The *albibarbis*-complex of *Efferia* Coquillett, 1910 from the Grand Canyon region, southwestern U.S.A., with three new species and new distribution records (Diptera: Asilidae)

Author(s): Aubrey G. Scarbrough, Lawrence E. Stevens, and C. Riley Nelson
Source: Pan-Pacific Entomologist, 88(1):58-86. 2012.
Published By: Pacific Coast Entomological Society
DOI: http://dx.doi.org/10.3956/2012-07.1
URL: http://www.bioone.org/doi/full/10.3956/2012-07.1

THE PAN-PACIFIC ENTOMOLOGIST
88(1):58–86, (2012)

The *albibarbis*-complex of *Efferia* Coquillett, 1910 from the Grand Canyon region, southwestern U.S.A., with three new species and new distribution records (Diptera: Asilidae)

Aubrey G. Scarbrough[1], Lawrence E. Stevens[2], & C. Riley Nelson[3]

[1]Department of Entomology Department, University of Arizona, Tucson, Arizona 85721
e-mail: saubrey05@gmail.com

[2]Biology Department, Museum of Northern Arizona, 3101 N. Ft. Valley Rd., Flagstaff, Arizona 86001
e-mail: farvana@aol.com

[3]Department of Biology, WIDB 401, Brigham Young University, Provo, Utah 84602
e-mail: rileynelson@byu.edu

Abstract. Six species of the *albibarbis* complex of *Efferia* Coquillett are reported from the Grand Canyon ecoregion on the southern Colorado Plateau in northern Arizona. The terminalia of *E. albibarbis* (Macquart), *E. bicolor* (Bellardi) *E. carbonaria* **sp. nov.**, *E. fisheri* **sp. nov.**, *E. tapeats* **sp. nov.,** and *E. zonata* (Hine) are figured and compared with congeners. *Efferia peralta* Wilcox and *E. vertebrata* (Bromley) are included as comparisons and possible members of the Grand Canyon faunas. The range of *E. bicolor* has been extended northward from central Arizona to within 51.5 km of the south rim of the Grand Canyon and into Nye County, Nevada. *Efferia fisheri* is recorded along the southern edge of the plateau at Payson, AZ, 169 km south of the GCNP. Taxonomic and distribution notes are provided. Wilcox's key of this complex is revised to include all species described since his publication. Four of the six species overlap in low-elevation perennial stream riparian zones and in adjacent colluvial brecchia habitats in the Grand Canyon region. *Efferia bicolor*, *E. fisheri*, and *E. zonata* overlap at higher elevations.

Key Words. Asilids, biogeography, Colorado Plateau, Grand Canyon National Park, new taxa.

Introduction

Efferia Coquillett is the largest and most conspicuous genus of asilids in the Americas with over 230 described species and many undescribed taxa, especially south of the United States (Fisher 2009). About 100 species occur in North America (Wilcox 1966, Fisher 2009), primarily occurring in arid and grasslands in the Southwest. At least 98 species are reported from Texas to California and the Four Corners states, and about 51 species are reported in Arizona (Geller-Grimm & Artigas 2003/2004). Ecoregional surveys commonly report *Efferia* as the most species-rich genus of asilids in the Southwest. For example, Nelson & Baumann (2001) reported at least 17 species in a survey of the Grand Staircase-Escalante National Monument (GSENM) in southern Utah. However, the asilids of the Grand Canyon ecoregion (GCE) in northern Arizona, and particularly in Grand Canyon, have received little attention. As part of a biological inventory, LES [Lawrence E. Stevens] and CRN [C. Riley Nelson] collected asilids across a variety of elevations in the study area. We present new distribution data on the species in this complex (genus *Albibarbefferia* by Artigas & Papavero 1997; subgenus by Geller-Grimm & Artigas 2003/2004) in the GCE region.

Hine (1919) and Wilcox (1966) arranged the North American species into eight groups or complexes based primarily on differences in wing venation and setation.

Later, Artigas & Papavero (1997) designated many groups to genera. However, Fisher (2009) considered several of their genera synonyms of *Efferia*, and noted significant variability in the characters that Artigas & Papavero used to justify their generic status. Fisher emphasized that the unique structure of the male and female terminalia is the most reliable basis for recognizing a monophyletic *Efferia*. Although the groups recognized by Hine and Wilcox were not based on phylogenetic analyses (Fisher 2009), they are useful in organizing the species. We followed Fisher's assessment in this study.

Study Area

Located on the lower Colorado Plateau, the Grand Canyon region is a large (140,000 km^2), geomorphically complex landscape that drains into the Grand Canyon (Fig. 1; Blakey & Ranney 2008, Stevens & Polhemus 2008). This ecoregion is dominated by a mid-elevation plateau that extends southward to the Mogollon Rim, which is the southern terminus of the Colorado Plateau. Numerous small peaks exist on the plateau and several large volcanic peaks approach or exceed elevations of 3500 m. Additionally the plateau contains large, long, and sheer escarpments. The middle and upper parts of the plateau between elevations of 1200–3400 m are covered by coniferous woodland and forests interspersed with large forest meadows. The Colorado River and its tributaries are deeply incised into the plateau, creating thousands of kilometers of ephemeral and perennial desert stream-riparian habitats with sand-boulder substrata and phreatophytic vegetation, as well as sand dune, bedrock, and colluvial brecchia habitats, all of which are favored by some species of *Efferia*. The GCE lies at the boundary between the Basin and Range and the Rocky Mountain geologic provinces, and includes four biomes: the Sonoran-Mohavean, Great Basin Desert, the Upper Colorado Plateau in northeastern Utah, western Colorado, northwestern New Mexico, extreme southwestern Wyoming [Intermountain region], and the Rocky Mountain biomes. As a consequence of its geologic history and topographic, climatic, and habitat diversity, the GCE is an ecotonal mixing zone for flora and fauna, with roughly equal proportions of neotropical, nearctic, and endogenic taxa (Stevens & Polhemus 2008).

Diagnosis of the *Albibarbis* Complex

The species in this complex mostly occur in the arid southwestern states of North America, and southward into Central America. They differ from other North American complexes by the following combination of characters: mesothorax usually broad, evenly curved dorsally, not strongly arched, and usually with short setae anteriorly, setae slightly shorter than pedicel never, never abundant or forming a crest except in *E. willistoni* (Hine) i.e., mesonotum highly arched with numerous setae, longer than scape, and forming an erect crest; mesonotal bristles sparse, dorsocentral bristles present behind transverse suture. Scutellum with short setae and usually 2–6 stout marginal bristles; costal margin of wing straight, sometimes slightly dilated (Fig. 25); vein R_4 branched at or beyond discal crossvein; vein R_5 curved anteriorly joining costa above wing apex (Wilcox 1966). Terminalia (Figs. 2–24, 26–40): Male genitalia erect with dorsal surface positioned anteriorly; epandria longer than wide with small apical process; gonostylus usually branched with erect or hooked spine; gonocoxite with abundant setae ventrally, usually dense basally, usually sparser and sometimes shorter apically; aedeagus with three perpendicular

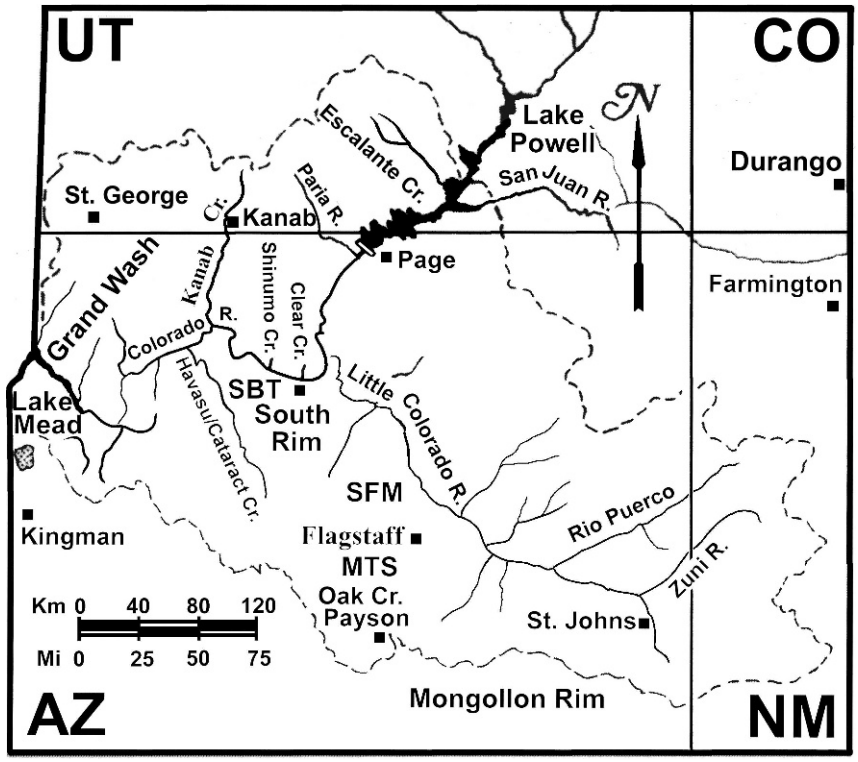


Figure 1. Map of the Grand Canyon region in southern Utah, northern Arizona. The southern margin of the Colorado Plateau is the Mogollon Rim. MTS—Middle Tovar Springs, SBT—South Bass Trail, SFM – San Francisco Mountains.

phallic tubules apically, each angled 45–60 degrees posteriorly from the phallus; female genitalia, usually longer than segments 6–7, and consisting of segments 8–9 and cercus; ovipositor strongly compressed laterally except oval in cross-section in *Efferia albibarbis* (Macquart); spermathecae ovate or oval, longer than wide; surface largely sclerotized with base narrowly membranous.

Methods and Materials

The descriptive terminology primarily follows McAlpine (1981), with the following clarifications. The term 'bristle' herein refers to the stout macrotrichia found on the thoracic dorsum, legs, and tarsi. All other macrotrichia are termed setae, and are usually distinguished by the shorter, weaker shaft. The term vestiture denotes a combination of bristles and setae.

Measurements were made using an ocular micrometer in the eyepiece of a Meiji dissecting microscope. Body length is the distance from the apical protrusion of the face to the apex of segment 7 of females or 8 of males (Bullington & Lavigne 1984, Cannings 2011). Wing length is the distance from the humeral crossvein to the apex of the wing. Scutal setae length is the average length of the acrostichal setae along the anterior arch of the mesonotum. Scutellar setae length is the length of the setae in the middle of the scutellum; setae across the base of the scutellum are slightly shorter, and those along the apical margin are slightly longer. Epandrium length is measured

from the extreme base to the apex, including the apical process; epandrium diameter is measured at the greatest width in lateral view approximately midway from base to apex. Ovipositor length is the distance from the base of segment 8 to the apex of the cercus; length/width ratio is the total length divided by the diameter. Length of segment 9, cercus, and spermatheca (measured separately) is the horizontal length from base to apex of these structures. Ground color refers to the color of the cuticle which is usually covered by tomentum, the microscopically superficial extensions of the cuticle (pollinosity of Wilcox 1966, pruinosity of McAlpine 1981).

Label data were recorded in a standard format with each line denoted by a forward slash [/]. A second label is indicated by a tilde symbol [~] preceded and followed by a blank space. Data from holotype labels were recorded unchanged. In all other sections, we omitted any information that is repeated many times, e.g., "Arizona, AZ., Coconino County", and then grouped all locality records from each county together separated by semicolons. Phrases, words, or abbreviations denoting collectors, e.g., collected by, Coll(s)ectors, collrs, etc. are omitted. Square brackets are used to clarify abbreviations or to provide useful information not found on labels.

Preparation of terminalia for study, illustration, and storage follow the techniques by Scarbrough & Perez-Gelabert (2008, 2009).

Identification Keys

Wilcox's (1966) key to the species of this group is herein revised, including new species described herein and those by Forbes (1987). The structure and wording of his original keys are maintained whenever possible. Changes include an update of morphological terminology (McAlpine 1981), clarification of certain details, and the omission of some wording. New illustrations of the terminalia of those species found in the survey and/or similar species that are likely to occur in the GCNP are included. Workers should consult Wilcox (1966) and Forbes (1987) for illustrations of male terminalia of species not found in this study.

Key to Species of the *Efferia albibarbis* Complex, Males

1. Large flies, usually 25–40 mm long (*neosimilis* Forbes 1987, & *bicolor* (Bellardi) 1861, sometimes < 18 mm) 2
- Smaller flies, usually < 21 mm. 9
2. Metathoracic tibiae bent forward and enlarged apically 3
- Metathoracic tibiae neither bent forward nor unusually enlarged apically . . . 7
3. Mystax white to yellow; apical 3/5 of metathoracic tibiae enlarged; scutellar setae white or yellowish; abdominal segments 6–7 white tomentose, 6 with black spot dorsally; body length 29–32 mm; (Texas) . . . . . *armata* (Hine) 1918
- Mystax not entirely pale, at least a few bristles black; apical 2/5 of metathoracic tibiae enlarged; scutellar setae mostly pale, sometimes black setae medially (*tagax*) or mostly (*neosimilis*); segments 6–7 entirely white tomentose 4
4. Gonocoxite with deep C- or U-shaped apical notch 5
- Gonocoxite without deep C- or U-shaped apical notch 6
5. Apical 4/5 of epandrium ventrally with spur or tooth-like process; gonocoxite with U-shaped notch, dorsal and ventral margins of notch about equal in length; femora black; metathoracic tibiae greatly enlarged; scutellar setae mostly or entirely black; body length 16.5–26 mm; (southern Arizona, New Mexico) . . . . . *neosimilis* Forbes 1987

- Apical 4/5 of epandrium ventrally without spur or tooth-like process, gonocoxite with C-shaped notch, dorsal margin of notch about twice as long as ventral margin; femora reddish dorsally; metathoracic tibiae moderately enlarged; scutellar setae white, at most sparse black setae medially; body length 21–28 mm; (southern Arizona, Texas). . . . . .*tagax* (Williston) 1885

6. Gonocoxite with wide shallow apical emargination, a prominent triangular flange dorsally and low mound-like process medially, apical corner ventrally acuminate and produced well beyond triangular flange; apical 4/5 of epandrium ventrally without spur-like process; body length 18.0–22.0 mm; (Northern Chihuahua, Mexico; New Mexico, Texas) . . . *incognita* Forbes 1987
- Gonocoxite without wide shallow apical emargination, dorsal flange elongate, well beyond deep rectangular notch ventrally, apex truncate; apical 4/5 of epandrium ventrally with spur-like process (see *bicolor*, Fig. 6); body length 19.5–25.0 mm; (Sonora, Sinaloa, Mexico) . . . . . *sonorensis* Forbes 1987

7. Head vestiture entirely pale yellowish; abdomen grayish-white tomentose with short white setae; costa not dilated, subcostal cell brownish; apical process of epandrium wide, strongly produced, diameter slightly greater than height; dorsal margin of gonocoxite elongate, forming a stout spine-like process apically; body length 25–34 mm; (Kansas, Oklahoma, Texas) . . . . . *leucocoma* (Williston) 1885
- Vestiture of mystax and palpi usually partly black; abdominal segments 2–5 or 2–6 black basally usually with short black setae (Nevada *E. bicolor* with mystax and abdominal tergites entirely whitish setose); costa dilated; apical process of epandrium neither strongly produced nor unusually wide; dorsal margin of gonocoxite not forming a stout spine-like process apically. 8

8. Mystax with only sparse black bristles; narrow base of abdominal segments usually with sparse black setae; usually 2 stout scutellar bristles, sometimes 2–4 weaker bristles laterally, discal setae white; epandrium with prominent triangular apical process and much smaller spur-like process ventrally at apical 4/5; terminalia (Figs. 7–9); body length 21–26 mm; (Arizona, California, Mexico, Mississippi, Nevada, New Mexico, Texas) . . . . . .*bicolor* (Bellardi) 1861
- Mystax with numerous black bristles; broad dorsum of abdominal segments black setose; usually 6 stout scutellar bristles, all or most discal setae black; epandrium without prominent triangular apical process and small spur-like process ventrally; body length 32–35 mm; (Texas) . . . . . .*grandis* (Hine) 1919

9. Mystax usually entirely pale; frons at vertex as wide as at antennae; abdominal segments 2–5 with 2 black spots dorsally; r-m crossvein at or slightly beyond middle of discal cell; terminalia as in Figs. 2–4; body length13–20 mm; (Coast to coast in United States, southern Canada, s. to Venezuela) . . . . . *albibarbis* (Macquart) 1838
- Mystax in part black; frons narrower at vertex than at antennae; r-m crossvein at apical 1/3 of discal cell or further beyond 10

10. Mystax mostly black, pale setae sparse; epandrium with tooth-like process at apical 4/5 ventrally, dorsal process with shallow notch, and short sparse fringe ventrally; gonocoxite with stout apical hook; gonostylus blade-like apically; aedeagus with paired erect flanges ventrally (Figs. 12–14); body length 13.0 mm; (Northern Arizona, Southern Utah). . . . . *carbonaria* **sp. nov.**

- Mystax mostly pale, sparse black bristles and setae mixed; epandrium without tooth-like process at apical 4/5 ventrally; terminalia differs from above 11
11. Abdomen entirely gray and light brown tomentose, setae white; scutellar setae and bristles white; tibiae and tarsi yellowish to brown; terminalia reddish-brown, apical flange of epandrium black; body length 14–17 mm; (Arizona) . . . . . *duncani* Wilcox 1966
- Abdominal tergites 2–5 black basally with short black setae 12
12. Femora black 13
- Femora brownish-yellow or yellow; terminalia as in Figs. 26–28; body length 12.8–16.9 mm; (Grand Canyon National Park) . . . . . *tapeats* **sp. nov.**
13. Terminalia wider than apical abdomen segments in dorsal view, gonocoxite ventrally with fringe of uniform length from base to apex, dense basally, increasingly sparse apically 14
- Terminalia narrower than apical abdomen in dorsal view, gonocoxal fringe variable in length and density 15
14. Epandrium long, widest on apical half, apical process narrow with uniform margin in lateral view; apical 1/2 of gonocoxite with parallel margins and uniformly diameter, apex truncate; gonostylus with short hooked process (Figs. 17–19); body length15.8 mm; (Northern Arizona). . . . . *fisheri* **sp. nov.**
- Epandrium shorter, wider at middle than apically, apical process wider, margin more irregular; apical 1/3 of gonocoxite tapered to pointed apex; gonostylus ventrally with longer stouter hooked process (Figs. 31–33); body length16–18 mm; (California). . . . . *vertebrata* (Bromley) 1940
15. Apical process of epandrium digitate with rounded apex; gonostylus with short hooked spine ventrally; terminalia as in Figs. 36–38; body length 15–19 mm; (Texas-Oklahoma, New Mexico, Arizona, Utah) . . .*zonata* (Hine) 1919
- Apical process of epandrium triangular; gonostylus with long, stout spine ventrally; terminalia as in Figs. 20–22;body length13–19 mm; (California) . . . . . *peralta* Wilcox 1966

Females

1. Large flies, usually 20–40 mm long (some specimens of *bicolor, incognita, neosimilis* $<$ 18 mm) 2
- Smaller flies, length $<$ 20 mm long 9
2. Mystax entirely white or yellow 3
- Mystax usually with several black bristles medially, sparse below and along oral margin laterally, remainder pale yellow or white (except Nevada specimens with only pale vestiture). 4
3. Scutellum mostly or entirely white setose; abdomen entirely yellowish-gray tomentose and white setose; scutellum with white setae and bristles; ovipositor tapers from base to apex, 5.9 mm long, 1/9 as wide at middle as long; body length 31 mm. . . . . *leucocoma*
- Scutellum mostly or entirely black setose; abdominal segments 2–5 black basally and black setose, 7 usually broadly black, 6–7 largely black setose; stout scutellar bristles black, setae largely white; ovipositor length 4.4–6.1 mm, 1/9 as wide at middle as long; body length 21.5–29.0 mm . . . .*armata*

4. Scutellum entirely white setose, setae as long as scape and pedicel combined, about 2/3 as long as marginal bristles; usually 2 stout marginal bristles, sometimes 2–3 thinner bristles laterally; 2–4 thin dorsocentral bristles; ovipositor length 3.8–6.2 mm, 1/8 as wide at middle as long, spermatheca narrow, 1.8 times longer than wide (Figs. 9–10); body length 14.0–27.0 mm . . . . . *bicolor*
- Scutellum with numerous or mostly black setae, length of setae variable, usually 4 or more stout marginal bristles 5
5. Thorax and femora dorsally reddish or reddish-yellow 6
- Femora black, sometimes with reddish tips; thorax black 7
6. Thorax entirely and femora dorsally dark red; 6 marginal scutellar bristles; ovipositor length 7.0 mm; body length 21.0–28.0 mm. . . . . *tagax*
- Thorax entirely and femora dorsally paler red or orangish; 4–7 scutellar bristles; ovipositor length 5.9–6.8 mm; body length 19.5–25.0 mm. . . *sonorensis*
7. Abdominal tergite 6 laterally and sternites entirely white setose 8
- Abdominal segments 6–7 black with black setae; ovipositor length 7.1 mm, 1/10 as wide at middle as long; body length 20.6–38.0 mm . . . . . *grandis*
8. Ovipositor length 3.9–4.5 mm, 1/4 as wide at middle as long; body length 16.6–24.0 mm . . . . . *neosimilis*
- Ovipositor longer and narrower, 5.2–6.3 mm long; about 1/6 as wide at middle as long; body length 18.0–23.0 mm . . . . . *incognita*
9. Femora brownish-yellow, narrow apices brown or blackish; ovipositor narrow, length 4.0–4.1 mm, 1/7 as wide at middle as long, spermatheca oval, 1.5 times longer than wide (Figs. 29–30); body length 12.8–16.3 mm . . . *tapeats*
- Femora entirely black; ovipositor and spermatheca differs from above 10
10. Mystax usually entirely white, at most 2–3 black bristles; frons at vertex as wide as at antennae; r-m crossvein at or near middle of discal cell; dark transverse bands of 2–4 or 5 tergites divided medially; ovipositor length 3.0 mm, (segment 8) oval or circular in cross-section basally; spermatheca narrow, twice as long as wide; tergite 8 2.8 mm long (Figs. 5–6); body length 16–19 mm . . . . . *albibarbis*
- Mystax with 7 or more black bristles; frons at vertex narrower than at antennae; r-m crossvein beyond middle of discal cell, usually at apical 1/3 of discal cell; dark bands or spots of 2–4 or 5 tergites if present never divided medially; ovipositor not unusually oval in cross-section basally; spermatheca variable 11
11. Mystax with mostly black, sparse white setae and bristles mixed; tibiae blackish laterally and apically; 6–8 thin seta-like dorsocentral bristles; ovipositor long and narrow, length 5.0–5.3 mm, 1/9 as wide at middle as long, spermatheca narrow, about 2 times longer than wide (Figs. 15–16); body length17.0–17.6 . . . . . *carbonaria*
- Mystax with mostly white, 7–14 black bristles and sparse black setae mixed; tibiae yellowish, apices blackish; 4–6 stout dorsocentral bristles; ovipositor and spermatheca variable 12
12. Abdominal segments 1–6 gray and brown tomentose, white setose; ovipositor short, length 3.8–4.4 mm, 1/6 as wide at middle as long; body length 16 mm . . . . . *duncani*
- Abdominal segments black basally and black setose. 13

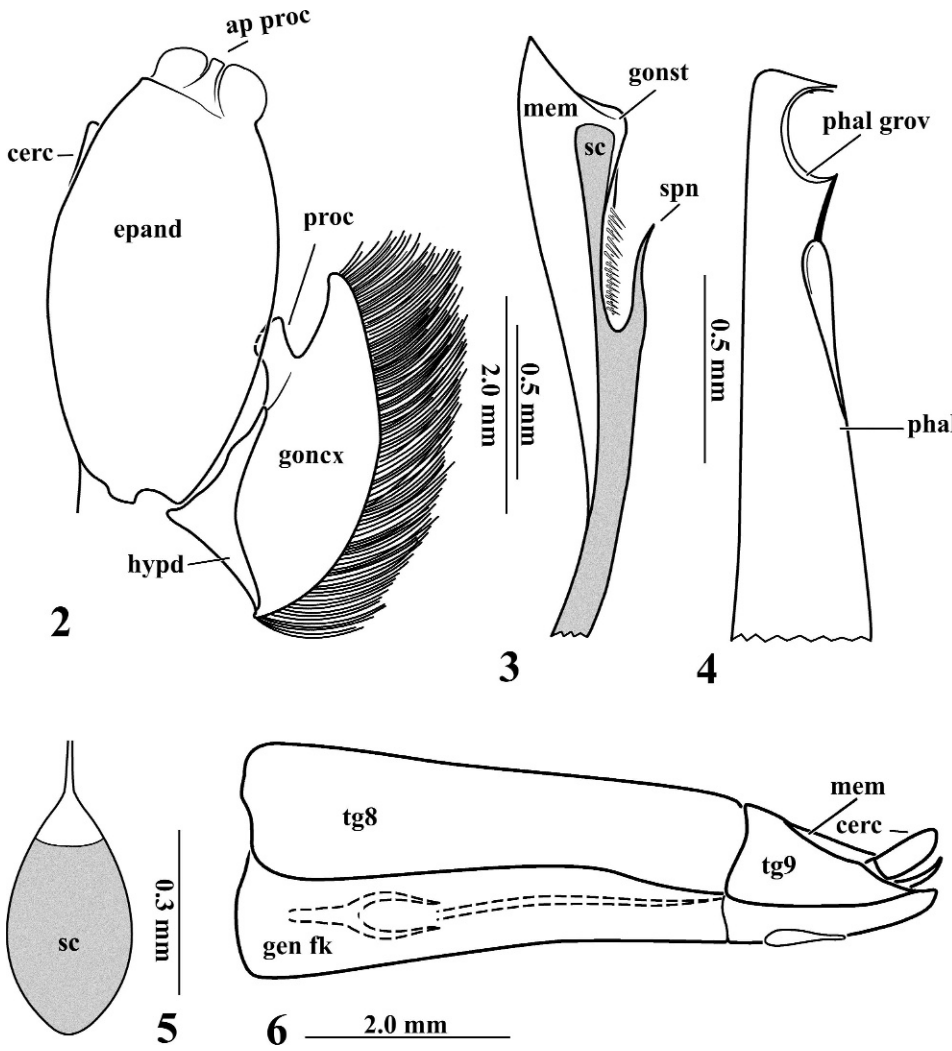
13. Metathoracic femora usually with 4 anteroventral bristles; mesonotum largely golden brown tomentose; abdominal segments 1–3 with erect white setae ventrally, tergite 3 with short black setae basally; ovipositor long, length 4.0–4.1 mm, 1/10 as wide at middle as long, spermatheca about twice as long as wide (Figs. 23–24); body length 16–18 mm . . . . . *peralta*
- Metathoracic femora usually with 5–7 anteroventral bristles; mesonotum mostly grayish tomentose; sternites 1–4 or 5 with erect white setae; spermatheca variable. 14
14. Scutellum with setae as long as or longer than scape and pedicel, usually largely white; katepisterna with tuft of setae (about 30); 5–6 bristles below metathoracic femora; ovipositor long, length 4.0–4.1 mm, 1/6 as wide at middle as long, spermatheca oval, 1.4–1.5 times as long as wide (Figs. 33–34); body length 16–18 mm . . . . . *vertebrata*
- Scutellum with shorter setae, not longer than scape, at least 1/2 black; katepisterna with sparser tuft of setae (about 15); metathoracic femora usually with 7 anteroventral bristles; ovipositor shorter, length 3.5–3.7 mm, 1/6 as wide at middle as long; spermatheca narrow, about twice as long as wide (Figs. 39–40); body length 15–18 mm . . . . . *zonata*

Taxa

Efferia albibarbis (Macquart) 1838
Figs. 2–6

Erax [*Er.*] *albibarbis* Macquart 1838: 117. Description (North America).
Er. barbatus, authors, not Fabricius, syn.
Er. pumilis Walker 1855: 640, syn. (Mexico, Veracruz).
Er. cinerescens Bellardi 1861: 39, syn. (Mexico, Veracruz).
Er. tricolor Bellardi 1861: 40, syn. (Mexico, nr. Mexico City).
Er. furax Williston 1885: 67, syn. (Washington).
Nerax albibarbis, Hull 1962: 478, syn.
Efferia albibarbis, Martin 1962: 251. Description, designated male neotype; Martin & Wilcox 1965: 393. Catalog; Wilcox 1966: 108. Description, figured male and female terminalia, keyed species; Martin & Papavero 1970: 62; Riley 1987:75. (Utah distribution); Papavero 2009: 15.

New records. Arizona, Coconino Co. [County], GCNP [Grand Canyon National Park]/Colo. R. Mi. [Colorado River Mile] 108 L/12.vii.2007; 670 m/L.E. Stevens (1♀, MNA); GCNP/Colo. R. Mi. 116.5 L/19.viii.2006; 735 m/J.D. Ledbetter (DIP 7.0010; 1♂, MNA); GCNP/Colo. R. Mi. 109 RL/18.viii.2006; 670 m/J.D. Ledbetter (DIP 7.0024; 1♀, MNA); GCNP/Shinumo Cr. 2 km up [from confluence with Colorado River]/12.vii.2007; 700 m/L.E. Stevens (2♀, MNA); GCNP/Shinumo Cr. [Creek] 3 km fr [from] mouth/11.vii.2007; 810 m/L.E. Stevens (1♂, 2♀, MNA); GCNP/Shinumo Cr. [Creek] nr lower trail Xing [crossing]/12.vii.2007; 690 m/L.E. Stevens (1♀, MNA); GCNP/Nankoweap Cr lower, CR Mi. 52R/25.v.2006; 855 m/L.E. Stevens (DIP 6.0083, 6.0098; 2♀, MNA); GRCA/Colo. R. Mi. 88R/27.v.2006; 735 m/L.E. Stevens (DIP 6.0086; 1♂, MNA); GRCA/209 Mile Channel/3.vi.2006; 400 m/L.E. Stevens (DIP 6.0094; 1♂, MNA); Mohave Co., GRCA/Kanab Cr. Mouth (CR MI 143R)/31.v.2006; 650 m/L.E. Stevens (DIP 6.0085, 6.0092, 6.0093, 6.0097; 2♂,



Figures 2–6. *Efferia albibarbis* (Macquart), male & female terminalia, lateral view. Figure 2. Intact terminalia. Figure 3. Gonostylus with long narrow spine posteriorly. Figure 4. Phallus with tubules and groove. Figure 5. Spermatheca. Figure 6. Ovipositor. Abbr.: ap proc = apical process of epandrium; cerc = cercus; epand = epandrium; gen fk = genital fork; goncx = gonocoxite; goncx proc = gonocoxal process; gonst spn = gonostylar spine; hypand = hypandrium; mem = membranous; phal grov = phallic groove; sc = sclerotized; st = sternite; tg = tergite.

2♀, MNA); HualIR [Hualapai Indian Reservation]/Spencer Cr. mouth/27.viii.2006; 365 m/J.D. Ledbetter (DIP 7.0023; 1♂, MNA); GCNP/Spencer Cr. mouth/ 27.viii.2006; 365 m/J.D. Ledbetter (DIP 7.0023, 7.0022; 1♂, 1♀, MNA); Yavapai Co., Private/Verde R. @ Granite Cr./Near Paulden/18.v.2008; 1208 m/L. & P. [Phoebe] Stevens (1♂, 1♀, MNA); C-TNF [Coconino-Tonto National Forest]/Fossil Cr. 10 km ds [downstream]/29.vii.2006; 1200 m/L.E. Stevens (DIP 6.0067; 1♀, MNA). Utah, Kane Co.,/Grand Staircase-Escalante/Natl. Mon. White House/ Cmpgd [Camp ground], 2 mi. S Paria/Contact Station and Hwy 89 ~ N 37.07953 W 111.88960,/elev. 1325 m 14.vi.2003/A.J. Nelson #0061 & J.E. Lee (2♂, BYU).

Remarks. Efferia albibarbis is distinguished from congeners by the broadly rounded protruding face and white tomentum and vestiture; face at antennae as wide as frons or vertex; two longitudinal rows of blackish spots on three or more tergites [usually only one per tergite in genus]; and the combined characters of the terminalia (Figs. 2–6). The gonocoxal process is erect, long, and slightly capitate apically (Fig. 2). In dry specimens the process is bent inward, appearing shorter and thumb-like in lateral view. The short (~ 3.0 mm) ovipositor is rigid, oval in cross-section in cross-section, not strongly compressed laterally as in most species, further distinguish females (Figs. 5–6).

Distribution & Habitats. This widespread species is found from northern South America throughout much of North America and southern Canada (Geller-Grimm & Artigas 2003/2004). Of the most common of the six *albibarbis* complex taxa taken in the Grand Canyon region, *Efferia albibarbis* is found along deep, narrow, canyon-bound, perennial streams, on barren to sparsely vegetated boulder and sand terraces, from 365 to1208 m in elevation. We collected it on the floor of Grand Canyon between Colorado River Miles 52 (Nankoweap Creek) and 246 (Spencer Creek), and it was also common in similar habitats in the upper Verde River drainage on the southern boundary of the GCE and throughout the GSENM to the north. We have yet to find it along ephemeral drainages in our region. *Efferia albibarbis* flies from late spring through summer, with collection dates from 18 May to 27 August.

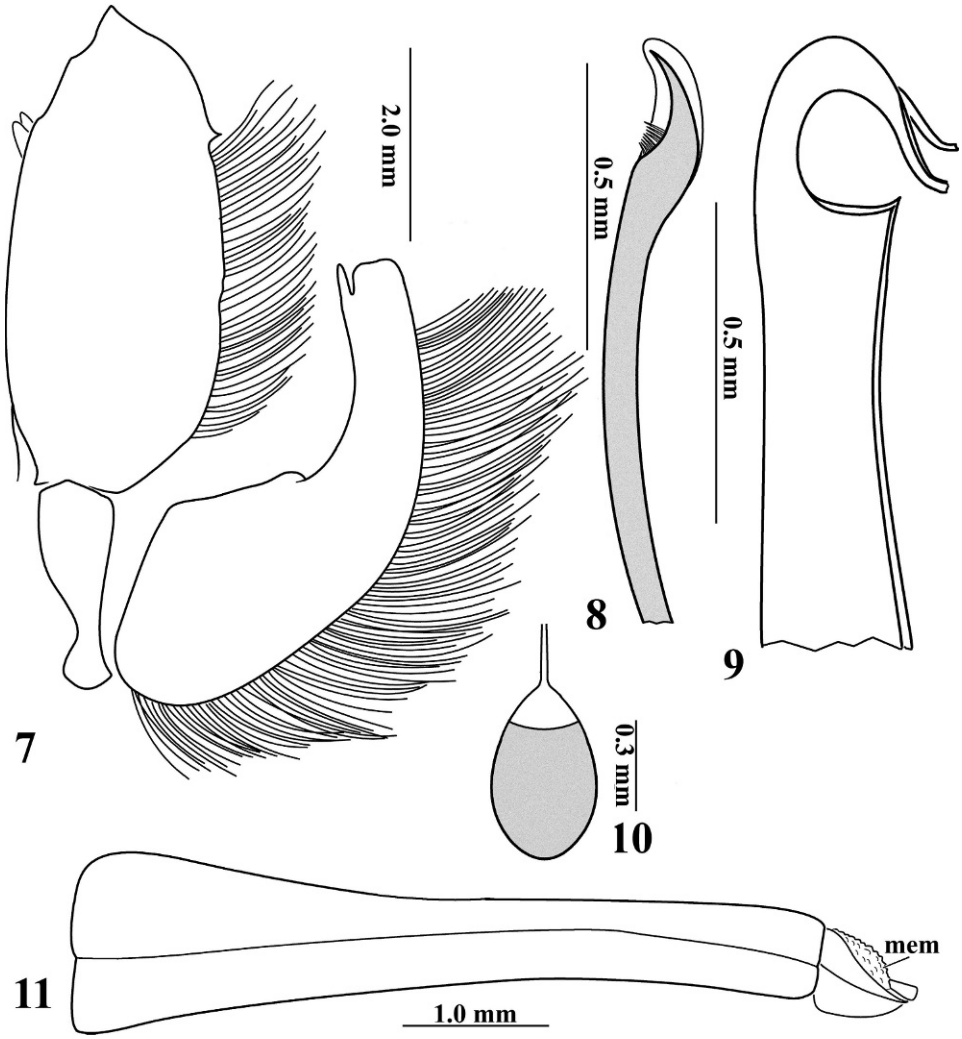
Efferia bicolor (Bellardi) 1861
Figs. 7–11

Erax bicolor 1861:47. (Mexico, nr. Mexico City); Hine 1919: 112. Description, figured male terminalia, keyed species. (Arizona, New Mexico, Mexico, Mississippi, Texas); Bromley 1934:109 (Texas).

Nerax bicolor, Hull 1962: 478, syn.

Efferia bicolor, Martin & Wilcox 1965: 394. Catalog; Wilcox 1966: 111. Redescribed, male and female terminalia illustrated, species keyed; Martin & Papavero 1970: 63; Papavero 2009: 15. Catalogue; Nelson 1987: 77. (Utah distribution).

New records. Arizona: Coconino Co., Hyde Park [437 m]/4.vi.66 ~ J.H. Davidson/J.M. Davidson/M.A. Cazier ~ *Efferia*/*bicolor*/Bell. '68/J. Wilcox (1♂, ASUT); 37 mi S. Grande [2000 m]/Canyon Rt. 64/6.vi.69 ~ M. Cazier/J. Bigelow ~ *Efferia*/*bicolor* Bell. 71/J. Wilcox (1♂, ASUT); Graham Co., Gila Valley [1995 m]/26.vii.1961/G.L.Arvizo/R. Hernandez (1♂, UAIC); Maricopa Co., Grand[e?] Reef Dam [1275 m]/19.1 × .'68 ~ Larry C. Antilla ~ 727 ~ *Efferia*/*bicolor* Bell. 71/J. Wilcox (1♂, ASUT); 3.2 mi SE/St. Johns [1731 m],/E. of Sierra/Estrellas 1050'/10.vi.1973 *Condila*/*lycioides* in/bloom (Gray)/Gray-thorn ~ Martin Kolner ~ *Efferia*/*bicolor* Bell. 75/J. Wilcox (1♂, ASUT); 3.2 mi SE/St. Johns,/E. of Sierra/Estrellas 1050'/22.vi.1973 ~ Martin Koler ~ *Efferia*/*bicolor* Bell. 75/J. Wilcox (1♀, ASUT). California: Imperial Co., 13 Mi. SW. Palo Verde [~ 444 m]/1.viii.1967 ~ J.D. Ledbetter/M.A. Cazier ~ *Efferia*/*bicolor*/Bell. '68/J. Wilcox (1♂, ASUT). Mexico: Sonora, Guaymas/area, Nacapule Canyon [300–600 m] 28°01′ N, 111°03 W/3.viii.2001 SIB, 2001.0051 (1♂, UAIC); Hermosillo [210 m], 12.viii.1959/Black light trap/WLNutting & FGWerner (1♂, UAIC). Texas: Brewster Co., Rio Grande/Big Bend/Nat. Park 16–17.v.'74 ~ Linda Draper/Oscar Francke/M.A. Cazier ~ *Efferia*/



Figures 7–11. *Efferia bicolor* (Bromley), male & female terminalia, lateral view. Figure 7. Intact terminalia. Figure 8. Gonostylus without spine posteriorly. Figure 9. Phallus with tubules and groove. Figure 10. Spermatheca. Figure 11. Ovipositor.

bicolor/Bell. '75/J. Wilcox (1♂, ASUT); Duval Co., 10 mi W. San/Diego [94 m]/ 12.v.1974 ~ Linda Draper/M.A. Cazier ~ *Efferia*/*bicolor*/Bell. '75/J. Wilcox (1♂, ASUT); Hudspeth Co., 4 mi E. Salt/Flat [1137 m]/5.v.1974 ~ Linda Draper/Oscar Francke/M.A. Cazier ~ *Efferia*/*bicolor*/Bell. '75/J. Wilcox (2♂, ASUT).

Additional Specimens Examined. Arizona: Cochise Co. 2 mi. N.E. Portal/6.vi.63/ M. Cazier, mountains ~ *Efferia*/*bicolor*/Bell. '64/J. Wilcox (1♂, ASUT); 2 mi. N.E. Portal/28.vi.62/M. Cazier ~ *Efferia*/*bicolor*/Bell. '64/J. Wilcox (1♂, ASUT); 2 mi. N.E. Portal/2.viii.63/M. Cazier ~ *Efferia*/*bicolor*/Bell. '64/J. Wilcox (1♂, 1♀, ASUT); 2.5 mi N.E. Portal/4700' [1400 m] El/2.viii.1975 ~ M.A. Cazier/and family ~ *Efferia*/*bicolor*/Bell. '71/J. Wilcox (1♀, ASUT); 5 Mi. N.E. Portal/21.vi.1964 ~ Jean H. Puckle/M.A. Mortenson/M.A. Cazier ~ *Efferia*/*bicolor*/Bell. '65/J. Wilcox

(1♂, ASUT); Portal/4700 ft. at/light 28.viii.64 ~ Jean H. Puckle/M.A. Mortenson/M.A. Cazier ~ *Efferia/bicolor*/Bell. '65/J. Wilcox (1♂, ASUT); same data except 2.vi.64/J.D. Ledbetter ~ *Efferia/bicolor*/Bell. '65/J. Wilcox (1♀, ASUT); 13.vi.63/Cazier, Mortenson ~ *Efferia/bicolor*/Bell. '64/J. Wilcox (1♂, ASUT). New Mexico: Hidalgo County, 16 Mi. N.E. Rodeo [1534 m]/N.M. 22.vi.64 ~ Jean H. Puckle/M.A. Mortenson/M.A. Cazier ~ *Efferia/bicolor*/Bell. '65/J. Wilcox (1♂, ASUT); same data except 29.vi.65 ~ J.H. Davidson/J.D. Ledbetter/M.A. Cazier ~ *Efferia/bicolor*/Bell. '66/J. Wilcox (2♀, ASUT). Nevada: Nye Co. AMNWR [Ash Meadows National Wildlife Refuge]/Marsh Spring/8–14.viii.2005; 715 m/H. Kloeppel (1♂, DIP 5.2974, MNA); AMNWR/Indian Springs North UV/8–14.viii.2005; 700 m/H. Kloeppel (1♀, DIP 5.2973, MNA); AMNWR/Roger Springs: UV light/11.viii.2005; 700 m/H. Kloeppel, K. Taylor (1♀, DIP 5.3315, MNA); AMNWR/Point of Rocks Spr. UV/8.viii.2005; 700 m/H. Kloeppel (1♀, DIP 5.2975, MNA).

Remarks. Efferia bicolor, a moderately large [usually > 22 mm] black species, is distinguished by a slightly dilated costal margin, reddish-yellow or yellow tibiae, long dense setae along the posterior margin of the gonocoxite, epandrium with a large pointed apical process, and in the combined characters of the terminalia (Figs. 7–11). Though similar to *E. sonorensis* Forbes (1987), *E. bicolor* is distinguished from the latter by the hooked apex of the gonocoxite and narrow parallel sided (not enlarged apically) metathoracic tibiae. *Efferia bicolor* is one of three species in Arizona that has a preapical tooth or spur projecting from the posterior margin of the epandrium. Although at least a few black bristles are usually found in the mystax, it is entirely pale yellow or whitish in the Nevada specimens reported here.

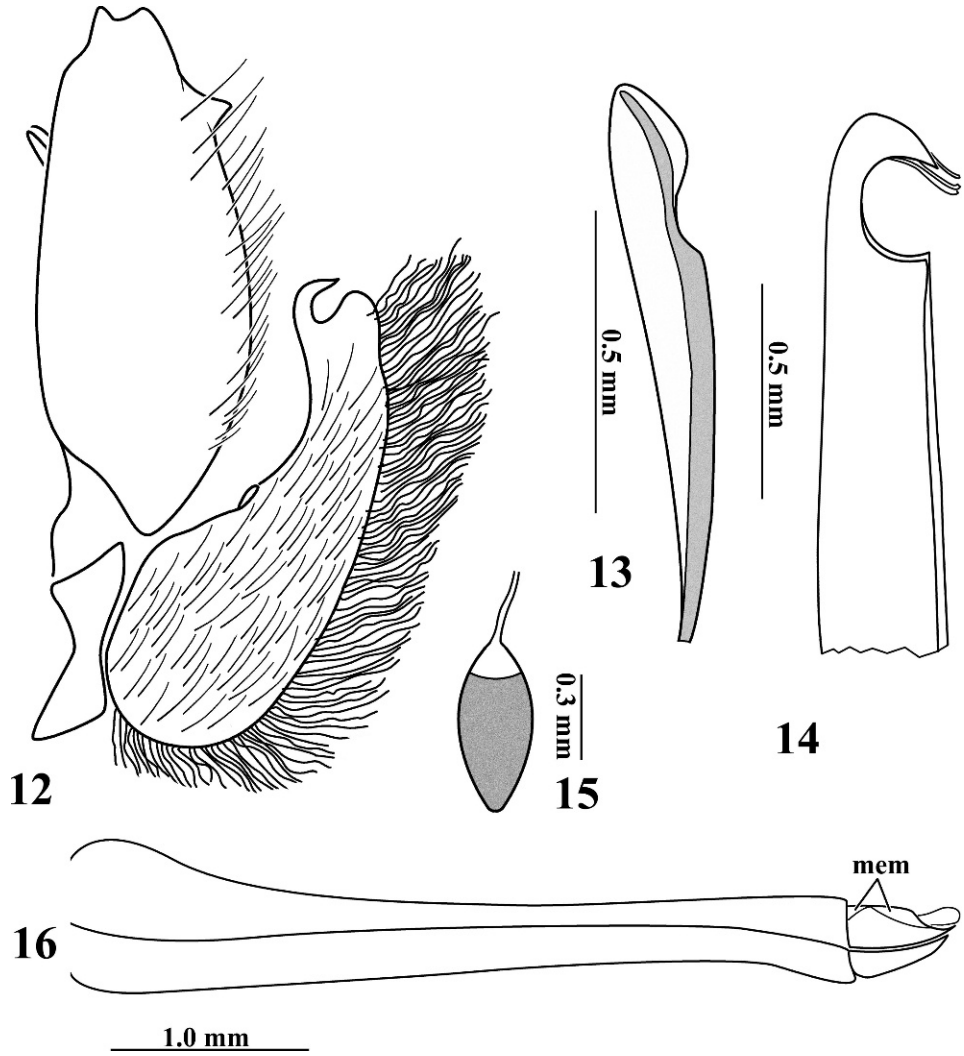
Distribution and Habitats. Bellardi (1861) described *E. bicolor* from females collected in northern Mexico. Hine (1919) later added 24 specimens from Arizona, Mexico, Mississippi, New Mexico, and Texas, gave a short description of the male, illustrated its terminalia, and noted the dilated wing and the long ovipositor (oviduct), 'as long as abdominal segments 4–7'. Bromley (1934) and Wilcox (1966) then reported the species from five localities in southern Texas and 5 counties in Arizona (Cochise, Gila, Graham, Maricopa, Pima, and Pinal) and southern California, respectively. Geller-Grimm & Artigas (2003/2004) listed the species from Mississippi and Oklahoma. Nelson (1987) reported the species from 5 counties in Utah, Washington County in the southwest and northward to Box Elder, Cache and Daggett Counties. Here we report its range further northward in Arizona to within a few miles of the south rim of the Grand Canyon National Park, Coconino County, AZ., and from Nye County in southern Nevada. This is the first record of *E. bicolor* from Nevada. *Efferia bicolor* flies from June to August at elevations up to 2000 meters, and is commonly found in open scrub vegetation and in open forests. It was captured on rocks and vegetation below trees.

Efferia carbonaria **sp. nov.**

Figs. 12–16

Male. Length 13.1 mm; wing 10.0 mm; face at antennae 0.8 mm, head width 2.7 mm, vertex 0.7 mm. Antennomeres from style to scape, 0.7:0.4:0.1:0.4.

Head. Black, white tomentose with mostly white setae, mystax with about 20 black bristles medially, 10 along epistomal margin laterally; palpi black setose, sparse white setae on basal 1/2 ventrally. Antennae black setose. Frons with black setae



Figures 12–16. *Efferia carbonaria* **sp. nov.,** male & female terminalia, lateral view. Figure 12. Intact terminalia. Figure 13. Gonostylus without spine posteriorly. Figure 14. Phallus with tubules and groove. Figure 15. Spermatheca. Figure 16. Ovipositor. Abbr. goncx hook = gonocoxal hook.

laterally, setae ventrally as long as or longer than scape; sides above tubercle parallel, about as wide as face at antennae. Ocellar setae thinner, shorter, posterior setae as long as combined length of basal 3 antennomeres. Occiput with 4–5 erect postocular bristles dorsally, 2–3 black mixed with sparse black setae.

Thorax. Black. Pronotum yellowish-gray tomentose, white setae and 4 bristles. Mesonotum brownish-gray tomentose, paler anteriorly, paired paramedial stripes black separated by a narrow brownish tomentose stripe medially; black setose dorsally, anterior setae 1/2–2/3 as long as scape, setae much longer posteriorly with sparse whitish setae; bristles black, 6 laterally and 1–4 thin dorsocentrals posteriorly, latter about 1/2 as long as lateral bristles. Scutellum brownish-gray or gray

tomentose; setae erect, entirely white, sparse black setae mixed medially, 2/3 as long as marginal bristles, apical setae about as long as bristles; 2 stout black marginal bristles plus 4 thinner bristles. Pleura brown to brownish-gray tomentose, darkest anteriorly, setae and bristles pale yellowish, sparse black setae on anepisternum dorsally and posteriorly, and katatergite. Halter yellow. Wing: Hyaline; costal margin straight, not dilated; costal cell pale brownish-yellow; veins dark reddish-brown or brown; costal vein black setose basally. Crossvein r-m just beyond apical 1/2 of cell d; stump vein slightly longer than basal diameter of cell m_4. Base of cell m_4 well beyond d. Vein R_5 merges with costa at or just above wing apex. Legs: Black with black bristles. Coxae brownish-gray tomentose with white vestiture. Trochanters and femora largely whitish setose, long setae ventrally, usually shorter blackish setae apically; prothoracic femora with long white or black setae dorsally; metathoracic femora with 4–5 bristles ventrally. Tibiae dark brownish-yellow or blackish anteriorly and laterally, paler posteriorly, narrow apices black; long white setae ventrally or laterally. Tarsi black with black bristles and setae.

Abdomen. Black, largely white tomentose and white setose; tergite 1 entirely, base of 2, wide sides and narrow apices of tergites 2–5, and tergites 6–7 entirely, white or grayish tomentose; tergites 2–5 with large blackish spots dorsally and black setae medially, black setae sparse on tergites 2–3, abundant and more widely spread on tergites 4–5, and segment 8 entirely black setose; white setae long laterally, shorter dorsally. Sternites 1–7 gray tomentose, white setose, setae long on sternites 1–3, shorter on 4–7.

Terminalia; (Figs. 12–14). Black, black setose. Epandium narrow, 2.5 times longer than wide, shallow notch along apical margin, fringe sparse ventrally, long apically. Gonocoxite uniformly narrow apically, slightly curved anteriorly, apex broadly rounded; fringe uniformly dense, slightly longer apically.

Female. Lengths, body 17.0–17.6 mm; wing 13.6–13.8 mm; face width at antennae 0.8–1.2 mm, head width 2.7–3.1 mm, vertex 0.7 mm. Antennomeres from style to scape, 0.7:0.4:0.1:0.4–0.9:0.4:0.2:0.4 mm. Ovipositor length 5.0–5.3 mm; midpoint 1/9 as wide as long.

Head. Face with black vestiture, pale setae sparse. Black postocular bristles extend to midlateral margin of eye, numerous stout bristles clustered at margin just before vertex. Thorax: Mesonotum with 8–10 dorsocentral bristles with thinner shorter bristles between thicker bristles, 3 thin shorter bristles before transverse suture. Scutellum white setose, dorsal setae about 1/2 as long as marginal bristles, those near apex longer, about 2/3 as long as marginal bristles; 6 marginal bristles plus shorter, thinner bristles. Legs: Metathoracic femora with 7–8 black bristles ventrally. Abdomen: Mostly gray tomentose with long white setae. Tergites 2–7 with wide sides and apical margins gray tomentose with white setae, each with large black spot dorsally and short black setae, at least medially on basal 2–3, more widespread on 4–7; wide sides and apical margins of gray tomentose. Terminalia (Figs. 15–16): Ovipositor length 5.3 mm, 1/9 as wide at middle as long. Spermatheca oval.

Types. Utah: Carbon Co., BLM [Bureau of Land Management] Gr. R. [Green River]/Cedar River Can. [Canyon],/29.vi.2008; 1400 m/J.D. Ledbetter (holotype ♂, MNA). Paratypes, Arizona: Coconino Co., Private/"Tovar Springs Middle" [Middle Tovar Springs], 16.vii.2009; 2070 m/M. Souter (DIP 10.1010, 1♀; DIP 10.1009, 1♀, MNA).

Etymology. Latin, *carbonaria* for the redundant black tibiae and Carbon County, the holotype locality. The name is feminine gender.

Remarks. The dull gray tomentose face, the black and white facial vestiture, palpus and antennae black setose; anterior mesonotal setae about as long as scape and pedicel combined; 4–6 marginal scutellar bristles; hyaline wings, costal margin straight; blackish tibiae; and the combined characters of the terminalia (Figs. 12–16) distinguish *E. carbonaria*. It is distinguished from congeners by the smaller size (body length 13.1 mm, wing 10.0 mm), the blackish tibiae, and long thin ovipositor (Figs. 15–16). The notched apical process of the epandrium, shapes of the phallus and gonocoxal hook, and the long abundant setae on the posterior margin of the gonocoxite further distinguish the species.

Distribution & Habitat. Efferia carbonaria ranges onto the Colorado Plateau, with habitats including a spring-fed meadow in ponderosa pine forest in northern Arizona, and along a perennial tributary of the Green River in east-central Utah. It flies at 1400 to 2070 m from late June to at least mid-July during the pre-monsoon period.

Efferia fisheri **sp. nov.**
Figs. 17–19

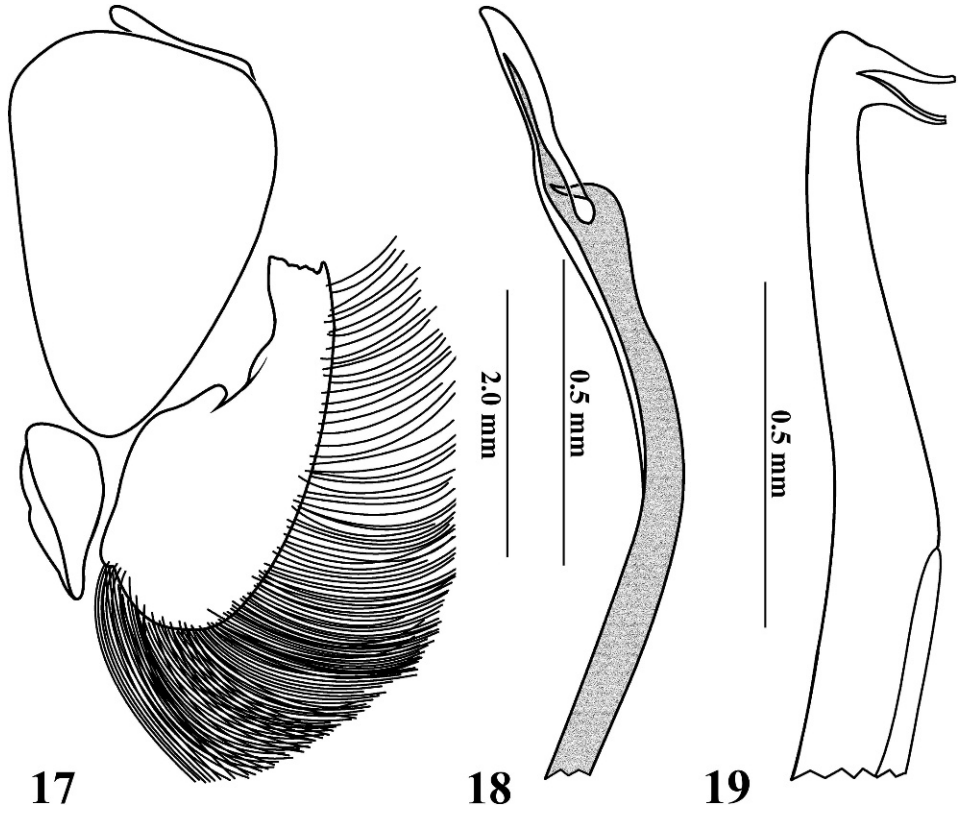
Male. Length 15.8 mm; wing 13.4 mm; maximum head width 3.5 mm; facial width at antennae 0.9 mm, width of vertex (narrowest point between eyes) 0.62 mm. Antennomeres from style to scape (in mm) = 0.8:0.4:0.2:0.5.

Head. Gray tomentose, thin along oral margin and apex of gibbosity, with thin white setae; cuticle black. Mystax with 13 black bristles scattered medially, 6–7 along oral margin. Palpus black setose, sparse white setae mixed ventrally. Antennae, frons, and occiput white setose. Ocular tubercle with 2 long black setae, longer than pedicel and scape combined; 5–7 black postocular bristles dorsally, thinner white bristles laterally.

Thorax. Mesonotum black with brownish-yellow tomentum mixed with gray posteriorly, areas shifting to golden yellow or dark brown depending on light angle. Apical 2/3 with wide longitudinal stripe and two lateral spots dark brown in dorsal view, stripe divided medially and bordered laterally with brownish-yellow tomentum; postpronotal spot golden yellow, sides yellowish-gray or gray. Vestiture black, setae along anterior arch of mesonotum as long as scape, dorsocentrals and acrostichal setae long and thin, those posteriorly about same length and thickness, anterior 3 dorsocentral thinner and 2/3 as long as posterior bristles, first one at transverse suture; 6 thicker bristles laterally with 1–2 additional, thinner, shorter bristles nearby. Scutellum with dull gray to yellowish-gray tomentum, setae widespread, mostly black, basal corners mixed with pale setae, setae about 1/4 as long as 6 stout black bristles. Pleura brownish-yellow anteriorly grading to gray beyond wing base; setae white generally weak and clustered on arched sclerites, scattered black setae along dorsal and posterior margin of anepisternum; katatergal bristles black. Halter knob reddish, stalk yellow grading to dull brown at base.

Wing. Venation typical of group. Veins brown to dark brown, basal veins reddish. Cells hyaline, cells r_1 brownish. Costal vein with short mostly black microtrichia, white microtrichia basally. Crossvein r-m at apical 1/3 of discal cell. Recurrent vein 1.5–2.0 times as long as r_4.

Legs. Coxae, trochanters, and femora black with abundant white setae and sparse black bristles; black setae apically on apical 1/3, mostly dorsally on first 2 femora, dorsal 1/3 dorsally and ventral 1/2 of metathoracic femora. Mesothoracic and



Figures 17–19. *Efferia fisheri* **sp. nov.,** male, lateral view. Figure 17. Intact terminalia. Figure 18. Gonostylus with short hooked spine posteriorly. Figure 19. Phallus with tubules and groove.

metathoracic femora with 5–7 black bristles anteroventrally. Tibiae brownish-yellow with apices narrowly reddish; bristles and short black setae anteriorly, prothoracic tibiae with fringe of long whitish setae. Tarsi reddish, with bristles and dorsal setae black; basal tarsomere of prothoracic tarsus with white setae laterally.

Abdomen. Black with mostly gray tomentum and white setae. Tergite 2 with narrow transverse spot medially, tergites 3–5 dark brown spot on basal 2/3 dorsally, tergite 6 with small basal spot, brown spots with brown often unusually long, and with extensive gray tomentum laterally extending across the apical margin of tergites, appearing banded in dorsal view; tergite 7 entirely white tomentose with white setae, tergite 8 shining black with black vestiture.

Terminalia; (Figs. 17–19). Brown. Swollen, slightly wider than the apical three abdominal segments in dorsal view.

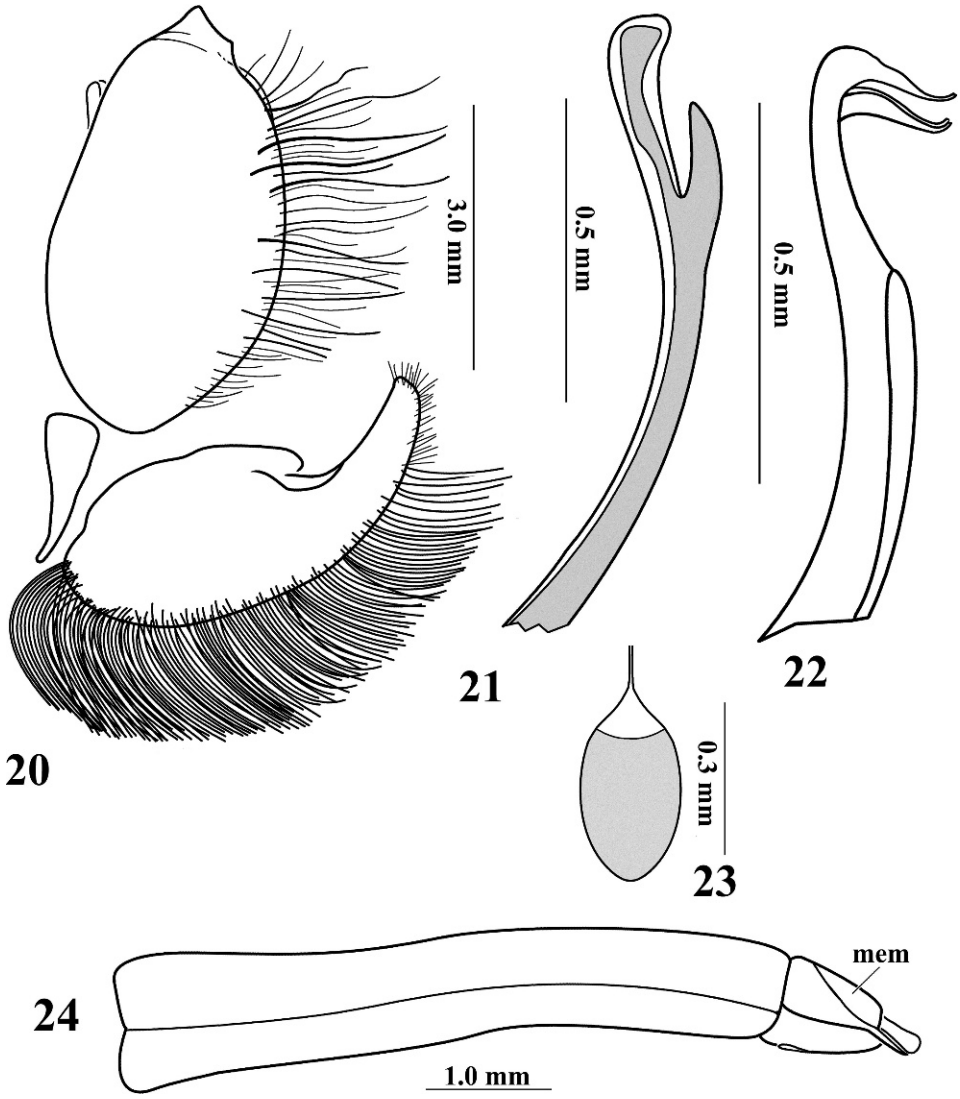
Female. Unknown.

Types. Arizona, Gila Co.,/11 mi N. of Payson/5100' 12.ix. 80/E. Fisher (♂ holotype, CAS).

Etymology. The species name is in honor of Eric Fisher who collected the holotype.

Distribution. Northern Arizona.

Remarks. Efferia fisheri will run to *E. vertebrata* in Wilcox's key. However, *E. fisheri* is distinguished by the characters of the male terminalia (Figs. 17–19). The



Figures 20–24. *Efferia peralta* Wilcox, male & female, lateral view. Figure 20. Intact terminalia. Figure 21. Gonostylus with thick erect spine posteriorly. Figure 22. Phallus with tubules and groove. Figure 23. Spermatheca. Figure 24. Ovipositor.

epandrium is more slender basally, wider on apical half, about 2/3 its vertical height, the slender digital apical process, the uniformly long gonocoxal setae, denser basally, the uniform wide on the apical 1/2, and the truncate apex. The short hooked process and shape of the phallus further distinguish the species.

Efferia peralta Wilcox 1966
Figs. 20–24

Efferia peralta Wilcox 1966: 115. Description, illustrated terminalia, keyed species; Papavero 2009: 15. Catalogue.

Specimens Examined. California: Orange Co./4.ix.[19]55 ~ J. Wilcox ~ Paratype/*Efferia*/*peralta*/Wilcox (1♂, EMFC); *peralta*/5.v.1952 ~ J. Wilcox ~ Paratype/*Efferia*/*peralta*/Wilcox (1♂, 1♀, EMFC). San Antonio/Canyon Ontario [282 m]/Cal. July 25, \'07 ~ Jas.S. Hine/Collector ~ red label, Paratype [of *E. zonata*, err. ident.] (1♂, 0359872, OSUC); San Diego Co./28.vi.19/EPVan Duzee ~ red label, Paratype [of *Erax zonatus*, err. ident.] (1♂, 0359873, OSUC);/28.vi.19/EPVan Duzee (1♀, 0359879, OSUC); 29. iv.13/EPVan Duzee ~ *Erax*/*zonatus*/Det. S.W. Bromley 38' [err. ident.] (1♂, 0359878, OSUC); Jacumba [~ 800 m],/27.vi.52 ~ D.J. & J.N./Knull ~ *Erax*/*zonata* Hine/Det./Martin '57 [err. ident.] (1♀, 0359881, OSUC); Jacumba/20.vii.49 ~ D.J. & J.N./Knull ~ *Erax*/*zonatus* Hine/Det./S.W. Bromley 1950 [err. ident.] (1♀, 0359880, OSUC).

Remarks. Efferia peralta is superficially similar to *E. zonata* but is distinguished by the combined characters of the terminalia (Figs. 2–24) especially the triangular apical process and the long setae of the epandrium. It is further distinguished by the long setae and the narrow apical 1/3 of the gonocoxite, and the thick spine of the gonostylus (Figs. 20–24).

Distribution. Southern California, San Diego & Orange counties. Its flight season ranges from 200 to 380 m in April through July, and September.

Efferia tapeats **sp. nov.**
Figs. 25–30

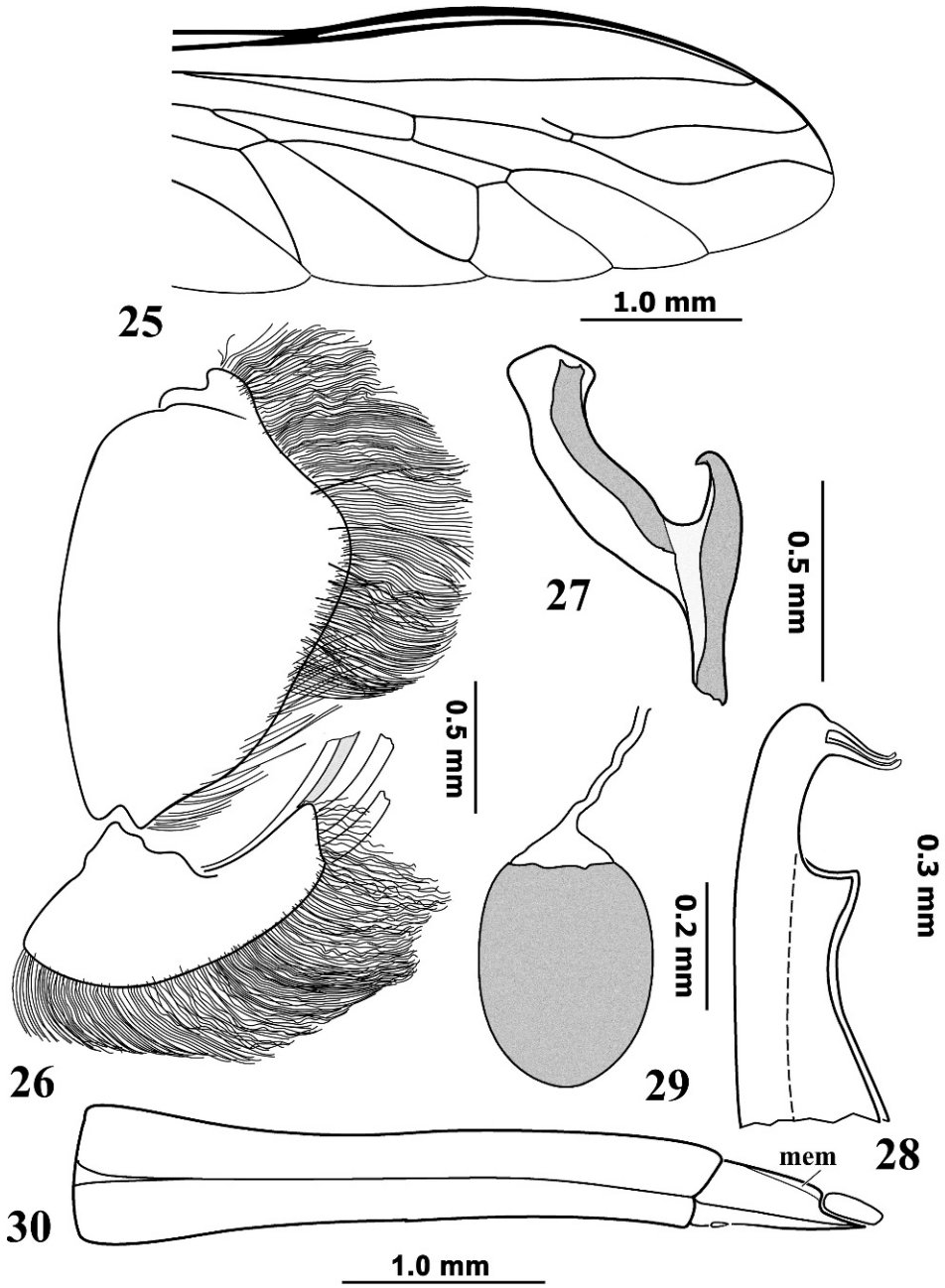
Male. Length 16.3–16.9 mm; wing 12.8–13.6 mm; face width at antennae 0.6–0.9 mm, head width 3.5–4.3 mm, vertex 0.5–0.7 mm. Antennal segments, 0.7:0.3:0.2:0.4–0.8:0.4:0.2:0.4 mm.

Head. Black, white tomentose with white setae and bristles, mystax with 4–6 black bristles; palpi black setose apically and dorsally, white on basal 1/2 or less ventrally. Antennae black, grayish tomentose, setae white; frons with long bristly ventrally, as long as or longer than scape; ocellar setae thinner shorter, subequal in length to scape.

Thorax. Black, mesonotum yellowish-gray tomentose, central stripe divided and lateral spots brown; black setose dorsally, about as long as pedicel, setae posteriorly much longer and thinner, whitish; bristles black, 6 laterally and 1–2 stout dorsocentrals posteriorly, latter short seta-like about 1/2 as long as posterior bristles. Scutellum yellowish-gray or gray tomentose; setae erect, entirely white or white with sparse black setae medially, most 1/2–2/3 as long as marginal bristles, apical setae about as long as bristles; 4–5 black marginal bristles. Pleura gray tomentose, slight tint of yellow anteriorly, setae and bristles white. Halter yellow. *Wing* (Fig. 25): Hyaline; costal cell brownish-yellow; veins reddish-brown or brown; costal margin only slightly dilated; costal vein whitish setose basally. Cell r_1 acutely pointed apically with vein R_{1+2+3} adjacent to costa, sometimes appearing fuse with it. Crossvein r-m at apical 1/3–1/4 of cell d; stump vein as long as or slightly longer than cell m_4. Base of cell m_4 well beyond cell d. Vein R_5 merge with costa at wing apex.

Legs. Coxae black, grayish tomentose, white setose. Trochanters, femora, and tibiae reddish-yellow or darker yellowish-brown, narrow margins of trochanters and apices of femora and tibiae black. Femora and tibiae whitish setose, short except long ventrally or laterally on prothoracic femora and tibiae; bristles black. Tarsi reddish-brown with black bristles, brownish-yellow setae ventrally, black setae dorsally; basal prothoracic tarsomere with sparse white setae laterally.

Abdomen. Grayish-white tomentose; tergites 2–5 with bases narrowly gray tomentose, wide black band or large spot on basal 1/2–2/3; setae white, long on



Figures 25–30. *Efferia tapeats* **sp. nov.,** male & female, lateral view. Figure 25. Male wing. Figure 26. Intact terminalia. Figure 27. Gonostylus with short apically hooked spine posteriorly. Figure 28. Phallus with tubules and groove. Figure 29. Spermatheca. Figure 30. Ovipositor.

sides, sometimes apically, shorter dull yellowish and black setae on black areas; tergites 6–7 entirely gray tomentose, with long white setae laterally, sometimes apically, shorter dorsally; tergites 8 black with sparse black setae. Sternites gray tomentose, long, white setae. Sternite 8 with long black bristly setae apically.

Terminalia; (Figs. 26–28). Brownish-yellow or reddish. Narrow, not wider than abdominal segments 6–8 in dorsal view, black setose except pale yellow on cercus. Epandrium triangular, 1.7 times longer than wide; apical process emarginated, fringe long, dense and black on dorsal 2/3 ventrally, shorter more sparse below. Phallus tubules triradiate, surface flat ventrally with deep wide groove and thin erect flange laterally, structure rectangular in cross-section. Gonostylus forked apically with short hooked process medially and longer wide flat branch laterally, sclerotized cuticle golden colored. Gonocoxite flat, curved dorsally to middle of epandrium, apex oblique with anterior corner slightly longer than ventral corner; fringe black with long, dense setae, only slightly longer apically than basally.

Female. Gray tomentose, mesonotum pale yellowish-gray. Length, 12.8–16.3 mm; wing 10.0–12.5 mm. Face width at antennae 0.8–0.9 mm, head width 3.6–4.0 mm, vertex 0.4–0.6 mm. Antennae 0.7:0.9:0.1:0.4–0.9:0.4:0.2:0.5 mm.

Face. Mystax with 7 black bristles; ocellar setae as long as pedicel. Thorax: Mesonotum with 3–4 dorsocentral bristles, yellowish-gray tomentose; 5 black marginal scutellar bristles, 1–2 thin. Wing: Costal margin straight, not dilated anteriorly; cell r_1 closed well before Costa, vein R_{1+2+3} distinct. Stump vein longer than basal diameter of cell r_4. Legs: Prothoracic femur with 2–3 long stout black bristles ventrally. Abdomen: Tergites 2–7 with black setae on black spots, white setae shorter and less abundant laterally and on sternites than in male; sternites 6–7 with scattered short black setae. Terminalia (Figs. 29–30): Length 4.0 mm. Segment 8 tapered apically, 7 times longer than diameter at middle, 3.5 mm. Spermathecae ovate, about 2 times as long as wide.

Types. Arizona: Coconino Co., GCNP/Clear Cr., 4 km up [from confluence with Colorado River]/12.ix.2005; 775 m/L.E. Stevens (holotype ♂, MNA). Paratypes: same data as holotype (1♀, MNA); GCNP/Colo. R. [Colorado River] Mi 108R [north bank] resting on *Aster* [*Chloracantha*] *spinosus* flower; 20.ix.2009; 670 m/L.E. Stevens (1♂, MNA); GCNP/S. [South] Bass Tr [Trail] in Supai Fmn. [Formation]/8.vii.2009; 1500 m/L.E. Stevens (1♀, MNA); GCNP/Colo. R. Mi 108R/Shinumo Cr. Mouth/21.ix.2009; 665 m/L.E. Stevens (1♀, MNA); GCNP/Colo. R. M. 108 L/12.vii.2007; 670 m/L.E. Stevens (1♂, MNA); Awatubi/Canyon (RM 58.2R) in Grand/Canyon Nat. Pk. 8.v.[19]92: M.E. Douglas, ASU (1♂, ASUT); GCNP/S. [South] Bass Trail, base of Tapeats (Fmn) [formation]/12.vii.2007; 900 m/L.E. Stevens (1♀, MNA); GCNP/Shinumo Cr. 3 km fr mouth/11.vii.2007; 810 m/L.E. Stevens (3♀, MNA); GCNP/S. [South] Bass Trail in Redwall Fmn/12.vii.2007; 1200 m/L.E. Stevens (1♀, MNA); same data except 13.vii.2007 (1♀, MNA); Mohave Co., HualIR/Peach Spr. Wash 4 km fr. CR [from Colorado River]/08.x.2008; 380 m/L.E. Stevens (1♀, MNA). Utah, UT. San Juan Co., GLCA/San Juan Spring #1/11.vii.2005; m./Coll. E. North (DIP 5.2198, 1♀, MNA).

Etymology. The species epithet *tapeats* refers to the massive cliff-forming unit of buff-brown Cambrian sandstone that forms the Tonto Platform in Grand Canyon. This species distribution roughly matches the exposure of this geologic formation in Grand Canyon. The species name is a noun in apposition, feminine gender.

Remarks. In addition to the characters in the key, *Efferia tapeats* is distinguished from congeners by the yellowish-gray or gray tomentose body; 5–6 marginal scutellar bristles; costa slightly dilated (Fig. 25), femora and tibiae pale brownish-yellow, apices blackish; abdominal tergites with large blackish tomentose spots dorsally; and the combined characters of the male terminalia (Figs. 26–28), especially

the wide triangular epandrium, the long black setal fringe on the epandrium and gonocoxite, and the distinctive characters of the phallus and gonostylus.

Efferia tapeats will key to couplet 10 in Wilcox (1966), which includes *E. zonata* (Hine) 1918, and *E. peralta* Wilcox 1966. Both *E. zonata* and *E. peralta* have black femora, the costal margin of the wing is straight and the epandria are elongate, not triangular. Additionally the epandrial fringe is sparser and the gonocoxal fringe is uniformly long along its entire length in *E. peralta*. It is shorter and contrastingly less dense apically in *E. zonata*. *E. tapeats* is distinguished from these species by the pale brownish-yellow legs, slightly dilated wings (Fig. 25), the triangular shape of the epandrium, and the long dense fringe of the epandrium and gonocoxite (Figs. 26–28). The female is further distinguished by the oval spermatheca (Fig. 30).

Distribution & Habitats. Efferia tapeats was taken along ephemeral and perennial sand and boulder-dominated riparian shorelines, and upslope on colluvial brecchia. It was collected in the GCNP in Arizona and on the Hualapai Indian Reservation in Coconino and Mohave counties. The holotype and paratype taken in Southern Utah extends its range upstream from Grand Canyon into tributaries leading into Glen Canyon. *Efferia tapeats* flies from July–October at elevations of 380–1500 m.

Efferia vertebrata (Bromley) 1940
Figs. 31–35

Erax vertebrata Bromley 1940: 14. Description. (California).
Nerax vertebrata, Hull 1962: 478, syn.
Efferia vertebrata (Bromley), Martin & Wilcox 1965: 396. Catalog; Wilcox 1966: 118. Illustrated terminalia, keyed species; Papavero 2009: 16.

Specimens Examined. California, Cal. Riverside Co./Menifee Vly (hills/on W. end) 33°39′ N/117°13′ W. 1800'el./7–27.viii.1980 ~ collected in/fly trap ~ E.M.Fisher ~ *Efferia*/*vertebrata* (Brom 83)/det. E.M. Fisher (1♂, EMFC); Idyllwild Calif./ 8.3.35/Jean Russell ~ *Erax*/*vertebrates*/Brom 41'/detr J. Wilcox (1♂, 1♀, EMFC); Inyo County;/Walker Creek, 5 km S Olaucha;/malaise in oak woodland nr. water:/ 16–30.vii.2010; M.E. Irwin; 1530 m;/36°14.56′ N, 118°03.46′ W (8 ♂, 4 ♀, UAIC).

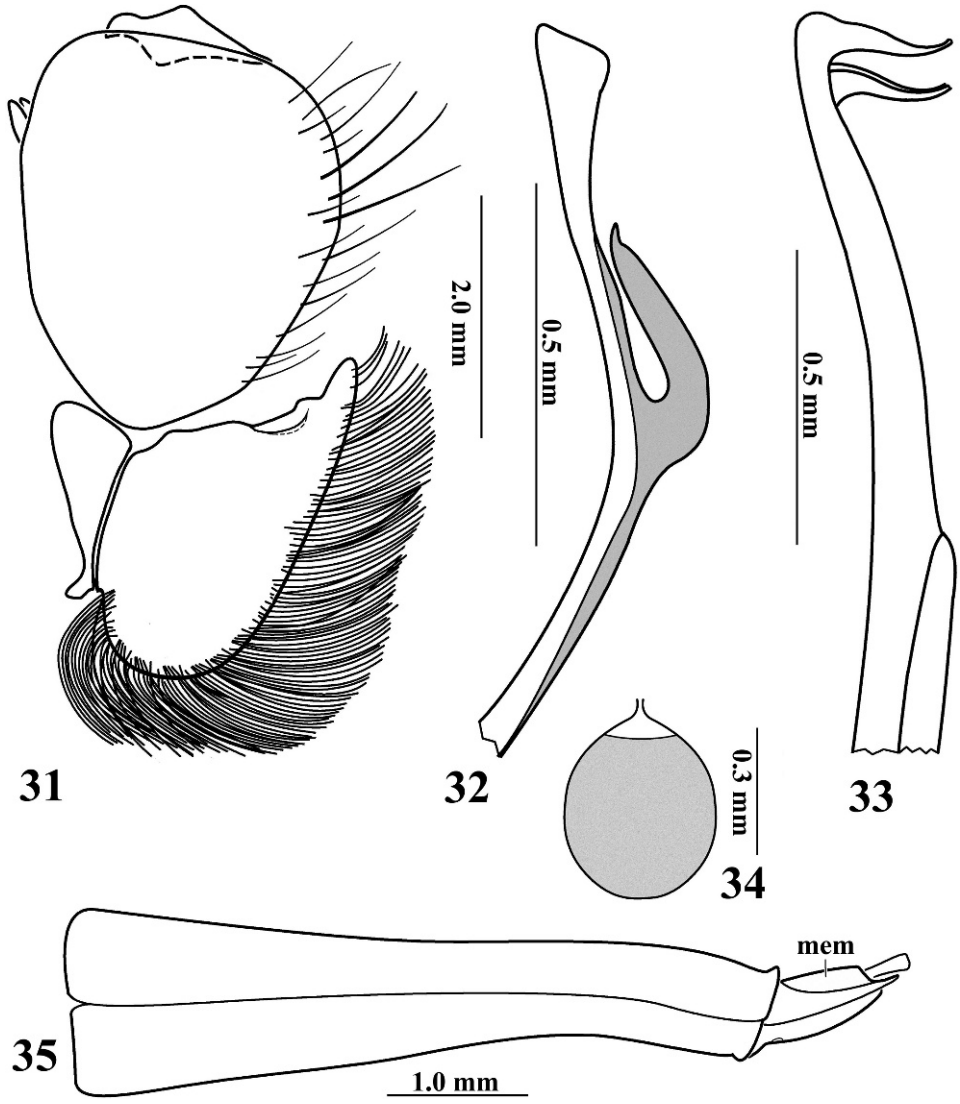
Remarks. Efferia vertebrata is distinguished by the tumid male terminalia which is wider than the apical 3–4 abdominal segments when view dorsally. Additionally, the epandrium is only slightly longer than wide; the apical process is wide, projecting well above the dorsal surface of the epandrium, and emarginate along its dorsal margin in lateral view. The narrow triangular apex of the gonocoxite and the long, stout spine-like process of the gonostylus further distinguish the species (Figs. 31–32). It is distinguished from *E. fisheri* by the combined characters of the terminalia (Figs. 31–35).

Distribution & Habitats. Southern California (Riverside and Inyo Counties).

Efferia vertebrata flies from 548 to 1629 meters in elevation during August. It was captured in oak woodlands near water.

Efferia zonata (Hine) 1919
Figs. 36–40

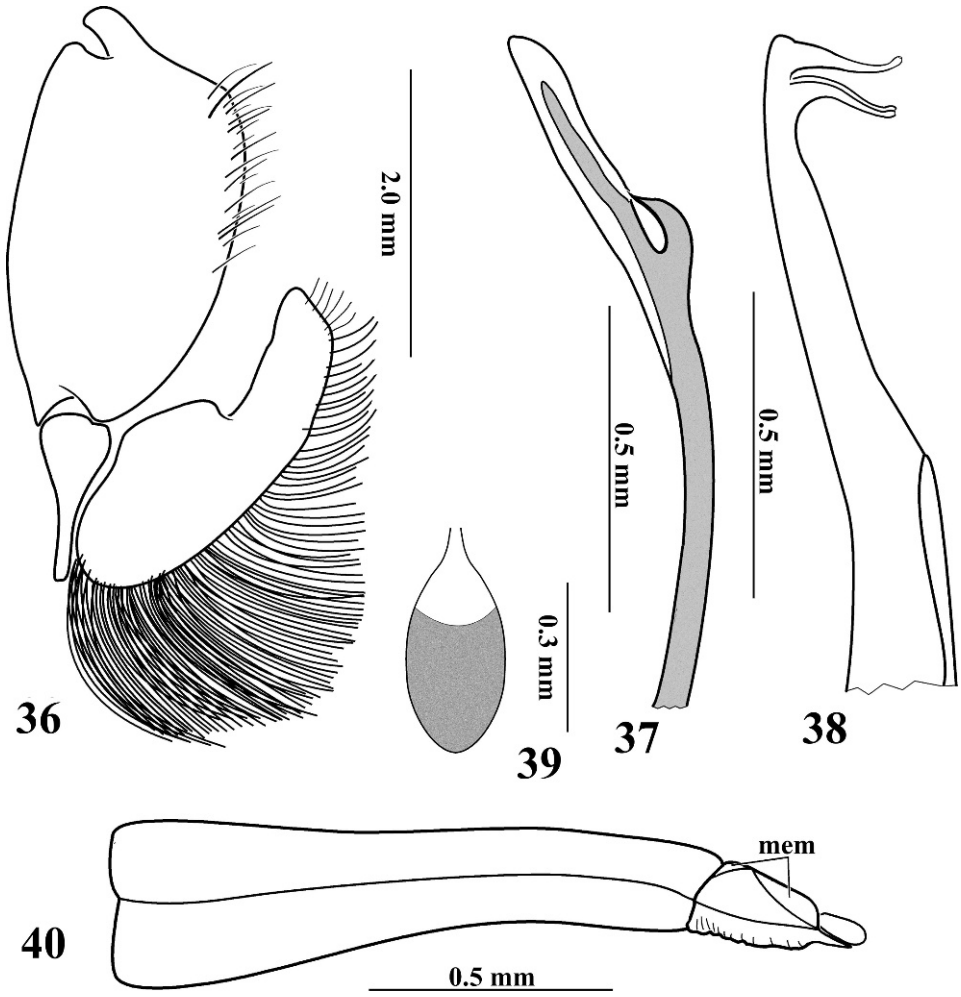
Erax zonata Hine 1919: 112. Description, North America.
Nerax zonata, Hull 1962: 478, syn.



Figures 31–35. *Efferia vertebrata* (Bromley), male & female, lateral view. Figure 31. Intact terminalia. Figure 32. Gonostylus with long thick spine posteriorly. Figure 33. Phallus with tubules and groove. Figure 34. Spermatheca. Figure 35. Ovipositor.

Efferia zonata (Hine), Martin & Wilcox 1965: 396. Catalog; Wilcox 1966: 139. Redescribed, illustrated terminalia, and keyed species. Riley 1987:79. Utah distribution.

Types Examined. Arizona: F.H. Snow/August 1905 ~ red label with the word Type ~ *Erax*/*zonatus*/Hine ~ (holotype ♂, 0319486, OSUC); F.H. Snow/August 1902 ~ red label, Allotype (1♂, 0359871, OSUC); F.H. Snow/August 1902 ~ red label, Paratype (1♂, 0359874, 1♀, 0359875, OSUC). **New records**. Arizona, Cochise Co., Cochise Strnghld [Stronghold]/Dragoon Mts./21.vii.1961/Werner, Nutting,



Figures 36–40. *Efferia zonata* (Hine), male & female terminalia, lateral view. Figure 36. Intact terminalia. Figure 37. Gonostylus with short slightly hooked spine posteriorly. Figure 38. Phallus with tubules and groove. Figure 39. Spermatheca. Figure 40. Ovipositor.

U.V. lt.trp. [light trap] (5♀, UAIC); Mineral Park 6500'/Dos Cabezas Mts.,/11. viii.1976/DSChandler ~ sweeping low/vegetation (1♀, UAIC); Herb Martyr Dam/ Chiricahua Mts.,/22.vii./1964, GDButler (1♀, UAIC); 3 mi NE. Portal/Chiricahua Mtns/22.vii./1964 G.D. Butler/Agava (1♀, UAIC); Coconino Co., Grand Canyon/ Ri. m,/July 14, 1913 ~ AKFisher (1♀, 0359876, OSUC); N.P./So. Rim/8.viii.69 ~ R.H.Davidson/*Efferia*/*zonata*/(Hine) '67/det. G.S. Forbes '89 (1♀, 0372986, OSUC); Oak Creek Can[y]on/6000 ft. August (1♀, 0359877, OSUC); Oak Cr. Cn., 4800'/ 10.viii.1962/F. Werner, J. Bequaert (1♂, 1♀, UAIC); GC/S. [south] Bass Tr [trail] in Supai Tr. [trace, trail]/8.vii.2009; 1500 m/L.E. Stevens (DIP 10.1008, 1♂; DIP 10.1006, 1♂; DIP 10.1007, 1♀, MNA); GCNP/S. [south] Bass Trail in Redwall Fmn/ 13.vii.2007; 1200 m/L.E. Stevens (1♂, MNA); HavlIR/Spr. Grapevine Hualapai Cyn/8.vii.2003; 1050 m/L.E. Stevens, M. Erhart (DIP 3.0935; 1♂, MNA); GC/S. [south] Bass Tr [trail] in Supai Tr. [trace, trail]/8.vii.2009; 1500 m/L.E. Stevens (DIP

10.1007; 1♀, MNA); GCNP/South Bass Pt./13.vii.2007; 2050 m/L.E. Stevens (1♀, MNA); Canyon L.[-Lake; Gila Co., Globe/30.3.[19]33/FHParker ~ FHParker/ collection (2♂, UAIC); 27.viii.1950/FHParker ~ FHParker/collection (1♀, UAIC); [Gila-Pinal-Graham Cos. 31°11′16″ N, 110°28′20″ W] San Carlos Lake/20.vii. [19]32 (1♀, UAIC); Maricopa/Co., Tempe, 14.i.71 ~ C.A. Bicteo ~ *Efferia*/*zonata* Hine '71/det. J. Wilcox (1♀, ASUT); 33°32′ N, 111°26′ W]/7.ix.1935/Parker ~ F.H.Parker/collection (1♀, AUIC); Canyon Lake, 11.x.73 B.A. Robertson ~ *Efferia*/*zonata*/(Hine) '75/det. J. Wilcox (1♀, ASUT); Pima Co. Sta./Rita Mts. N. end Rose/mont area 31°48–53′ N, 110°42–47′ W,/4400-/6175' El. Anamax mine/ inventory 1975–1976/J. Busacca & C. Olson ~ Ridge Area/Sec. 24 5400'/11.viii.1975 UV light (1♀, UAIC); Madera Cn. [Canyon], Sta.[Santa] Rita Mts. 8.vi.1961/P.H. Johnson (1♀, UAIC); Cochise Strongh./Dragoon Mts./5.viii. [19]55/Butler-Noon (1♀, UAIC); Brown Cn, Babo-/quivari Mts. 4.viii.1962/FWerner, PJohnson (1♀, UAIC); Bear Cn., Hwy. mi. 12/Sta. Catalina Mts., 14.vii.1961 Werner/Nutting, UV lt.trp/(1♀, UAIC); Pinal Co., nr First/water Cr. 2000'/6 mi. NW Weaver's/Needle/ Superstition Mts./23.i.1973 ~ Jim Vaaler/Martin Koler ~ *Efferia*/*zonata* Hine '75/ det. J. Wilcox (1♀, ASUT); Pinal Mts./17.vi.1933/Lot 183 ~ FHParker/collection (1♀, UAIC); Yavapai Co., 8 mi. E. Ashfork,/3.ix.1959 WLNutting (1♀, UAIC). Utah: Capital Reef/Nat. Mon./21.vii.67 ~ W.E. &/C.A. Triplehorn ~ *Efferia*/ *zonata*/(Hine)/det. J. Wilcox'67 (1♂, 0372985, OSUC); Bryce Can. [Canyon] N.P. [National Park]/UT. 23.vii.67/W.E. &/C.A. Triplehorn ~ *Efferia*/*zonata*/(Hine)/det. J. Wilcox '67 (1♂, 0372984; 1♀, 0372982, OSUC); Box Elder Co./Round Hill/1 mi. N Mantua/5.vii.1986/C. Riley Nelson (1♂, 3♀, BYU); Garfield Co./3 miles W. of Egypt off/Hole in the Rock rd./37°34′21 N, 111°15′31 W/31.v.2000/C.R. Nelson/ no.7068A & Texas folks ~ Grand Staircase-Escalante National Monument Survey (GSENMS) (1♂, BYU); Right Hand Collet Canyon,/spring jct. Smokey Mtn. Rd./ 37°32′33 N, 111°38′25 W,/7.vii.2000 ~ E.C. Green/W.N. Mendel no.73/M. Moody/ C.R. Nelson no.7095 ~ GSENMS (2♀, BYU); Grand Staircase-Escalante/National Monument, Boulder/Mail Trail, E of Sand Creek ~ N 37.85243 W 111.47305,/elev. 2022 m, 8.viii.2003,/A.J. Nelson no. 0178 & J.E. Lee (1♂*, BYU); tenaja area, Hwy 12,/above Escalante River/37°45′ N, 111°27′ W, ~ 20.vi.2002/R.W. Baumann, S.M. Clark & P. Fugal (1♂*, BYU); Grand Staircase-Escalante/National Monument/ Upper Calf Creek Trail/N 37.85971 W 111.43759,/elev. 1960 m, 23.vi.2003,/A.J. Nelson no. 0076 & J.E. Lee (1♂*, BYU); Right Hand/Collet Canyon off/Smokey Mtn. Rd. 37°32′58 N, 111°38′20 W,/11.viii.2000 ~ E.C. Green/W.N. Mendel no.106/ C.R. Nelson no.7129 ~ GSENMS (1♂, 1♀, BYU); Grand Staircase-Escalante/ National Monument. Right/Hand Collet Canyon, jct. ~ Smoky Mountain Road,/N 37°32′33″ W, 111°38′25″/30–31.vii.2001/C.R. Nelson no.7302 (1♀, BYU); Right Hand Collet Canyon/spring jct. Smoky Mtn. Rd.,/37°32′33 N, 111°38′25 W,/ 7.vii.2000 (2♀, BYU); Grand Staircase-Escalante/National Monument. Calf/Creek, Calf Creek Cmpgd., ~ N 37.78342 W 111.41482/elev. 1628 m, 7–8.vii.2003,/A. J. Nelson no. 0111& J. E. Lee (1♀, BYU); Kane Co. GSENM/Willis Creek Skutumpah Rd./37.482° N, 112.079° W/elev. 1823 m, 5.vii.2003, C.R. Nelson (1♂*, BYU); Snake River above jct./Paria River/37°20′44 N, 112°00′29 W,/26.vii.2000/WN Mendel no.91/M. Moody ~ GSENMS (1♂*, 1♀, BYU); Grand Staircase-Escalante/Natl. Mon., Kitchen Corral/Point on Kitchen Corral Rd. Upper Calf Creek Trail/N 37°10′34″ W, 112°03′19″ W ~ 2.vii.2001,/N. Martinez,/M. Moody,/ E.C. Green no.206 (1♂*, BYU); Grand Staircase-Escalante/Natl. Mon., Wire Pass

Trail/jct. Buckskin Pass Rd. S of/House Rock Valley Rd. ~ 37°00′47″ N, 112°10′13″ W/3.vii.2001,/K.A. Clarke, M. Moody/E.C. Green no.208 (2♂*, BYU); Dip Tank Canyon/spring jct. Smokey Mtn. Rd.,/37°19′22 N, 111°38′58 W,/5–6.vii.2000 ~ E.C. Green/W.N. Mendel no.68/M. Moody/C.R. Nelson/no.7093 ~ GSENMS (3♀, BYU); same location, except 3–4.viii.2000 ~ E.C. Green/W.N. Mendel no.97/M. Moody/C.R. Nelson/no.7112 ~ GSENMS (3♀, BYU); East Fork of the Virgin River/0.5 mi. E of Mineral Gulch,/37.177° N, 112.786° W,/28–29.vii.2002, C.R. Nelson (1♀, BYU); Water Canyon, Cottonwood,/Point Wilderness,/N of Hwy 389,/37°04′07″ N, 112°37′49″ W ~ 6.vii.2001/K. A. Clarke/E.C. Green no. 211 (1♀, BYU); Cottonwood Point/Wilderness. north end of/Hwy 389, 37°04′07″ N/112°37′50″ W. 5.vii.2001,/K. A. Clarke, E.C. Green no.210 (2♀, BYU); Grand Staircase-Escalante/Natl. Mon., Kitchen Corral/Point on Kitchen Corral Rd. Upper Calf Creek Trail/N 37°10′34″ W, 112°03′19″ W ~ 2.vii.2001,/N. Martinez,/M. Moody,/E.C. Green no. 206 (3♀, BYU); Grand Staircase-Escalante/Natl. Mon., Seaman Spring,/10–25.vii.2001, E.C. Green/Malaise trap, no. 241 (1♀, BYU); GSENM,/50-Mile Mountain, Pleasant Grove/111.154° W, elev. 2255 m, 19.viii.2003, C.R. Nelson (1♀, BYU); 50 MileMtn./Steer Canyon above jct./Pleasant Groove Creek,/37°17′34 N, 111°10′01 W/8.viii.2000 ~ H.A. Barter,/E.C. Green,/W.N. Mendel,/M. Moody, C.R. Nelson no. 7123 ~ GSENMS (1♀, BYU); Early Weed Bench, off/Hole in the Rock Rd.,/37°31′15″ N, 111°11′28″ W,/5277 ft., 3.v.2000,/KT. Huntzinger, WN. Mendel/, C.R. Nelson ~ GSENMS (1♀, BYU); Sheep/Creek below Skutumpah/Rd. 37°29′44 N, 112°03′56 W, 5824 ft./17.vii.2000, ECGreen, WNMendel no.85 ~ GSENMS (1♀, BYU); Tooele Co. I-80/rest area, ca 60 mi. E/Wendover, 26.viii.1989/C.R. Nelson & family/no.53938 (1♀, BYU); Utah Co. 12/mi. E Thistle Hwy/6/50, Wheeler/Sawmill, 21–22.vii./1989, C.R. Nelson &/family no.5372 (1♂, BYU). TEXAS: Valverde Co. 20 mi. W./Comstock/11.vi.1974 ~ Linda Draper/Oscar Francke/Mont. A. Cazier ~ *Efferia/zonata* Hine '75/det. J. Wilcox (1♀, ASUT); 20 mi. W./Comstock/11.vi.1974 ~ Linda Draper/Oscar Francke/Mont. A. Cazier ~ *Efferia/zonata* Hine '75/det. J. Wilcox (1♀, ASUT).

Remarks. The male of *Efferia zonata* is distinguished from congeners by the combined characters of the terminalia (Figs. 36–40). Wilcox noted that the setation pattern on the gonocoxite, e.g., long, dense setae basally, much sparser and shorter on the apical half (see Wilcox, page 106, Fig. 22), and the shallow groove along the posterior margin of the epandrium are diagnostic of the species. Additionally, the dorsal thumb-like epandrial process, the short curved spine-like process of the gonostylus, and the shape of the phallus further distinguish the species.

The identity of *Efferia zonata* reported from California, Texas, and eastward is uncertain. Wilcox (1966) failed to find specimens of *E. zonata* from California and questioned the identification of Hine's paratypes from that state. He further suggested that they were probably *E. peralta* or *E. vertebrata*. Our examination of the types of these three species revealed that the California paratypes of *E. zonata* are *E. peralta*. Recent malaise samples taken from several locations in California, Oregon, and Washington did not yield any specimens of *E. zonata*. The yellowish tomentum of the mesonotum and long setae on the apical half of the gonocoxite and posterior margin of the epandrium, and the combined structures of the terminalia (see Figs. 20–24, 31–40) are distinctive.

Wilcox also found some variation in specimens of *E. zonata* from Nevada but only stated that they were intermediates between *E. zonata* and *E. vertebrata*. We

also report that males captured in the Grand Staircase-Escalante National Monument, Utah, are atypical. They possess abundant long setae along the entire ventral margin of the gonocoxite, similar to that found in *E. vertebrata*, rather than the short apical setae in the type series of *E. zonata*. Additionally, veins in the wing are largely pale, and the costal margin is slightly produced. However, dissected terminalia are otherwise essentially identical to the typical *E. zonata*. The Utah specimens with long gonocoxal setae are noted with an asterisk in the 'new records' section.

Distribution and Habitats. The range of *E. zonata* is probably much more limited than previously recorded (see Geller-Grimm & Artigas 2003/2004). A more extensive study is necessary to document its complete distribution.

In the GCE we found *E. zonata* on dry bedrock and colluvial brecchia surfaces between elevations of 1050 to 2000 m, more removed from the riparian terraces than the other *albibarbis* complex taxa. In the GESNM this species is almost invariably found on slickrock and dry bedrock.

Biogeography

Aerographic analyses of insects in the large, deep canyon landscape of the Grand Canyon region reveal several discrete regional biogeographic patterns. 1) The region has a relatively high biodiversity due to ecotonal mixing of Mexican-Neotropical, Nearctic, and occasionally (e.g., Odonata) Pacific Coast taxa (Polhemus & Polhemus 1976; Stevens & Bailowitz 2009). However, 2) species richness generally attenuates with elevation, latitude, and distance up the Colorado River drainage. 3) Regional biodiversity is usually greater for more vagile taxa (e.g., butterflies, dragonflies; Garth 1950; Stevens & Bailowitz 2005, 2009) compared to less vagile taxa (e.g., land snails, cicindelid tiger beetles; Baequart & Miller 1973, Spamer & Bogan 1993, Stevens & Huber 2004). However, 4) rarity, isolation, and endemism are greater among low vagility taxa (Stevens & Polhemus 2008). While desert corridor and across-canyon barrier effects predominate over refuge or null biogeographic effects on areography, rather many examples exist of isolated, (particularly) neotropical taxa (Stevens & Huber 2004, Stevens & Bailowitz 2005, Stevens & Polhemus 2008). These patterns generally apply to the *albibarbis* complex reported here. These taxa are potentially or actually vagile, and thus the regional diversity of this group is relatively higher than might be expected for such mobile species.

Overlap of the Six Species are Noteworthy. Efferia zonata overlaps with all species regardless of elevation. *Efferia bicolor* and *E. fisheri* are high elevation species on the plateau. All other species overlap at low elevations in the central Grand Canyon, and the co-occurrence of four ecologically similar taxa challenges the Gaussian niche-overlap paradigm. For example, all species in the complex except *E. bicolor* and *E. fisheri* species co-occur in the lower Shinumo Creek drainage in central Grand Canyon. Similar patterns of co-occurrence have been reported among tiger beetles (Coleoptera: Cicindelidae), with 17 co-occurring species in the Willcox Playa in southern Arizona (Pearson & Vogler 2001). Overlap in range may be more likely among generalist predators, as compared to more specialized predators, like Asilidae. Also, the greater concentration of insect prey in desert riparian zones may relax selection pressures and permit coexistence of already-derived sister taxa (Holstein 1984, Pearson & Knisley 1985, Kochner 2005). Resolution of the high diversity of coexisting members of the albibarbis taxa will require detailed

differential analyses of life histories and genetics to clarify ecological differences, isolation mechanisms, and evolution.

Acknowledgments

Funding for this research was provided in part by the Annenburg Foundation/ Explore Program, and we thank Charles A. Weingarten and Thomas Pollak for their support of LES's work. Additional research funding was provided for CRN by the Grand Staircase Escalante National Monument and the Kanab Field Office of the Bureau of Land Management. We thank the Museum of Northern Arizona (MNA) and Brigham Young University (BYU) for office and administrative support. Specimens collected by LES were obtained under National Park Scientific Collecting Permits OMB 1024-0026; 9602-09-03; 9606-06-01; 9602-28-01; 9610-09-002; 9803-10-001; 0002-20-001; GRCA-2001-SCI-0031; GRCA-2004-SCI-0004; GRCA-2005-SCI-0026;GRCA-2006-SCI-0009,0012, 0013; GRCA-2008-SCI-0011; and GRCA-2009-SCI-0015, 0045. We thank the Hualapai Tribe for permission Collection Permit No. 3772. Luciana Musetti of the Charles A. Triplehorn Insect Collection (OSUC), Ohio State University, provided a loan of the types of *E. zonata*. Many thanks to Eric Fisher (EMFC), retired California Department of Food and Agriculture, El Dorado Hills, CA, for advice and assistance over many years and a loan of *Efferia* related to this study; Michael Irwin, Professor Emeritus, NRES, University of Illinois, Urbana, IL, for the inclusion of recently collected specimens of *E. vertebrata*. Aaron Smith and Anthony Gill of The Frank F. Hasbrouck Insect Collection, Arizona State University, Tempe, (ASUT) and Shawn Clark of the Monte L. Bean Life Sciences Museum, Insect Collection, Brigham Young University (BYU), Provo, are acknowledged for arranging specimen loans. We also thank Eric Fisher, William Grogan, Florida State Collection of Arthropods, Museum of Entomology, Gainesville, and R.A. Cannings, Royal British Columbia Museum, Victoria, British Columbia, Canada for valuable suggestions and constructive comments on an earlier draft of the manuscript; and to the faculty and staff of the University of Arizona, Entomology Department (UAIC), particularly Carl Olson, for his support of this work for AGS.

Literature Cited

Artigas, J. N. & N. Papavero. 1997. The American genera of Asilidae (Diptera): keys for identification with an atlas of female spermatheca and other morphological details. IX. 2. Subfamily Asilinae Leach—*Efferia* group, with the proposal of five new genera and a catalogue of the Neotropical species. *Arquivos de Zoologia* 34(4):65–95.

Bellardi, L. 1861. Saggio di Ditterologia Messicana. *Memorie della Reale Accademia delle Scienze di Torino* 21(2):103–199, figures 1–5. pls. 1–2 [reprint 1–99 pls. 1–2] (11–88. pl. 1).

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. The University of Arizona Press, Tucson, pp. 1–271.

Blakey, R. & W. Ranney. 2008. *Ancient Landscapes of the Colorado Plateau*. Grand Canyon Association, pp. 1–176.

Bromley, S. W. 1940. New U.S.A. robber flies (Diptera: Asilidae). *Bulletin of the Brooklyn Entomological Society* 35(1):13–21.

Bullington, S. W. & R. J. Lavigne. 1984. Description and habitat of *Efferia kondratieffi* sp. nov. with notes on *Efferia aestuans* (L.) (Diptera: Asilidae). *Annals of the Entomological Society of America* 77:404–413.

Cannings, R. A. 2011. *Efferia okanagana,* a new species of robber fly (Diptera: Asilidae) from the grasslands of southern British Columbia, Canada, with notes on taxonomy, biology, distribution and conservation status. *The Canadian Entomologist* 143:578–593.

Fisher, E. M. 2009. Asilidae of Central America, pp. 585–632. *In*: Borkent, B. V. A. Brown, J. M. Cumming, D. M. Wood, N. E. Woodley & M. A. Zumbado (Eds.). *Manual of Central American Diptera.* Volume 1. NRC Research Press, Ottawa, 714 pp.

Coquillett, D. W. 1910. The type-species of the North American genera of Diptera. *Proceedings of the United States National Museum* 37:499–647. Washington, DC

Forbes, G. S. 1987. The status of *Efferia similis* (Williston), with description of three new Nearctic *Efferia* species in the *albibarbis* group (Diptera: Asilidae). *The Pan-Pacific Entomologist* 63(3):292–300.

Garth, John S. 1950. *Butterflies of Grand Canyon National Park*. Grand Canyon Natural History Association, Bulletin 11, pp. 1–53, map.

Geller-Grimm, Fritz & J. N. Artigas. 2003/2004. Catalogue of the Nearctic species (Asilidae). Available from http://www. geller-grimm. de/genera/nearctic/catspecies. html (accessed 1 February 2012).

Hine, J. S. 1918. Notes on robber flies from southwest Texas, collected by the Bryant Walker Expedition, with a description of a new species of *Erax*. *Occasional Papers of the Museum of Zoology* 61:1–7.

Hine, J. S. 1919. Robberflies of the genus *Erax*. *Annals of the Entomological Society of America* 12(2):103–157.

Holstein, G. 1984. California riparian forests: deciduous islands in an evergreen sea, pp. 2–22. *In*: R. E. Warner & K. M. Hendrix (Eds.). *California Riparian Systems: Ecology, Conservation & Productive Management*. University of California Press, Berkeley, pp. 1–1035.

Hull, F. M. 1962. Robber flies of the world. The genera of the family Asilidae. *Smithsonian Institute, Bulletin* 294(2):433–907. 1536 figs.

Kochner, T. D. 2005. Evolutionary biology: Ghost of speciation past. *Nature* 435:29–30.

Macquart, P. J. M. 1838. Diptères exotiques nouveaux ou peu connus. *Mémoires de la Société royale des Sciences de l'Agriculture et des Artes* 1(2):5–207, 14 pls. (14–172), Lille.

Martin, C. H. 1962. Changes on the status of *Efferia barbata* (Fabr.) & *Efferia albibarbis* (Macq.) (Diptera: Asilidae). *Journal of the Kansas Entomological Society* 35(2):247–253.

Martin, C. H. & J. Wilcox. 1965. Family Asilidae, pp. 360–401. *In*: A. Stone, C. Sabrosky, W. Wirth, R. Foote, J. Coulson & J. (Eds.). *A Catalog of the Diptera of North America*. Agriculture Handbook No. 276, Agricultural Research Service, United States Department of Agriculture, Washington DC, pp. 1–6996.

Martin, C. H. & N. Papavero. 1970. Family Asilidae, *in* N. Papavero (Ed.). *A Catalogue of the Diptera of the Americas South of the United States,* 35b:1–139, Museu de Zoologia, Universidade de São Paulo, São Paulo.

McAlpine, J. F. 1981. Morphology & terminology — adults, pp. 9–63. *In*: J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth & D. M. Wood (Eds.). *Manuel of Nearctic Diptera.* Volume 1. Agriculture Canada. Monograph 27, Ottawa, 674 pp.

Nelson, C. R. 1987. The robber flies of Utah (Diptera: Asilidae). *Great Basin Naturalist* 47(1):38–90.

Nelson, C. R. & R. W. Baumann. 2001. Invertebrates, arthropods (primarily insects) on the Grand Staircase-Escalante National Monument. Asilidae, 15–17, *Bureau of Land Management report, Grand Staircase-Escalante National Monument, Kanab*, 1–97 pp. + 16 figs.

Papavero, N. 2009. Catalogue of neotropical Diptera. Asilidae. *Neotropical Diptera* 17:1–178.

Pearson, D. L. & C. B. Knisley. 1985. Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). *Oikos* 45:161–168.

Pearson, D. L. & A. P. Vogler. 2001. *Tiger Beetles: The Evolution, Ecology & Diversity of the Cicindelids*. Cornell University Press, Ithaca, pp. 1–352.

Perla, B. S. & L. E. Stevens. 2008. Biodiversity and productivity at an undisturbed spring, in comparison with adjacent grazed riparian and upland habitats, pp. 230–243. *In*: L. E. Stevens & V. J. Meretsky (Eds.). *Aridland Springs in North America: Ecology & Conservation*. University of Arizona Press, Tucson, pp. xiv + 1–432.

Scarbrough, A. G. & D. E. Perez-Gilabert. 2008. Review of the West Indian species of *Efferia* Coquillett (Diptera: Asilidae): Part I. Bahamas, Cayman Islands, Cuba & Jamaica. *Insect Mundi* 49:1–29.

Scarbrough, A. G. & D. E. Perez-Gelabert. 2009. Review of the West Indian species of *Efferia* Coquillett (Diptera: Asilidae) with 13 new species & checklist: Part II. Hispaniola, Puerto Rico & Lesser Antilles including Tobago & Trinidad. *Zootaxa* 1994:1–66.

Stevens, L. E. & R. A. Bailowitz. 2005. Distribution of *Brechmorhoga* clubskimmers (Odonata: Libellulidae) in the Grand Canyon region. *Western North American Naturalist* 65:170–174.

Stevens, L. E. & R. A. Bailowitz. 2009. Odonata biogeography in the Grand Canyon ecoregion, southwestern U.S.A. *Annals of the Entomological Society of America* 102(2):261–274.

Stevens, L. E. & R. L. Huber. 2004. Biogeography of tiger beetles (Cicindelidae) in the Grand Canyon Ecoregion, Arizona & Utah. *Cicindela* 35:41–64.

Stevens, L. E. & J. T. Polhemus. 2008. Biogeography of aquatic and semi-aquatic Heteroptera in the Grand Canyon ecoregion, southwestern U.S.A. *Monographs of the Western North American Naturalist* 4:38–76.

Spamer, E. E. & A. E. Bogan. 1993. Mollusca of the Grand Canyon and vicinity, Arizona: New and revised data on diversity and distributions, with notes on Pleistocene-Holocene mollusks of the Grand Canyon region. *Proceedings of the Academy of Natural Sciences of Philadelphia* 244:21–68.

Walker, F. 1855. List of specimens in the dipterous insects in the British Museum, London, Suppl. 3, Part 7, pp. 507–775, 5 pls.

Wilcox, J. 1966. *Efferia* Coquillett in America North of Mexico (Diptera: Asilidae). *Proceedings of the California Academy of Sciences* 34(2):85–254.

Williston, S. W. 1885. On the North American Diptera (Part II). *Transactions of the American Entomological Society* 12(2):53–76.

Received 10 Feb 2012; Accepted 4 Apr 2012 by M. Hauser; Publication date 27 July 2012.