weakly concave before mediolateral process, process not protrudent (refer to figures in Hurd & Linsley, 1976); penis valve not elongate, only slightly surpassing gonostylar apices, with strong ventral subapical ridge extending to thin lateral process bearing setae (refer to figures in Hurd & Linsley, 1976).

INCLUDED SPECIES: *Notoxaea ferruginea* (Friese, 1898).



Figures 25–27. Photographs of male of *Alloxaea brevivalpis* (Ascher, Engel, & Griswold). 25. Lateral habitus. 26. Dorsal habitus. 27. Facial view.

Genus *Alloxaea* Ascher, Engel, & Griswold

Oxaea (*Alloxaea*) Ascher, Engel, & Griswold, 2006: 542. Type species: *Oxaea* (*Alloxaea*) *brevivalpis* Ascher, Engel, & Griswold, 2006, by original designation. Graf & Moure, 2007: 16 [elevated to generic rank].



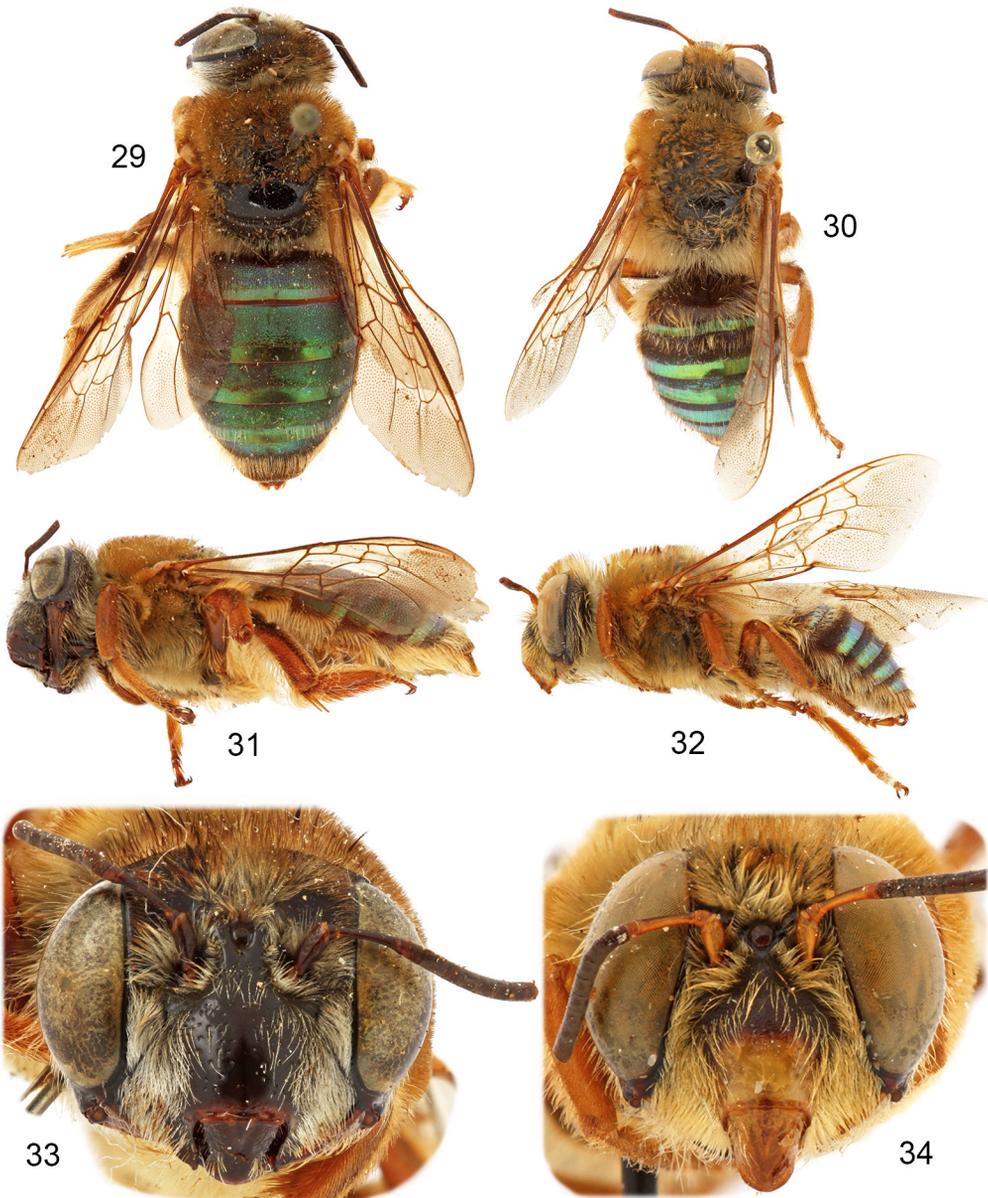
Figure 28. Photograph of dorsal habitus of holotype female of *Oxaea (Oxaea) festiva* Smith.

DIAGNOSIS: Male without pale maculations on clypeus, labrum, mandible, and antenna (Fig. 27); mandible simple apically (Fig. 27); maxillary palpi composed of three palpomeres; metasomal terga brownish black or black with faint metallic highlights, not partly reddish (Figs. 25, 26); metasomal tergum VI with long, conspicuous tufts of brown to yellow brown setae at sides; apical margin of male metasomal sternum VIII deeply emarginate medially; gonobase greatly reduced, ringlike, much wider than long, not tapering basally (refer to figures in Ascher *et al.*, 2006); gonostylus partially (albeit weakly) differentiated from gonocoxae, with setae apicolaterally; outer lateral apex of volsella without dorsal lobed extension, outer margin from broadly-rounded ventral apex to widest point apical from apodeme deeply concave before protrudent mediolateral process (refer to figures in Ascher *et al.*, 2006); penis valve not elongate, not surpassing gonostylar apices, without ventral subapical ridge or process (refer to figures in Ascher *et al.*, 2006). Female remains unknown.

INCLUDED SPECIES: *Alloxaea brevipalpis* (Ascher, Engel, & Griswold, 2006).

Genus *Oxaea* Klug

DIAGNOSIS: Male often with pale maculations on clypeus, labrum, mandible, and basal antennal articles (Fig. 34); mandible simple apically (Fig. 38); maxillary palpi absent; metasomal terga with or without metallic coloration, otherwise brownish black, black (Figs. 28–30, 35–37), or partly or largely reddish; metasomal tergum VI (male) and tergum V (female) with long, conspicuous tufts of white or black setae at sides (Figs. 31, 32); apical margin of male metasomal sternum VIII deeply emarginate medially (refer to figures in Hurd & Linsley, 1976); gonobase greatly reduced, ringlike, much wider than long, not tapering basally; gonostylus not differentiated from gono-



Figures 29–34. Photographs of *Oxaea (Oxaea) flavescens* Klug. 29. Dorsal habitus of female. 30. Dorsal habitus of male. 31. Lateral habitus of female. 32. Lateral habitus of male. 33. Facial view of female. 34. Facial view of male.

coxae, apex without setae (refer to figures in Hurd & Linsley, 1976); outer lateral apex of volsella without dorsal lobed extension, apex and outer margin variable; penis valve sometimes elongate, slightly to greatly surpassing gonostylar apices, without ventral subapical ridge or process.

Subgenus *Oxaea* Klug
(Figs. 28–38)



Figure 35. Photograph of dorsal habitus of lectotype male of *Oxaea (Oxaea) flavescens* Klug.

Oxaea Klug, 1807a: 261. Type species: *Oxaea flavescens* Klug, 1807a, monobasic.

Dasyglossa Illiger in Klug, 1807b: 217 [no valid species included]. Klug, 1810: 44 [first included valid species]. Type species: *Oxaea flavescens* Klug, 1807a, by designation of Sandhouse, 1943: 544.

DIAGNOSIS: Metasomal terga with bright metallic coloration, frequently as metallic green, purple, or bluish-green bands (Figs. 28–32, 35, 37); male mandible without basal tooth (Fig. 38); outer lateral margin of volsella from narrow apex to widest point apical from apodeme straight, mediolateral angle not pronounced (refer to figures in Hurd & Linsley, 1976); penis valve elongate, slender, greatly surpassing gonostylar apices (refer to figures in Hurd & Linsley, 1976).

INCLUDED SPECIES: *Oxaea (Oxaea) austera* Gerstaecker, 1867; *O. (O.) festiva* Smith, 1854 (Fig. 28); *O. (O.) flavescens* Klug, 1807a [lectotype (Fig. 35) designation by Engel, 2006]; *O. (O.) fuscescens* Sichel, 1865; and *O. (O.) stenocoryphe* Moure, 1947.

***Rhodoxaea* Engel, new subgenus**

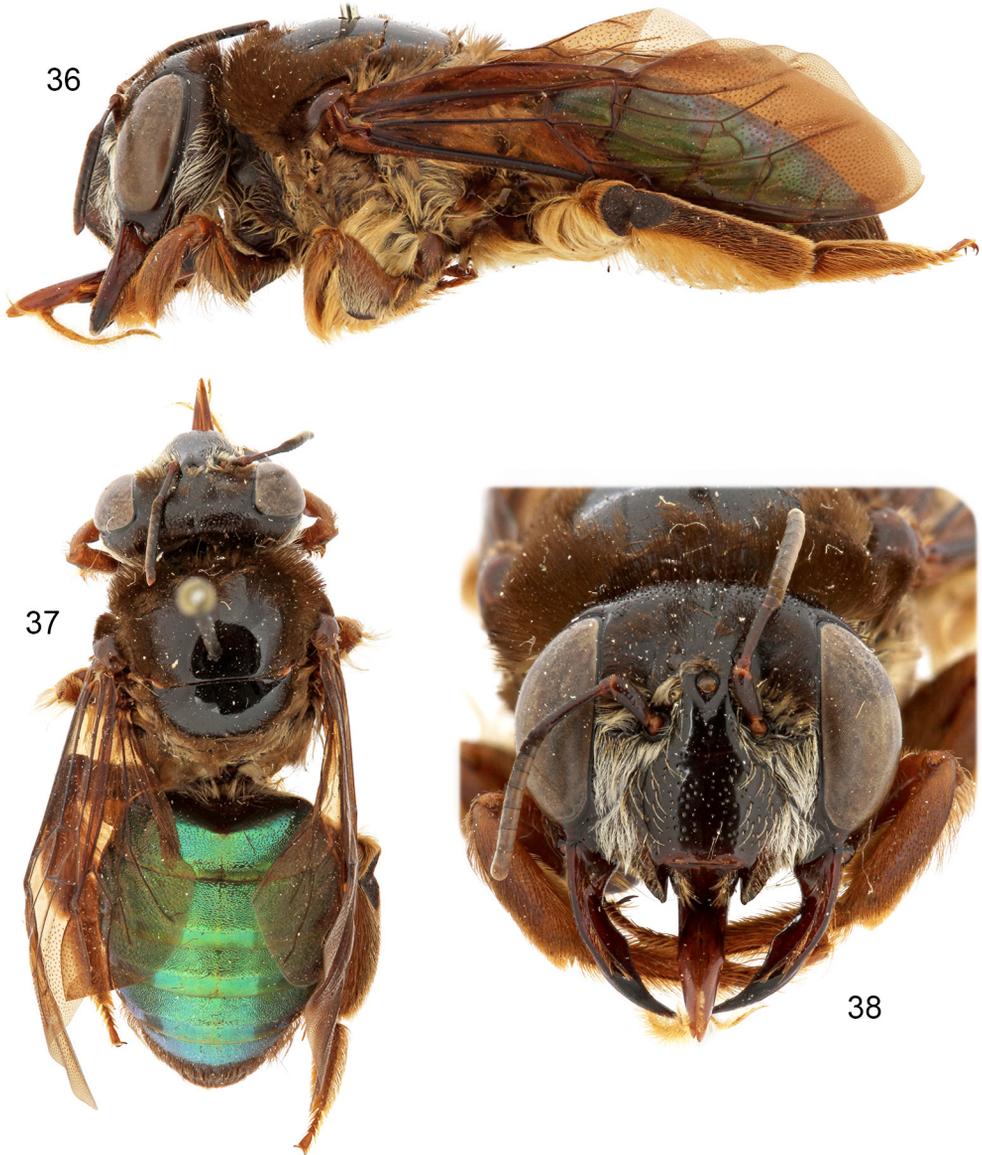
ZooBank: urn:lsid:zoobank.org:act:7C965A2E-D909-477F-986F-78761F730E8D

TYPE SPECIES: *Oxaea rufa* Friese, 1899.

DIAGNOSIS: Metasomal terga largely red, with exceedingly faint iridescence on terga II–IV; tergum VI dark brown to black. Scopa with pubescence off-white. Male remains undescribed. This is an enigmatic oxaeine from Bahia and Pará in Brazil, and is in need of greater investigation.

ETYMOLOGY: The new subgeneric name is a combination of *rhodon* (Greek, meaning “red”) and *Oxaea*, type genus of the subfamily. The gender of the name is feminine.

INCLUDED SPECIES: *Oxaea (Rhodoxaea) rufa* Friese, 1899.



Figures 36–38. Photographs of female of *Oxaea* (*Oxaea*) *stenocoryphe* Moure. 36. Lateral habitus. 37. Dorsal habitus. 38. Facial view.

Percnoxaea Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:78EF25E3-F2F0-47DB-88EF-9F3AF1084207

TYPE SPECIES: *Oxaea schwarzi* Moure & Seabra, 1962.

DIAGNOSIS: Metasomal terga brownish black or black, at most weakly metallic, never bright metallic green; male mandible with basal tooth or at least basal high-arched ridge present (refer to figures in Moure & Seabra, 1962, Moure & Urban, 1963, and Graf & Urban, 2008); outer lateral margin of volsella from broadly-rounded apex to widest point apical from apodeme deeply concave before protrudent mediolater-

al process (refer to figures in Moure & Seabra, 1962); penis valve not elongate, only slightly surpassing gonostylar apices (refer to figures in Moure & Seabra, 1962, and Moure & Urban, 1963).

ETYMOLOGY: The new subgeneric name is a combination of *perknos* (Greek, meaning "dark-colored") and *Oxaea*, type genus of the subfamily. The gender of the name is feminine.

INCLUDED SPECIES: *Oxaea (Percnoxaea) alvarengai* Moure & Urban, 1963; *O. (P.) mourei* Graf, 1992; *O. (P.) schwarzi* Moure & Seabra, 1962; and *O. (P.) sooretama* Graf & Urban, 2008. Graf & Urban (2008) provide a key to the species.

Practical Key to Genera and Subgenera of Oxaeinae
(modified from Hurd & Linsley, 1976)

1. Maxillary palpus present, with six or three palpomeres; male gonostylus partly differentiated from gonocoxa, sometimes only weakly so, and setose 2
- Maxillary palpus absent; male gonostylus not recognizable, apex without setae (*Oxaea* Klug *s.l.*) 6
- 2(1). Maxillary palpus with six palpomeres; mesosomal dorsum with pubescence variously colored, but never as below 3
- Maxillary palpus with three palpomeres; mesoscutum and mesoscutellum with strongly contrasting dark versus pale pubescence (Fig. 26) [Ecuador] *Alloxaea* Ascher, Engel, & Griswold
- 3(2). Mandible simple apically (*e.g.*, Fig. 38); clypeus and mandible of male without pale maculations 4
- Mandible with preapical tooth on inner margin; clypeus and mandible of male with pale maculations (Fig. 23) [Argentina, Paraguay, Brazil] *Notoxaea* Hurd & Linsley
- 4(3). Metasomal tergum VI of male and tergum V of female with lateral tufts of long white setae; apical margin of male sternum VIII emarginate medially (*Mesoxaea* Hurd & Linsley *s.l.*) 5
- Metasomal tergum VI of male and tergum V of female without conspicuous lateral tufts of long white setae (Figs. 2, 4); apical margin of male sternum VIII convex, not emarginate [USA & Mexico] *Protoxaea* Cockerell & Porter
- 5(4). Mesosomal dorsum of female with dark brown to black pubescence (Figs. 7, 8); male with forewing heavily infusate throughout [USA & Mexico] *Mesoxaea* Hurd & Linsley *s.str.*
- Mesosomal dorsum of female with pale pubescence (Figs. 13, 14); male forewing hyaline clear in basal two-thirds, only infusate in apical third [USA & Mexico] *Heteroxaea* n. subgen.
- 6(1). Metasomal terga dark with weak or bright metallic coloration 7
- Metasomal terga largely red [Brazil] *Rhodoxaea* n. subgen.
- 7(6). Metasomal terga with bright metallic coloration, frequently as metallic green or bluish-green bands (Figs. 28–30, 35, 37) [South America] *Oxaea* Klug *s.str.*
- Metasomal terga dark, at most weakly metallic, never bright metallic green [Brazil, Argentina] *Percnoxaea* n. subgen.

ACKNOWLEDGEMENTS

This work has been supported by U.S. National Science Foundation grant DBI-1057366. Production of photographs and their arrangement was supported by the Engel Illustration Fund of the University of Kansas College of Liberal Arts & Sciences, and by Laura C.V. Breitkreuz. Two reviewers are graciously thanked for their helpful comments. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

REFERENCES

- Alcock, J. 1975. A day in the life of *Protoxaea gloriosa*. *Insect World Digest* 2(5): 10–13.
- Alcock, J. 1990. Body size and territorial behavior in the bee *Protoxaea gloriosa* (Fox) (Hymenoptera: Oxaeidae). *Pan-Pacific Entomologist* 66(2): 157–161.
- Alexander, B.A., & C.D. Michener. 1995. Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* 55(11): 377–424.
- Ascher, J.S. 2003. Evidence for the phylogenetic position of *Nolanomelissa* from nuclear EF-1 α sequence data. In: Melo, G.A.R., & I. Alves-dos-Santos (Eds.), *Apoidea Neotropica: Homenagem aos 90 Anos de Jesus Santiago Moure*: 107–108. Editora UNESC [Universidade do Extremo Sul Catarinense]; Criciúma, Brazil; xvi+320 pp. [Nota bene: This brief but important paper is presented as an appendix to a work by J.G. Rozen, Jr., on the systematics and biology of *Nolanomelissa* Rozen (Panurginae: Nolanomelissini)]
- Ascher, J.S., M.S. Engel, & T.L. Griswold. 2006. A new subgenus and species of *Oxaea* from Ecuador (Hymenoptera: Andrenidae). *Polskie Pismo Entomologiczne* 75(4): 539–552.
- Ashmead, W.H. 1899. Classification of the bees, or the superfamily Apoidea. *Transactions of the American Entomological Society* 26: 49–100.
- Bullock, S.H., R. Ayala, D. Rodríguez-Zamora, D.L. Quiroz-García, & M. de la Luz Arreguin-Sánchez. 1991. Nest provision and pollen foraging in three Mexican species of solitary bees (Hymenoptera: Apoidea). *Pan-Pacific Entomologist* 67(3): 171–176.
- Camargo, J.M.F., G. Gottsberger, & I. Silberbauer-Gottsberger. 1984. On the phenology and flower visiting behavior of *Oxaea flavescens* (Klug) (Oxaeinae, Andrenidae, Hymenoptera) in São Paulo, Brazil. *Beiträge zur Biologie der Pflanzen* 59(2): 159–179.
- Cameron, P. 1901. Description of a new genus and five new species of aculeate Hymenoptera from the Santa Fé Mountains, New Mexico. *Transactions of the American Entomological Society* 27: 311–316.
- Cockerell, T.D.A. 1936. Records of western bees. *American Museum Novitates* 831: 1–6.
- Cockerell, T.D.A., & W. Porter. 1899. Contributions from the New Mexico Biological Station. VII. Observations on bees, with descriptions of new genera and species. *Annals and Magazine of Natural History, Series 7* 4(24): 403–421.
- Engel, M.S. 2001. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.
- Engel, M.S. 2006. *Oxaea flavescens* Klug 1807: Stabilization by designation of a lectotype (Hymenoptera: Andrenidae). *Polskie Pismo Entomologiczne* 75(3): 439–442.
- Engel, M.S. 2011. Systematic melittology: Where to from here? *Systematic Entomology* 36(1): 2–15.
- Fox, W.J. 1893. Synopsis of the N. American species of *Megacilissa*. *Psyche* 6(203): 421–422.
- Friese, H. 1898. Monographie der Bienengattungen *Megacilissa*, *Caupolicana*, *Diphaglossa*, und *Oxaea*. *Annalen des kaiserlich-königlichen naturhistorischen Hofsmuseum, Wien* 13(1): 59–86.
- Friese, H. 1899. Monographie der Bienengattungen *Megacilissa*, *Caupolicana*, *Diphaglossa*, und *Oxaea*. *Annalen des kaiserlich-königlichen naturhistorischen Hofsmuseum, Wien* 14(3): 239–246.
- Friese, H. 1912. Neue und wenig bekannte Bienenarten der neotropischen Region. *Archiv für Naturgeschichte, Abtheilung A* 78(6): 198–226.
- Gerstaecker, [C.E.]A. 1867. Bericht über die wissenschaftlichen Leistungen im Gebiete der Entomologie während der Jahre 1865–66. Zweite Hälfte. *Archiv für Naturgeschichte* 33(2): 305–533. [Nota bene: The section on Hymenoptera encompasses pp. 305–347, with the description of *O. austera* in a footnote to p. 318]

- Gonzalez, V.H., T. Griswold, & M.S. Engel. 2013. Obtaining a better taxonomic understanding of native bees: Where do we start? *Systematic Entomology* 38(4): 645–653.
- Graf, V. 1966. A posição sistemática de Oxaeinae (Hymenoptera-Apoidea). *Ciência e Cultura* 18(2): 137–138.
- Graf, V. 1972. Contribuição ao estudo da anatomia da cabeça dos Apoidea II — A musculatura do complexo lábio-maxilar. *Boletim da Universidade Federal do Paraná, Zoologia* 5(3): 139–173.
- Graf, V. 1992. Uma nova espécie de *Oxaea* Klug (Oxaeinae, Andrenidae, Hymenoptera) do sul do Brasil. *Revista Brasileira de Zoologia* 9(1–2): 153–155.
- Graf, V., & J.S. Moure. 2007. Oxaeini Ashmead, 1899. In: Moure, J.S., D. Urban, & G.A.R. Melo (Eds.), *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*: 16–19. Sociedade Brasileira de Entomologia; Curitiba, Brazil; xiv+1058 pp. [updated online at: <http://www.moure.cria.org.br/catalogue>; last accessed 20 July 2015].
- Graf, V., & D. Urban. 2008. Uma espécie nova de *Oxaea* Klug (Hymenoptera, Apidae, Andreninae) do Espírito Santo, Brasil e notas complementares. *Revista Brasileira de Entomologia* 52(3): 407–410.
- Grimaldi, D., & M.S. Engel. 2007. Why descriptive science still matters. *BioScience* 57(8): 646–647.
- Guerino, A.C., & C. da Cruz-Landim. 1999. A new type of sternal gland present in *Oxaea flavescens* (Hymenoptera, Oxaeinae): Location and histology. *Cytobios* 97(385): 71–77.
- Guerino, A.C., & C. da Cruz-Landim. 2002. Ultra-estrutura de glândulas abdominais tegumentares em *Oxaea flavescens* (Hymenoptera, Andrenidae, Oxaeinae). *Iheringia, Série Zoologia* 92(4): 37–45.
- Hurd, P.D., Jr., & E.G. Linsley. 1976. The bee family Oxaeidae with a revision of the North American species (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* 220: 1–75.
- Klug, J.C.F. 1807a. *Oxaea*, eine neue Gattung aus der Ordnung der Piezaten. *Gesellschaft Naturforschender Freunde zu Berlin, Magazin für neuesten Entdeckungen in der gesammten Naturkunde* 1: 261–263.
- Klug, J.C.F. 1807b. Kritische Revision der Bienengattungen in Fabricius neuem Piezaten-systeme, mit Berücksichtigung der Kirbyschen Bienenfamilien und Illiger's Monographie im fünften Bande des Magazins. *Magazin für Insektenkunde* 6: 200–228.
- Klug, J.C.F. 1810. Einige neue Piezategattungen. *Gesellschaft Naturforschender Freunde zu Berlin, Magazin für neuesten Entdeckungen in der gesammten Naturkunde* 4: 31–45, +1 pl.
- Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History* 82(6): 151–326.
- Michener, C.D. 2007. *The Bees of the World* [2nd Edition]. John Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., +20 pls.
- Moure, J.S., & C.A.C. Seabra. 1962. A new species of the genus *Oxaea* from Brazil (Hymenoptera: Apidae). *Journal of the New York Entomological Society* 70(4): 235–238.
- Moure, J.S. 1947. Notas sobre algunas abejas de la Provincia de Salta (Hymen. Apoidea). *Revista de la Sociedad Entomológica Argentina* 13: 218–253.
- Moure, J.S., & D. Urban. 1963. Uma nova espécie de “*Oxaea*” de Mato Grosso, Brasil (Hymenoptera, Apoidea). *Revista Brasileira de Biologia* 23(4): 361–364.
- Oliveira, F.F., de, & M. Siqueira de Castro. 2002. Nota sobre o comportamento de agregação dos machos de *Oxaea austera* Gerstaecker (Hymenoptera, Apoidea, Oxaeinae) na caatinga do Estado da Bahia, Brasil. *Revista Brasileira de Zoologia* 19(1): 301–303.
- Popov, V.V. 1941. Family Oxaeidae and processes of morphological reduction in bees (Hymenoptera, Apoidea). *Comptes Rendus de l'Académie des Sciences de l'URSS [Doklady Akademii Nauk SSSR]* 30(1): 82–85.
- Popov, V.V. 1945. On the morphological reduction in the male genitalia of bees (Hymenoptera, Apoidea). *Zoologicheskii Zhurnal* 24(6): 329–336. [In Russian, with English summary]
- Roberts, R.B. 1973. Nest architecture and immature stages of the bee *Oxaea flavescens* and the status of Oxaeidae (Hymenoptera). *Journal of the Kansas Entomological Society* 46(4): 437–446.
- Rozen, J.G., Jr. 1964. Phylogenetic-taxonomic significance of last instar of *Protoxaea gloriosa* Fox, with descriptions of first and last instars (Hymenoptera: Apoidea). *Journal of the New York Entomological Society* 72(4): 223–230.

- Rozen, J.G., Jr. 1965. The biology and immature stages of *Melitturga clavicornis* (Latreille) and of *Sphecodes albilabris* (Kirby) and the recognition of the Oxaeidae at the family level (Hymenoptera, Apoidea). *American Museum Novitates* 2224: 1–18.
- Rozen, J.G., Jr. 1993. Phylogenetic relationships of *Euherbstia* with other short-tongued bees (Hymenoptera: Apoidea). *American Museum Novitates* 3060: 1–17.
- Rozen, M.A., & J.G. Rozen, Jr. 2010. The pupa of the bee *Protoxaea gloriosa* (Hymenoptera: Andrenidae: Oxaeinae). *Journal of the Kansas Entomological Society* 83(1): 76–79.
- Sandhouse, G.A. 1943. The type species of the genera and subgenera of bees. *Proceedings of the United States National Museum* 92(3156): 519–619.
- Sarzetti, L.C., J.F. Genise, & M. Victoria Sanchez. 2014. Nest architecture of *Oxaea austera* (Andrenidae, Oxaeinae) and its significance for the interpretation of Uruguayan fossil bee cells. *Journal of Hymenoptera Research* 39: 59–70.
- Serrão, J.E., S. Marques-Silva, & G.F. Martins. 2004. The rectum of *Oxaea flavescens* (Andrenidae) has a specialized structure among bees. *Micron* 35(4): 245–253.
- Sichel, J. 1865. Études hyménoptérologiques: Essai d'une monographie du genre *Oxaea* Klug. *Annales de la Société Entomologique de France, Série 4* 5: 331–334.
- Smith, F. 1854. *Catalogue of Hymenopterous Insects in the Collection of the British Museum, Part 2, Apidae*. British Museum; London, UK; 199–465 pp., pls. vii–xii.

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The *Journal of Melittology* was established at the University of Kansas through the efforts of Michael S. Engel, Victor H. Gonzalez, Ismael A. Hinojosa-Díaz, and Charles D. Michener in 2013 and each article is published as its own number, with issues appearing online as soon as they are ready. Papers are composed using Microsoft Word® and Adobe InDesign® in Lawrence, Kansas, USA.

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ISSN 2325-4467