The Drosophila (Sophophora) obscura species group in the Americas (Diptera: Drosophilidae): review, revisions, and three new species

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The *Drosophila* (*Sophophora*) *obscura* species group in the Americas (Diptera: Drosophilidae): review, revisions, and three new species

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ABSTRACT

Flies in the *Drosophila* (*Sophophora*) *obscura* species group are among the most common native drosophilids in northern temperate and boreal forests; southward, into cool, montane tropical forests they are rare and localized, but diverse. Of the world's 48 species, 18 occur in the New World, including three new neotropical species described here. Here, all New World species are diagnosed, many with images and the use of some new morphological features such as female terminalia (oviscapt and spermathecal structure). A basic phylogenetic scheme of relationships based on 19 morphological characters corresponds well with molecular trees.

Type series have been rediscovered of *D. algonquin*, *athabasca*, *azteca*, *narragansett*, and *seminole* (all described by Sturtevant and Dobzhansky in 1936), from which a lectotype is designated for each of the first four species and the holotype is recognized for *seminole*. *Drosophila narragansett* from the eastern United States, which has been found only once in 60 years, is redescribed in detail from historical material; *D. seminole* is found to be a synonym of *narragansett*. The three new species are *Drosophila chibcha*, n. sp. (from Costa Rica to Venezuela and Peru), *D. olmeca*, n. sp. (from southern Mexico), both of these in the *affinis* subgroup; and *D. zapoteca*, n. sp. (from Guatemala), in the *pseudoobscura* subgroup. Significant new distributional and host records are reported for various species.

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INTRODUCTION

Among the most common wild species of Drosophilidae in temperate and boreal forests throughout the Holarctic Region are small, dark species belonging to the *Drosophila obscura* species group (figs. 1–5). It is one of nine such groups in the large subgenus *Sophophora*. Species in the *obscura* group also occur in the tropics of the New World, Africa, and Asia, but here they are generally rare and relegated to cool montane forests.

The study of certain New World species in this group was formative to the New Synthesis in evolutionary biology, particularly the role played by a series of 43 papers by Theodosius Dobzhansky and his students and colleagues, *The Genetics of Natural Populations* (Dobzhansky and Powell, 1975; Lewontin et al., 2003). The western North American species *Drosophila pseudoobscura* was an early subject (Frolova and Astaurow, 1929; Lancefield, 1929) and the primary focus of Dobzhansky and his students (Dobzhansky and Epling, 1944; Dobzhansky and Powell, 1975). The subtle morphological differences among species in the *obscura* group, even for the male genitalia, required in some cases the use of crossing experiments and chromosomes to identify them, which, given their abundance in nature, promoted their use in population biology. As a result, the *obscura* group contributed to extensive understanding of hybridization, behavioral and genetic isolating mechanisms, chromosomal inversion polymorphisms, dispersal, sex-ratio meiotic drive, genetic variation in natural populations, and other important aspects of evolutionary processes. Moreover, relationships among species are very well known (discussed below, Relationships and Groupings), providing a critical foundation for every aspect of comparative biology in the group.

Two particularly interesting topics of *obscura*-group biology warrant brief mention, the first being far-northern distributions and cold tolerances. Species diversity in the family Drosophilidae is predominantly tropical, so it is remarkable that some *obscura*-group species are among the most cold-tolerant drosophilids. In Scandinavia, which has been extremely well surveyed (Baechli et al., 2004), five *obscura*-group species extend into northernmost districts of Finland, Norway, and Sweden, at and above 68°N. These include *D. alpina* Burla and *D. subsilvestris* Hardy and Kaneshiro (which diapause as a pupa), *D. bifasciata* Pomini and *obscura* Fallén (which diapause as adults), and *D. eskoi* Lakovaara and Lankinen (diapause stage unknown) (Goto et al., 1999). Not too surprisingly, species that extend the farthest north are strikingly more effective at withstanding cold temperatures that easily kill other species (Gilbert and Huey, 2001). Northern limits of the North American species are poorly surveyed by comparison, with only *D. athabasca* Sturtevant and Dobzhansky known from 69°N in Northwest Territories, Canada (fig. 1), details of which are given under that species below. Flies in the o*bscura* group, which are generally easy to culture, would seem to be ideal subjects for studying responses to climate change.

Another salient aspect of their biology concerns sex-ratio meiotic drive, which is reviewed in Werner and Jaenike (2017) and Werner et al. (2020a, 2020b). In meiotic drive, meiosis is "subverted," so that some alleles are inherited in greater proportions than 50%. In sex ratio (SR), male fruit flies have X-linked alleles that causes them to sire all females. In the absence of counter-balancing selection, SR can become fixed and lead to local or entire species extinc-

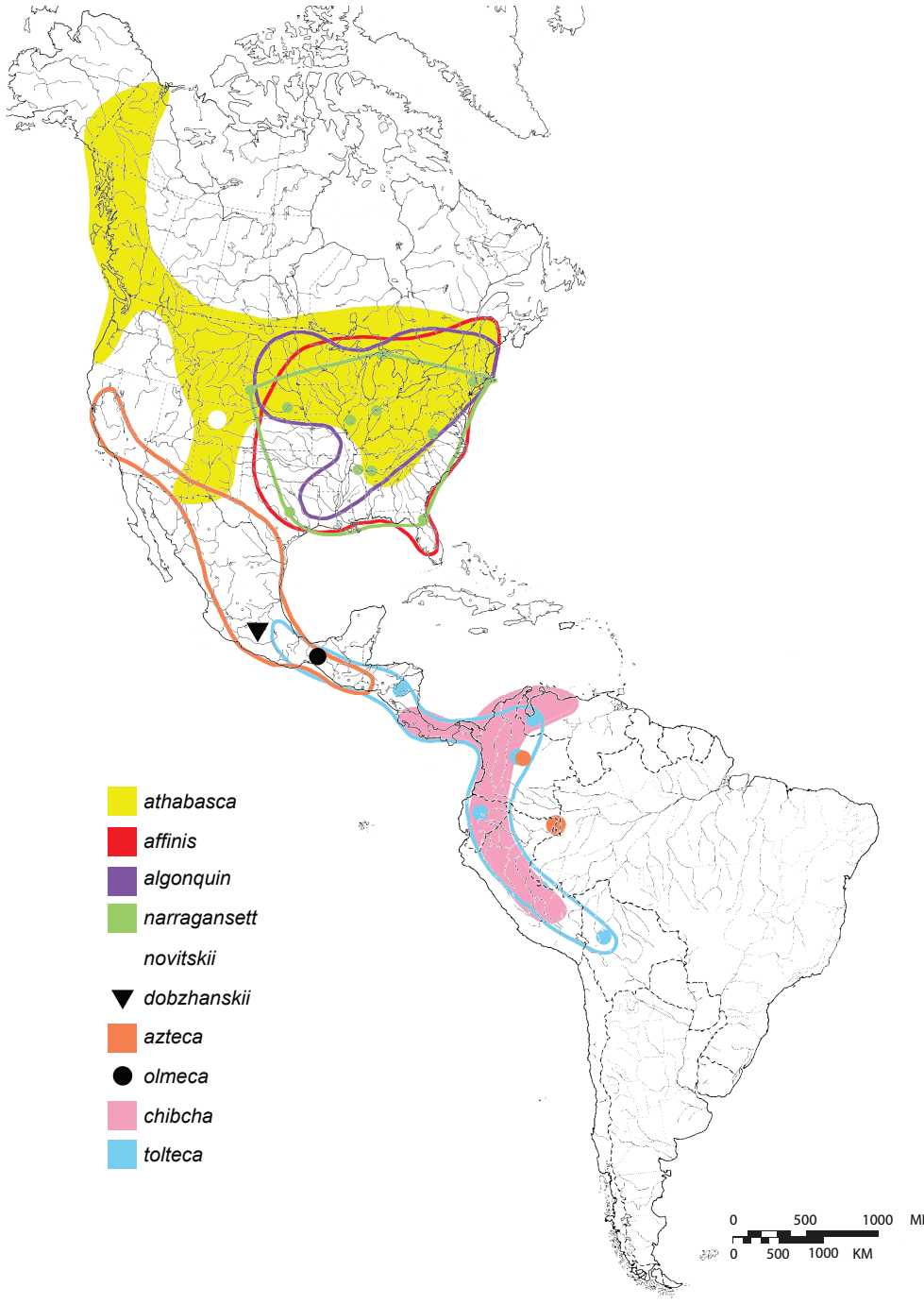

FIG. 1. Distribution map of species in the *affinis* subgroup. Distributions derived from Miller (1958), M. Miller et al. (2017), new records provided in the present paper, and more recent published reports. For distributions of species in the *pseudoobscura* group, see Dobzhansky and Epling (1944) and Heed and O'Grady (2000). Distribution boundaries are approximate, especially northernmost boundaries.

TABLE 1. World species of the *Drosophila* (*Sophophora*) *obscura* species group.

Subgroup and Species	Distribution
***affinis* subgroup**	
affinis Sturtevant, 1916	E North America
algonquin Sturtevant and Dobzhansky, 1936	NE North America
athabasca Sturtevant and Dobzhansky, 1936	N North America
azteca Sturtevant and Dobzhansky, 1936	SW U.S. to Colombia
chibcha, n. sp.	Costa Rica to Venezuela, Peru
dobzhanskii Patterson, 1943	Central Mexico
helvetica Burla, 1948	N Europe
narragansett Sturtevant and Dobzhansky, 1936	E United States
novitskii Sulerud and Miller, 1966	Colorado, United States
olmeca, n. sp.	Chiapas, Mexico
tolteca Patterson and Mainland, 1944	S Mexico to possibly Bolivia
***microlabis* subgroup**	
kitumensis Tsacas 1985	Kenya
microlabis Seguy, 1938	Kenya
***obscura* subgroup**	
ambigua Pomini, 1940	Palearctic
bifasciata Pomini, 1940	N Palearctic, Taiwan, Japan
cariouae Tsacas 1985	Kenya
dianensis Gao & Watabe 2003	Yunnan, China
eniwae Takada, Beppu, Toda, 1979	Hokkaido, Japan
epiobscura Parshad and Duggal, 1967	N India
eskoi Lakovaara and Lankinen, 1974	Scandinavia
frolovae Wheeler, 1949	Central Mexico
glabra Chen & Gao, 2015	Guangxi, China
hideakii Gao & Toda, 2009	Borneo
hypercephala Gao & Toda, 2009	Borneo
imaii Moriwaki and Okada, 1967	Japan
krimbasi Tsacas, 1985	Kenya
limingi Gao & Watabe, 2003	Yunnan, China
obscura Fallén, 1823	Europe
quadrangula Gao and Toda, 2009	Borneo
solstitialis Chen, 1994	China
subobscura Collin,1936	W Palearctic
subsilvestris Hardy & Kaneshiro, 1968	Europe
tristis Fallén, 1823	Europe
tsukubaensis Takamori and Okada, 1983	Honshu, Japan

TABLE 1 *continued*

Subgroup and Species	Distribution
***pseudoobscura* subgroup**	
cuauhtemoci Felix and Dobzhansky, 1976	Central Mexico
lowei Heed, Crumpacker, Ehrman, 1968	SW United States
maya Heed and O'Grady, 2000	Central America
miranda Dobzhansky, 1935	Pacific NW N. America
persimilis Dobzhansky and Epling, 1944	W North America
pseudoobscura Frolova, 1929	W North America
zapoteca, n. sp.	Guatemala
***sinobscura* subgroup**	
hubeiensis Sperlich and Watabe, 1997	Hubei, China
luguensis Gao and Toda, 2003	Yunnan, China
sinobscura Watabe, 1996	Taiwan
***subobscura* subgroup**	
guanche Monclús, 1976	Canary Islands
madeirensis Monclús, 1984	Madeira Is.
unplaced species	
alpina Burla, 1948	N Palearctic to Japan
inexspectata Tsacas, 1988	Japan

tion (Jaenike, 1996). SR was first discovered in two species of the *obscura* group: *Drosophila affinis* and *D. athabasca* (Gershenson, 1928; Sturtevant and Dobzhansky, 1936b). Although SR has not been found in *D. algonquin*, it does occur in other *Drosophila* species groups, in the following species: *D. neotestacea* Grimaldi, James, and Jaenike, *D. quinaria* Loew, and *D. recens* Wheeler (James and Jaenike, 1990; Jaenike, 1996). It is likely that SR occurs in more species of the *obscura* group. Given that the frequency of SR among males can vary from 3%–30%, depending on the species (James and Jaenike, 1990; Jaenike, 1996), its impact on natural populations may help explain the decline and extreme rarity of certain species, like *Drosophila narragansett*, discussed below.

Of the 48 species in the *obscura* group all but two are classified into six subgroups, the two other species being unclassified (table 1). Most species (30) are from the Old World. With the exception of a few species that have been introduced to nonnative areas (e.g., *D. subobscur*a, *D. pseudoobscura*), the New and Old World faunas have no species in common, not even Beringial ones, a fact that Wheeler (1981) also observed. This is unusual because the group is largely Holarctic, and the boreal species have very broad distributions.

This study started modestly, like many projects do, in this case as a search for the type specimens of five North American species of the *obscura* group. The authors of *Drosophila* (*Sophophora*) *algonquin*, *athabasca*, *azteca*, *narragansett*, and *seminole* reported that the types were deposited in the American Museum of Natural History (Sturtevant and Dobzhansky, 1936: 577–578), but there has never been a record of them at the AMNH, either in the collec-

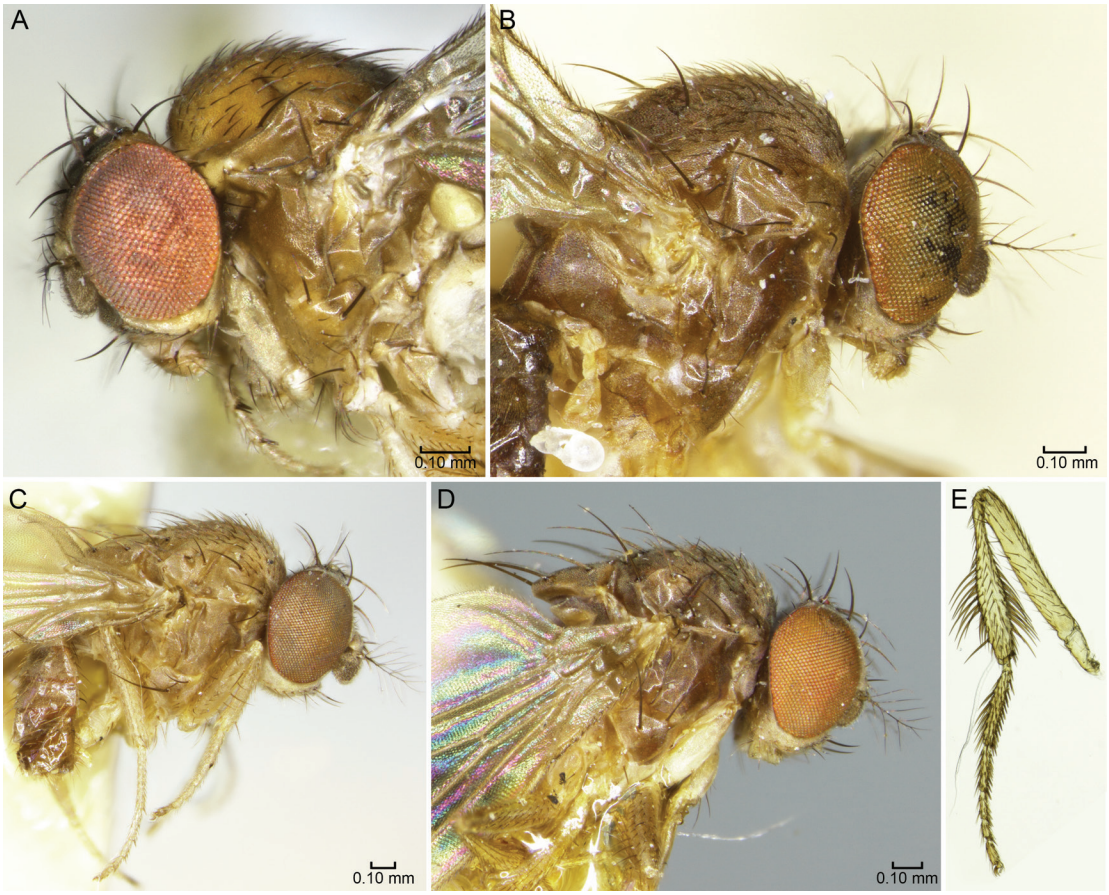

FIG. 2. Heads and thoraces (lateral view) of representative New World species of the *obscura* group (A–D), and a male midleg of *D. cuauhtemoci* (E). **A.** *D. chibcha* holotype, n. sp. (ASG 05); **B.** *D. maya* holotype. **C.** *D. narragansett* paralectotype male. **D.** *D. seminole* holotype. **E.** *D. cuauhtemoci*, male midleg (lateral view), paratype.

tion or recorded in accession records or correspondence archives. For decades, the types were assumed to be either in the AMNH (Brake and Baechli, 2008) or lost. The first two of these species are common and widespread; the latter two rare and poorly known, which is why the study of their types is so significant.

Knowing that Sturtevant's drosophilid collection was transferred from the California Institute of Technology to the USNM in 1970 and that these specimens were not in the USNM type collection, I searched the general USNM Diptera collection in June 2022. The type series were indeed there, unmarked as such by Sturtevant. Sometime in the 1970s USDA-SEL dipterist George C. Steyskal (at the USNM from 1962–1979) applied torn strips of paper penciled with "type" onto the pins of three specimens.

Here the lectotypes are formally reported, now properly labeled and separated, for four of the species and the holotype for *D. seminole*. I am also taking this opportunity to provide new diagnostic and other morphological information on the group; describe three distinctive, new

Neotropical species; synonymize a North American species, as well as add significant new distribution and ecological records. The primary types of Sturtevant and Dobzhansky (1936) remain at the USNM with their paralectotype series.

METHODS AND MATERIALS

The study relied entirely on point- and slide-mounted specimens from five collections whose acronyms below are used in the species accounts:

AMNH, American Museum of Natural History, New York, New York
CUIC, Cornell University Insect Collection, Ithaca, New York
MNCR, Museo Nacional de Costa Rica (former INBio collection), San José, Costa Rica
UCDBM, University of California, Davis, Bohart Museum of Entomology
USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC

Representative specimens were selected for dissection and each was given a unique, sequential number (ASG01, 02...). For males, a foreleg was removed and cleared in hot lactic acid, rinsed in water, dehydrated in 70% ethanol, and mounted in glycerin jelly for standardized orientation of the sex comb(s). For males and females terminalia were studied by snipping off the posterior half of the abdomen, clearing in 10% KOH, and then preparing as for the legs. Before the warm glycerin jelly solidified, the hypandrium + aedeagus and associated appendages were disarticulated from the epandrium using fine tungsten needles. Slide-mounted structures were illustrated with use of a drawing tube on a Wild compound microscope at 200–400×, and further studied with a Nikon Eclipse at the same magnifications also using phase contrast and DIC lighting. All dissections, preserved in minute blocks of glycerin jelly, are stored in small genitalia vials on the same pin as the rest of the specimen. For future observations the glycerin jelly can be easily dissolved from around the dissection using KOH. Male and female terminalic structures are illustrated since some important diagnostic features are too faint, minute, or obscure to resolve well with photomicrography. Standard measurements follow the protocols given in Baechli et al. (2004), made using a Nikon SMZ1500 stereoscope with Nikon Elements© software, which was also used for photomicrography. The photos serve mainly to show coloration and pollinosity of the heads and thoraces (figs. 2–5). Label data are cited verbatim, with emendations in [brackets]; a slash between spaces (" / ") indicates the beginning of a separate label.

In the male genitalia, postgonites pivot outward (laterally) when extruded, which causes the aedeagus to project farther beyond the edge of the hypandrium. To facilitate and accurately compare genitalia, specimens were selected (where possible) that had the periphallic appendages folded against the aedeagus.

Lakovaara and Saura (1982) mentioned that the "only efficient" method for collecting *obscura*-group flies is with fermenting baits. Such bait traps *are* efficient for Holarctic species, attract many flies, and are important for making live cultures, but it also needs noting that

FIG. 3. Frontal view of heads of representative species in the *D. pseudoobscura* subgroup. **A.** *D. lowei*, male paratype (A19.2); **B.** *D. maya*, male holotype (44.12A). **C.** *D. pseudoobscura*, male. **D.** *cuauhtemoci*, male paratype (face and antennae only) (ASG 39).

almost all the new records and species reported here from the neotropics are of specimens captured in passive Malaise and flight-intercept traps (e.g., Borkent et al., 2018). Bait traps seem much less effective for *obscura*-group flies in tropical montane forests.

Past *Drosophila* Geneticists: The renowned early geneticist Alfred H. Sturtevant adhered well to taxonomic practices earlier in his career, as did another brilliant geneticist, Harrison D. Stalker, who maintained a small reference and voucher collection that is thankfully preserved in the USNM. Other geneticists and evolutionary biologists of the 1930s–1970s, however, such as Dobzhansky, were remiss in their taxonomic practices. Despite his careful research, D.D. Miller left virtually no voucher specimens, even of the rare species *D. narra-*

FIG. 4. Frontal view of heads of representative species of the *affinis* subgroup. **A.** *D. affinis*, male. **B.** *D. chibcha*, n. sp., male holotype (ASG 05); **C.** *D. tolteca*, male (ASG 23); **D.** *zapoteca*, n. sp., male holotype (ASG 20). Note differences in development of the facial carina compared with faces in figure 3.

gansett and the types of *novitskii*, which he described. This is hardly unique. Few or no specimens of North American species were archived by W.P. Spencer (who described many species), nor by G.B. Mainland (who surveyed Mexico for *Drosophila*) and others. In fact, for this study, I was unable to locate types of four species: *Drosophila* (*Sophophora*) *novitskii* Sulerud and Miller, *D.* (*S.*) *persimilis* Dobzhansky and Epling, *D.* (*S.*) *pseudoobscura* Frolova, and *D.* (*S.*) *tolteca* Patterson and Mainland.

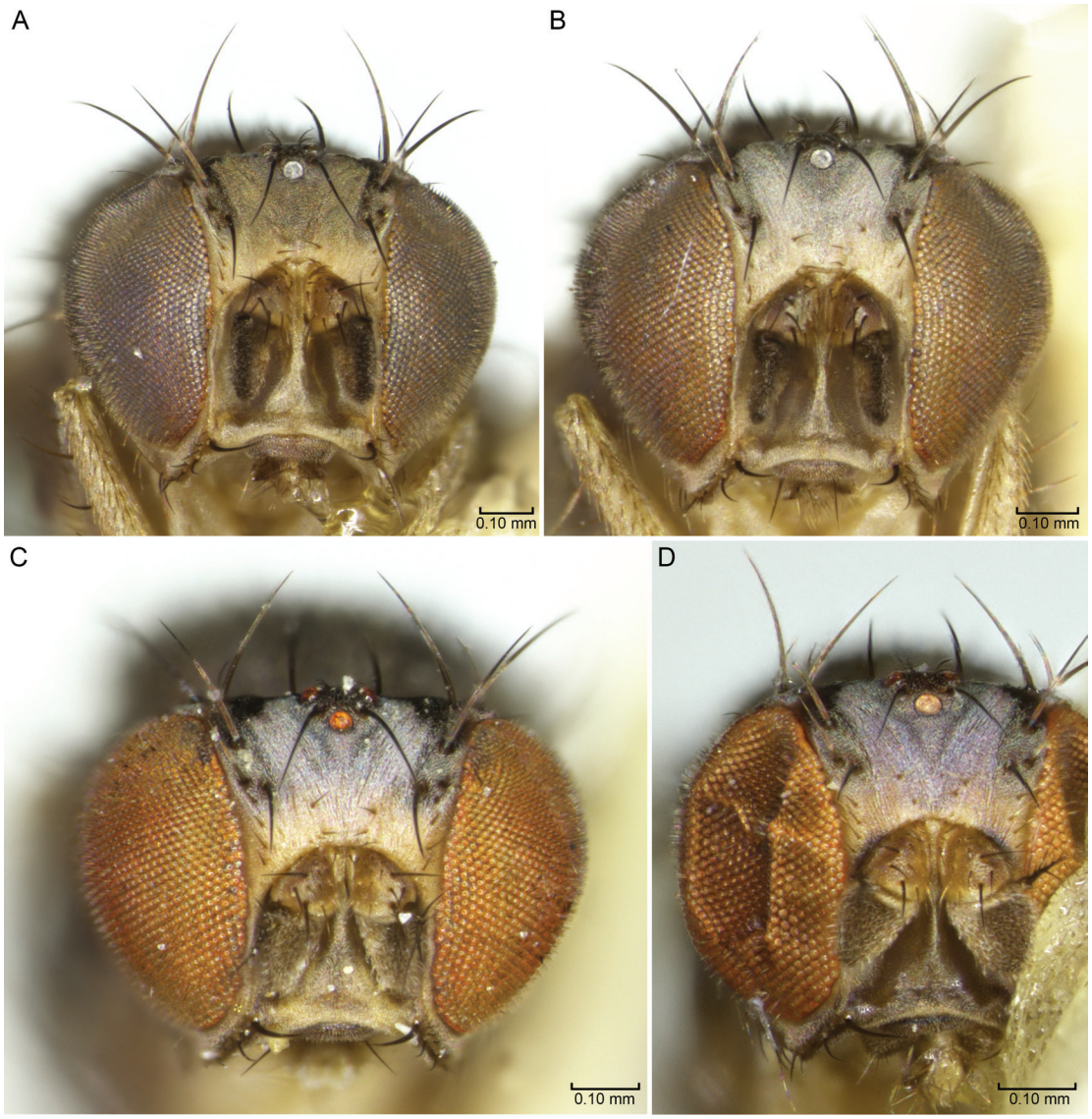

FIG. 5. Frontal view of heads of *Drosophila narragansett* (including *seminole*, new synonym) and the related species *D. olmeca*, n. sp. **A.** *D. narragansett*, female paralectotype (ASG 11); **B.** *D. narragansett*, male paralectotype (ASG 10); **C.** *D. seminole*, male holotype; **D.** *D. olmeca*, n. sp., male holotype (ASG 25).

Distributions are summarized based on data from D.D. Miller (1958), Werner and Jaenike (2017), Werner et al. (2020a, 2020b), M. Miller et al. (2017), other references as specified, and from label data of specimens in the collections cited above and as noted. An identification key to species in the *pseudoobscura* subgroup is provided by Heed and O'Grady (2000), and to the *affinis* subgroup by Sulerud and Miller (1966), both updated with the diagnoses of new and known species and the synonymy reported here.

SYSTEMATICS

The *Drosophila (Sophophora) obscura* Species Group

Diagnosis: Dark, blackish-brown flies (occasionally light brown) (figs. 1–5), head and thorax integument generally dull and slightly pollinose, male abdomen always entirely dark, female abdomen entirely dark or in some species with dark abdominal bands; male testes bright yellow to orange or red (visible even through pleural membrane of abdomen); arista with 3–4 dorsal, 2 ventral branches (all usually short); genal seta-1 not enlarged, much smaller than vibrissa; eye with dense ommatrichia; male foretarsus with comb ("sex comb") of thick, sclerotized setae ("teeth") on ta_1 and ta_2 (the latter lost in several species or reduced to 1 tooth in the *affinis* subgroup); male with ventral epandrial lobe bilobate, inner lobe closely adpressed laterally to surstylus; pair of sclerites (remnants of tergite 7) fused to tergite 6, articulate with inner margins of epandrium. Male genitalia rather uniform: aedeagus membranous, flanked by pair of sclerotized valves; postgonites slender, elongate, each with lateral row of minute sensilla trichodea; posterolateral corners of hypandrium articulating with pair of pointed lobes. Sperm occur in short and long forms, the latter involved in fertilization (Snook and Karr, 1998).

Relationships and Groupings

Relationships among species of the *obscura* group have been well explored. Studies have used hybridization (e.g., Dobzhansky and Epling, 1944), polytene chromosome inversions (e.g., Dobzhansky and Epling, 1944; D.D. Miller, 1977), enzyme electrophoresis (e.g., Lakovaara and Saura, 1982), mtDNA restriction sites (Barrio et al., 1992), and DNA sequencing (e.g., Barrio and Ayala, 1997; Gleason et al., 1997; Goto et al., 1999; O'Grady, 1999; Barmina and Kopp, 2007; Gao et al., 2007; Finet et al., 2021). Unsurprisingly, with morphological variation among most species so subtle, there have been very few such comparative studies of the *obscura* group. Brown (1965) provided a quantitative study of 24 morphological features in the group, but the characters used and the phenetic analysis produced a phylogeny that makes "little sense" (Lakovaara and Saura, 1982). There are, however, informative and even newly discovered morphological characters in the group, presented below, which correspond with the molecular trees (fig. 6).

Remarkably, the results on relationships among disparate cytological, electrophoretic, and molecular studies from the past 60–80 years agree well. Monophyly of the New World species (including the Palearctic species *D. helvetica*) is now accepted, although there is uncertainty about the poorly known species *D. frolovae* (known from one site in Mexico), which has been placed in the *obscura* subgroup based on the sex combs (Wheeler, 1949, 1981, see below).

There has been disagreement as to whether the Old World species are monophyletic (Lakovaara and Saura, 1982; O'Grady, 1999) or paraphyletic with respect to the New World ones (Barmina and Kopp, 2007; Gao et al., 2007; Finet et al., 2021). A sex comb with numerous teeth on male protarsomere-2 (at least 5 teeth and generally more than 10) in the Old World species is

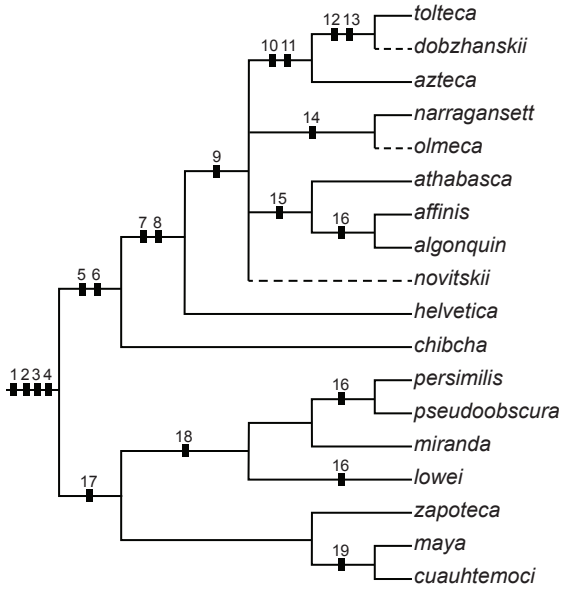

FIG. 6. Cladogram of 19 morphological characters for the New World species of the *Drosophila obscura* group. Numbers on the nodes correspond to synapomorphies in table 2. Nodes without any morphological characters are based on molecular trees (see text).

convergent with the double sex comb on protarsomeres-1 and -2 in the *montium* subgroup of the *melanogaster* group. Most Old World species (and some New World ones) have a broad facial carina (fig. 3); in many of the New World species (i.e., *affinis* subgroup) the carina is short, low, and very thin (figs. 4, 5).

Among the New World species the *pseudoobscura* subgroup forms a clade defined by having micropapillae on the valves of the aedeagus. Species in this subgroup also tend to have a broader (even flat) facial carina and more teeth on both ta_1 and ta_2 of the male protarsal sex comb. Within the subgroup is a smaller clade consisting of *lowei* + (*miranda* + (*persimilis* + *pseudoobscura*)), which is highly supported genetically (Lakovaara and Saura, 1982; O'Grady, 1999; Finet et al., 2021), and morphologically by eight rows of acrostichals (a character formerly used to define the entire *pseudoobscura* subgroup).

The *affinis* subgroup is defined morphologically by two distinctive features: a reduced number of teeth (0–2, most commonly 1) on protarsomere 2 (ta_2), and (occurring in all species except *D. chibcha*, n. sp.) by the inner lobe of the ventral epandrial lobe having furrows at the base (figs. 11A, B; 12A–D). The widespread Palearctic species *D. helvetica* possesses both these features and clearly belongs to the *affinis* subgroup, as has been recognized for some time (Lakovaara and Saura, 1982; Baechli et al., 2004). Within this subgroup, *D. affinis* + *athabasca* + *algonquin* form one clade, another clade consists of (*tolteca* + *azteca*) [and possibly *dobzhanskii*] + (*narragansett* + *olmeca*). The sister species *tolteca* + *azteca* have a patch of dense microtrichia amongst the epandrial lobe furrows (Miller and Sanger, 1969; fig. 11C, 12E), although the ta_1 sex combs are rather divergent (fig. 9). The males of *D. narragansett* + *olmeca* have silvery shagreenation on the frons (fig. 5); their sex combs are very similar. Placements of *D. dobzhanskii*, *novitskii*, and *olmeca* are ambiguous (denoted by dashed lines in fig. 6), lacking characters of one sex. *Drosophila frolovae* is not included since it appears to be in the *obscura* subgroup.

Drosophila affinis Subgroup

Diagnosis: Male protarsomere-2 with 0—2 (mostly commonly 1) sclerotized teeth on the sex comb; inner lobe of ventral epandrial lobe with fine, irregular furrows. Acrostichal setulae in 6 rows.

TABLE 2. Morphological synapomorphies of New World *obscura* group species (numbers correspond to those in fig. 6).

1. Male testes bright yellow or orange to commonly red.
2. Ventral epandrial lobe with an inner lobe closely adpressed to surstylus.
3. Males with sex combs on protarsomeres ta_1 and ta_2 (rarely absent on ta_2).
4. Aedeagus with pair of lateral valves.
5. Male protarsomere ta_2 with 2 or fewer teeth.
6. Facial carina narrow, shallow, and short, without flattened edge.
7. Base of inner lobe of ventral epandrial lobe with fine, irregular furrows.
8. Spermatheca with well developed apical indentation extending into end of sleeve.
9. Male protarsomere ta_2 with 0 or 1 tooth (sometimes tooth is very small).
10. Base of inner lobe of ventral epandrial lobe with dense microtrichia.
11. Testes coiled (vs. ellipsoid or folded just once).
12. Male protarsomere ta_1 with numerous (7–18) teeth.
13. Tooth on male ta_2 minute.
14. Male frons with fine, silvery shagreenation.
15. Spermathecal capsule squat, width >1.5× the height.
16. Male protarsomere ta_1 signficantly shorter than ta_2.
17. Aedeagal valves with micropapillae.
18. Acrostichal setulae in 8 rows (vs. 6).
19. Male protarsomere ta_2 with 3 teeth.

Drosophila (*Sophophora*) *affinis* Sturtevant

Figures 4A, 7A, 9A; 11A, B; 14A

Drosophila affinis Sturtevant, 1916: 334.

Diagnosis: A small, very common species in eastern North America, thorax color varying from light brown to black-brown (Werner and Jaenike, 2017: 83); carina very narrow, short; male sex comb with ta_1 usually with 4–5 teeth (ranging from 4–7 [Sulerud and Miller, 1966), ta_2 with 1 slender tooth; ta_1 distinctly shorter (0.88×) than ta_2; base of inner ventral epandrial lobe with furrows, no microtrichia.

Type: Holotype: ♂ + puparium: bred banana [written] / Kushla, Ala[bama] IV.25.15 AH Sturtevant / TYPE Drosophila affinis Sturt. [red label] / Amer. Mus. Nat. Hist. Dept. Invertebrates No. 24134. In AMNH. The adult and its puparium are mounted on separate points on the same pin.

Specimens Examined: Besides type (above), the following material (all in AMNH): UNITED STATES: ALABAMA: Kushla, Ala. VI.13.14, A.H. Sturtevant / Paratype (1). GEORGIA: large series, Georgia, Liberty Co., St. Catherine's Is., 11-20/IV/88, Grimaldi (two dissected: ASG28♀, ASG29 ♂). MAINE: Mount Desert Isle, ME 29 June-3 July 1982, J. Jaenike (7). MASSACHUSETTS: 5 mi W Ipswich, Mass / July 1948 M.R. Wheeler (8). NEW JERSEY: Morris Co., Pompton Plains, vi.10.2012, D. Grimaldi, on *Lysurus borealis* fungus (rotten fish smell) (17); N Brnswck [New Brunswick] NJ / Metatype VI/20 [Sturtevant coll.] (9). NEW YORK: New York [City], X.12.14, A.H. Sturtevant / Metatype (1); Chenango Valley St. Park, IV/15-V/6, 1982, D.A. Grimaldi (6); Trumansburg, VI/16-22/83, D. Grimaldi, coll. (22). NORTH CAROLINA: Alum Cave Bluffs, Great Smoky Mountains, VII/18-22/82; Clingman's Dome, Great Smoky Mountains, VII/18-22/82, J. Jaenike (11); Raleigh, VIII/3/82, J. Jaenike (3). TEXAS: Houston, Harris Co., White Oak Bayou, VI/20/83, J. Jaenike (7). VERMONT: Mad Brook Farm, E. Charleston, Orlean Co., VT VII/15-25/82, D. Grimaldi (4).

Distribution: The eastern half of North America, including prairie states; from Texas, Florida, and the Gulf coast in the south, to Maine, southern Ontario and Québec in the north, west to Minnesota (Miller, 1958; M. Miller et al., 2017).

Comments: The main breeding sites of this very abundant species have not been determined. These flies are attracted to a variety of substrates and will breed in low levels in such varied host plants as decaying spadices of skunk cabbage (*Symplocarpus foetidus*: Araceae) (Grimaldi and Jaenike, 1983), and fruits of mayapple and huckleberry (respectively, *Podophyllum peltatus*: Berberidaceae; and *Gaylussacia* spp., *Vaccinium* spp.: Ericaceae) (Carson and Stalker, 1951). I have also found them attracted to *Lysurus borealis* fungus (Phallaceae), which has the smell of rotten fish (full record given above), but it wasn't determined whether they were breeding in the fungus. The species has not been found to breed in mushrooms, despite all the efforts in breeding flies from various macrofungi (e.g., Werner and Jaenike, 2017).

An interesting aspect of the natural history of *D. affinis* is their attraction in significant numbers to the flowers of pawpaw (*Asimina triloba*: Annonaceae) (Martin, 2021; Goodrich et al., 2023). Various drosophilids are the most abundant visitors to the flowers, and *D. affinis* is the most abundant fruit fly visitor. The tree has a distribution throughout eastern North America similar to that of *D. affinis*. The flowering of pawpaw occurs in the early spring, the flowers smelling yeasty and fermenting; it is unknown whether *D. affinis* is a significant pollinator of this plant, whether they breed in its flowers and fruits, or possibly even both.

Drosophila (*Sophophora*) *algonquin* Sturtevant and Dobzhansky

Figures 9B, 14C

Drosophila (*Sophophora*) *algonquin* Sturtevant and Dobzhansky, 1936: 575.

Diagnosis: Color of thorax varying from light brown to dark black-brown (Werner and Jaenike, 2017: 79). Like *affinis*, ♂ ta_1 shorter (0.82×) than ta_2; males easily distinguished from *affinis* and *athabasca* by the larger sex comb on ta_1, with generally 7–9 long teeth (ranging 5–10; Sulerud and Miller, 1966); ta_2 with 1 tooth; base of inner ventral epandrial lobe with furrows, no microtrichia.

Type: Lectotype, ♂, selected by myself from a series of 8 ♀, 14 ♂, all labeled as "Woods Hole Mass. [printed]/Stock 25 [written]/A.H. Sturtevant Collection 1970 [printed]." Lectotype labeled by D.G. 12 June 2023. In the USNM. Steyskal did not add a penciled note to any specimen as the type.

Specimens Examined: Besides the type series (above), the following: MASSACHUSETTS: 5 mi. W Ipswich Mass / July 1948, MR Wheeler (5). NEBRASKA: 1 mi. W Haigler, VIII/24/50, 2070.11 [culture no.], M.R. Wheeler (2). NEW YORK: Chenango Valley St. Pk. [State Park], N.Y., IV/15-V/6 1982, D.A. Grimaldi / 1 ♂, ASG 32 (AMNH); Trumansburg, NY VI/16-22/1983, D. Grimaldi, coll. (4). VERMONT: Mad Brook Farm, E. Charleston, Orlean Co., VT VII/15-25/82, D. Grimaldi (3).

Distribution: Eastern North America, except for some southeastern U.S. states (Alabama, Georgia, Florida, South Carolina).

Drosophila (*Sophophora*) *athabasca* Sturtevant and Dobzhansky

Figures 7B, 9C, 14B

Drosophila (*Sophophora*) *athabasca* Sturtevant and Dobzhansky, 1936: 576; *D. athabasca mahican* Sturtevant and Dobzhansky, 1936.

Diagnosis: Like *affinis* and *algonquin*, thorax color varying from light brown to deep black-brown. Carina very narrow, short; male sex comb on ta_1 typically with 4 teeth (ranging from 3–5; Sulerud and Miller, 1966), ta_2 with 1 tooth; male ta_1 noticeably longer than (1.23×) ta_2; base of inner ventral epandrial lobe with furrows, no microtrichia; surstylus with row of 8–10 prensisetae; spermatheca very flattened, squat, width 2× the height (vs. 1.7× or less).

Type: Lectotype, ♂, selected from series of 7 specimens all labeled as "Grav [i.e., Gravina Island, Alaska: handwritten] / A.H. Sturtevant Collection 1970 [printed]." The male specimen to which Steyskal attached a penciled note "athabasca type" was labeled 12 June 2023 by me as the lectotype. In the USNM.

Specimens Examined: Besides type series (above), the following specimens: CANADA: Northwest Territories, Aklavik, May 24–July 25, 1931, Bryant [coll.] [68.24438, -134.97486], based on a series of six specimens caught on different days during May and July. UNITED STATES: NEW JERSEY: Bergen Co., Ridgewood, IV/87, Anne Soll / bred: spadices (ASG30 ♀, ASG31♂) (AMNH). NEW YORK: Sullivan Co., Mongaup Lake, 3 mi N Debruce, 1/VI/68, hillside hardwood forest, carrion trap #316, S. Peck (9♂, 23♀).

Distribution: Northern North America, extending further southward in the east along the Appalachians, in central North America along the Rockies, and in the west along the Cascades. A new, very northern record for the species is the record given above from Aklavik, Northwest Territories. The species had previously been recorded from nearby Inuvik, NWT and Tuktoyaktuk, NWT, on the Arctic coast (Toda, 1981; Takada and Toda, 1982). The flies are clearly resident in this tundra, where the only woody plants are shrubby birches (*Betula papyrifera*: Betlulaceae) and some willows (*Salix* spp.: Salicaceae); this is not too surprising given their attraction to such varied substrates as skunk cabbage and even carrion.

Comments: Three "semispecies" have been circumscribed for *D. athabasca*: western-northern (to which the type locality of the species belongs; distributed in the northern portions of eastern North America and northwestern N. America), and "semispecies" eastern A (northeastern North America) and eastern B (some coastal areas within northeastern U.S.). Their existence was originally based on significant differences in male courtship songs (Miller, 1958; Miller et al., 1975; Chang and Miller, 1978), then confirmed with isozymes (Jaenike et al., 1978), mtDNA sequences (Yoon and Aquadro, 1994), and genomes (Wong Miller et al., 2017). The "typical" form of *athabasca* reported by Sturtevant and Dobzhansky (1936)—the nominal subspecies—corresponds to flies from the western-northern "semispecies"; their subspecies *mahican* corresponds to "semispecies" eastern A and/or B. Sturtevant and Dobzhansky (1936) reported that *D. athabasca mahican* Sturtevant and Dobzhansky is somewhat lighter (thorax, legs, frons) than *athabasca athabasca*, but I have not found this to

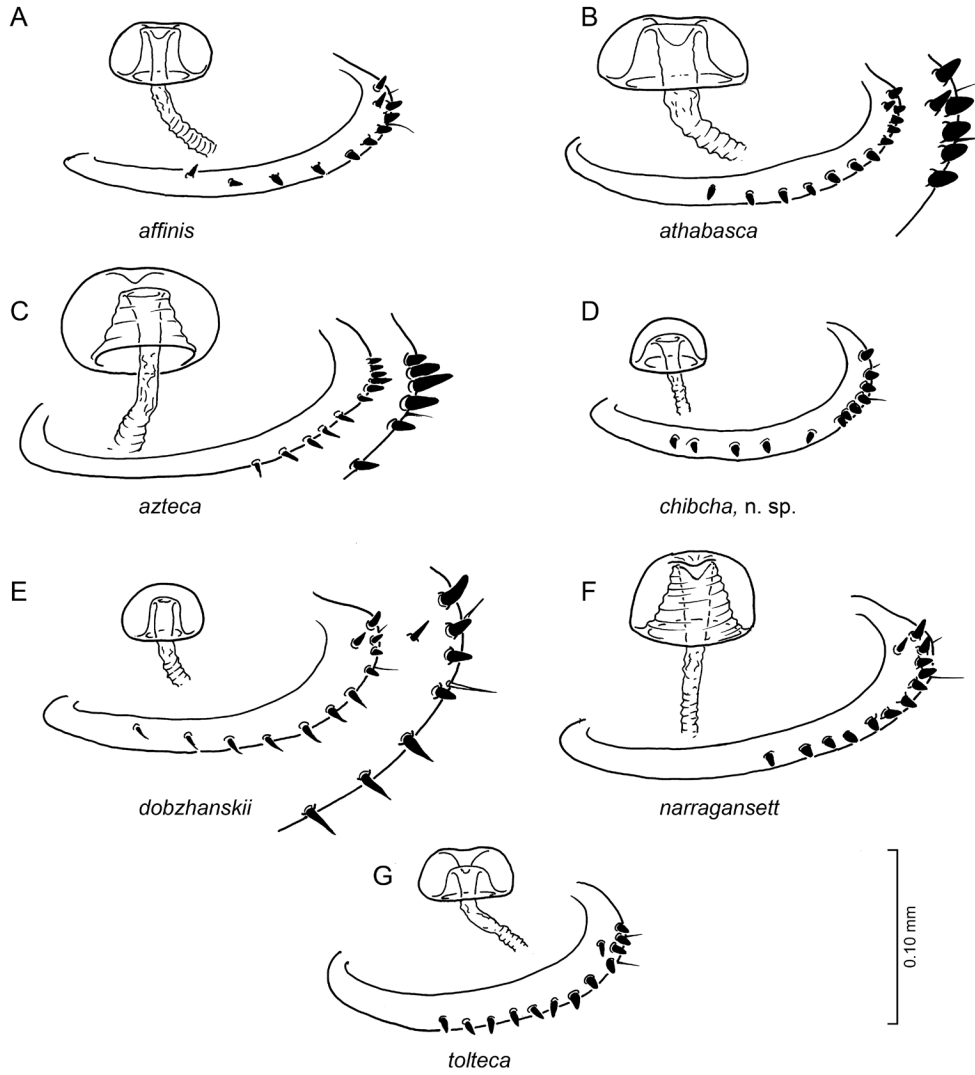

FIG. 7. Oviscapts and spermathecae (lateral views) of species in the *affinis* subgroup, with apical details for three species. **A.** *D. affinis* (ASG 28); **B.** *D. athabasca* (ASG 30); **C.** *D. azteca* (ASG 15); **D.** *D. chibcha*, n. sp. (ASG 17); **E.** *D. dobzhanskii* (ASG 33); **F.** *D. narragansett* (ASG 11); **G.** *D. tolteca* (ASG 24).

be consistent, and think that more northern or higher elevation populations may be darker in general because of cooler temperatures.

Though hybrids among "semispecies" are fully viable and fertile they rarely interbreed even in areas of sympatry, a separation reinforced by female mating preference toward male courtship (Yukilevich et al 2016). Not surprisingly, much of the genomic divergence is on the X chromosome, estimated to have originated only about 20,000 years ago (ca. 4×10^4 generations) (Wong Miller et al., 2017). I was unable to detect morphological differences among semispecies in a blind test using cultures from each of them, which were provided years ago

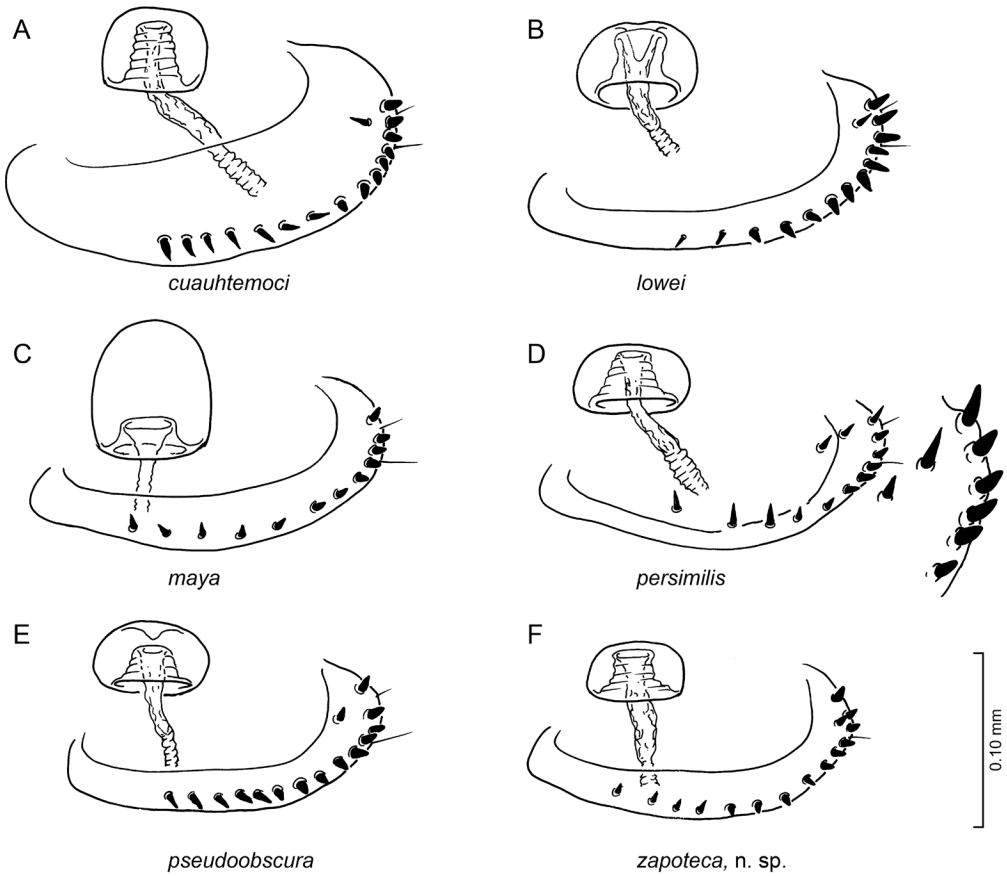

FIG. 8. Oviscapts and spermathecae (lateral views) of species in the *pseudoobscura* subgroup, with a detail for *D. persimilis*. **A.** *D. cuauhtemoci* (ASG 39); **B.** *D. lowei* (ASG 26); **C.** *D. maya* (ASG 19); **D.** *D. persimilis* (ASG 37); **E.** *D. pseudoobscura* (ASG 34); **F.** *D. zapoteca* (ASG 21).

by Carol Yoon (Yoon and Aquadro, 1994). Given that the semispecies, or subspecies, are not morphologically distinguishable they should continue to be classified as one species despite the behavioral and genetic differences. This is a compelling example of incipient speciation.

Drosophila (*Sophophora*) *azteca* Sturtevant and Dobzhansky

Figures 7C, 9D–E, 11C

Drosophila (*Sophophora*) *azteca* Sturtevant and Dobzhansky, 1936: 577.

Diagnosis: Thorax dark black-brown. Male sex comb on ta_1 typically with 4–5 teeth (ranging from 3–7; Sulerud and Miller, 1966), ta_2 with 1 tooth; length of male ta_1 slightly longer (1.14×) than ta_2; base of inner ventral epandrial lobe with furrows and microtrichia (a feature shared with *tolteca*: Miller and Sanger, 1969; fig. 11); surstylus with 5–6 prensisetae.

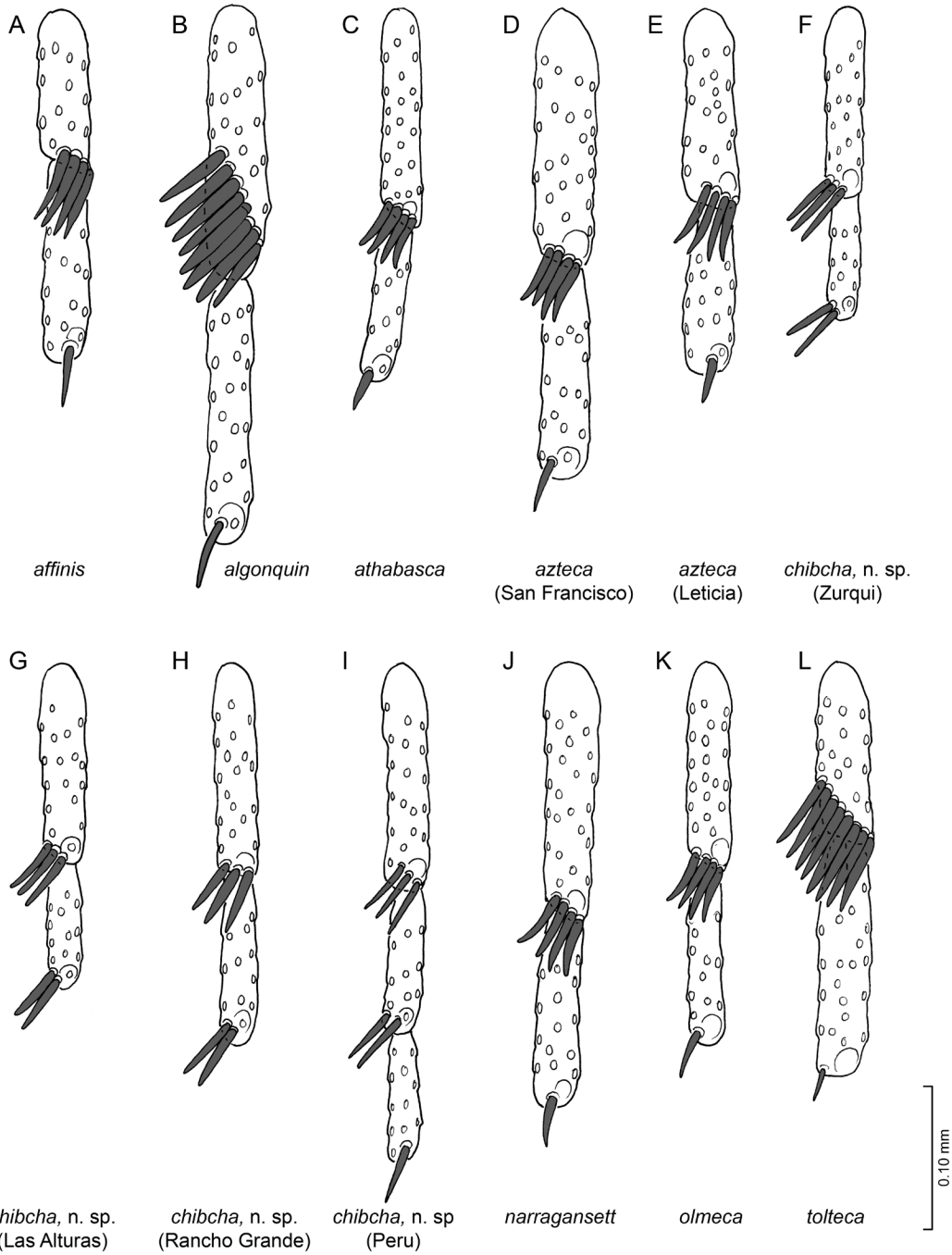

FIG. 9. Protarsal male sex combs (tarsomeres ta_1 and ta_2, and ta_3 for *D. chibcha* from Peru) of species in the *affinis* subgroup. **A**. *D. affinis* (ASG 29); **B.** *D. algonquin* (ASG 32); **C.** *D. athabasca* (ASG 31); **D.** *D. azteca* (ASG 13: San Franciso, CA); **E.** *D. azteca* (ASG 06: Leticia, Colombia); **F.** *D. chibcha*, n. sp. (ASG 04: Zurqui, Costa Rica); **G.** *D. chibcha*, n. sp. (ASG 05: Las Alturas, Costa Rica); **H.** *D. chibcha* (ASG 07: Rancho Grande, Venezuela); **I.** *D. chibcha* (ASG 08: Wayqecha, Peru); **J.** *D. narragansett* (ASG 10); **K.** *D. olmeca* (ASG 25); **L.** *D. tolteca* (ASG 23). All to the same scale.

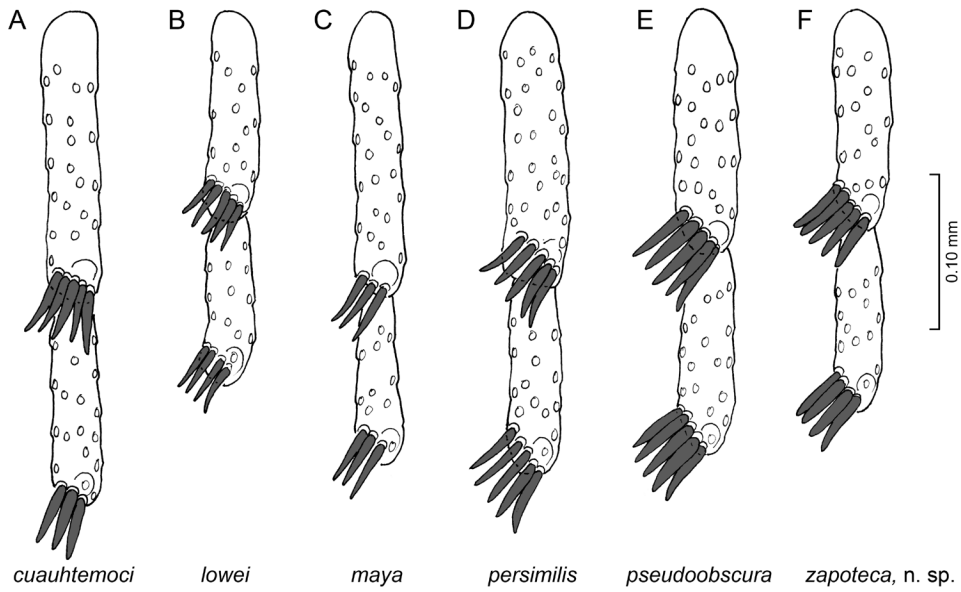

FIG. 10. Protarsal male sex combs of species in the *D. pseudoobscura* subgroup. **A.** *D. cuauhtemoci*; **B.** *D. lowei* (ASG 40); **C.** *D. maya* (ASG 41); **D.** *D. persimilis* (ASG 36); **E.** *D. pseudoobscura* (ASG 35); **F.** *D. zapoteca* (ASG 01). All to the same scale.

Type: Lectotype, ♂, selected from series of 2 ♂ and 6 ♀ specimens all labeled as just "Oax 2 [i.e., Oaxaca, Mexico; handwritten]/A.H. Sturtevant Collection 1970 [printed]." In the original description the type locality is mentioned as being "Oaxaca: Cerro San Jose" (Sturtevant and Dobzhansky, 1936). The male specimen to which Steyskal (in his writing) attached a penciled note "azteca type" was labeled 12 June 2023 by me as the lectotype. In the USNM.

Specimens Examined: Besides the type series (above), the following (all in the AMNH): COLOMBIA: Leticia, Colombia, VI/64, Sarah Pipkin, 1♂ (dissected, ASG06). EL SALVADOR: Volcan Santa Ana, 5670 ft. 26.6 / Rep de El Salvador / Nov 1953 W.B. Heed, 2 ♂ (1 dissected, ASG16). MEXICO: 26 mi. E Zamora, Mich[oacan], Mex / MR Wheeler, FA Cowan, Aug. 1947 / 1795.5 (1♂, dissected, ASG14). UNITED STATES: California: Kern Co., Kern River Canyon 7/49, M.R. Wheeler (1♂); Lobos Creek, San Francisco, Calif. VII/20/62 / WE Kelson Collector / emerged VII/24-26/62, reared from spittlebug (7 specimens, 2 dissected: ASG13 [♂], ASG15 [♀]).

Distribution: Miller (1958) indicated that this species occurs from northern California through Arizona, New Mexico, southern Texas, throughout Mexico to Guatemala. It has also been reported from El Salvador (Heed, 1957) and central Colombia (Cundimarca, above 1600 m) (Villamizar and Alvarez, 2010). To this can be added the most southerly record from South America, from Leticia, Colombia (cited above). This locality is very unusual for *azteca* or any *obscura*-group species in the tropics, since it lies on the upper Amazon River, at the southernmost tip of Colombia adjacent to Peru and Brazil, at an elevation of only about 100 m. The closely related *D. tolteca* supposedly prefers lower elevations in the neotropics, but the Leticia specimen is clearly distinguished from *tolteca* (figs. 9d, E; 11C; cf. figs. 9l, 12E).

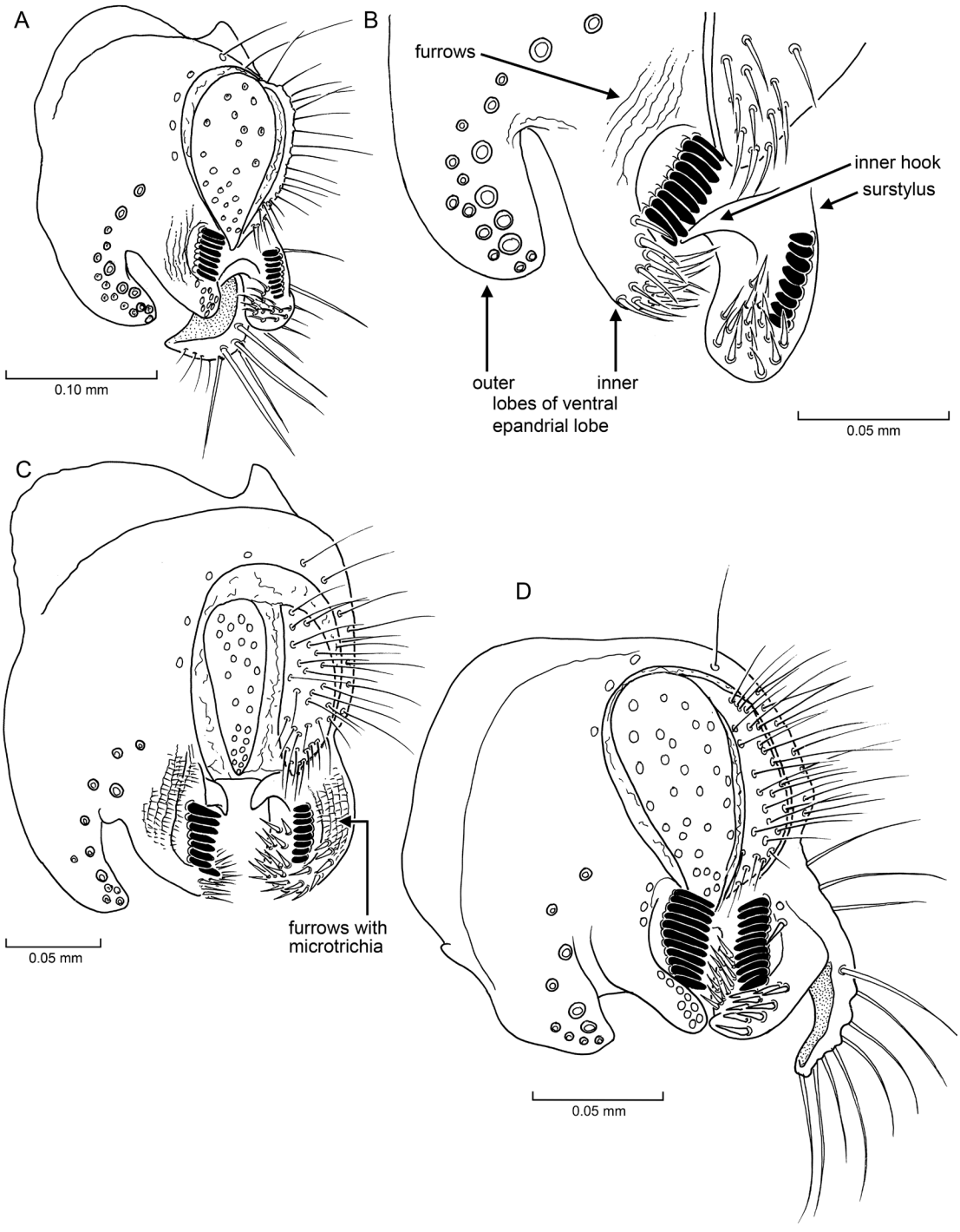

FIG. 11. Epandria (male tergite VIII) and associated structures in representative species of the *affinis* subgroup. **A.** *D. affinis* (ASG 29); **B.** *D. affinis*, detail of A; **C.** *D. azteca* (ASG 13); **D.** *D. chibcha*, n. sp. (ASG 05).

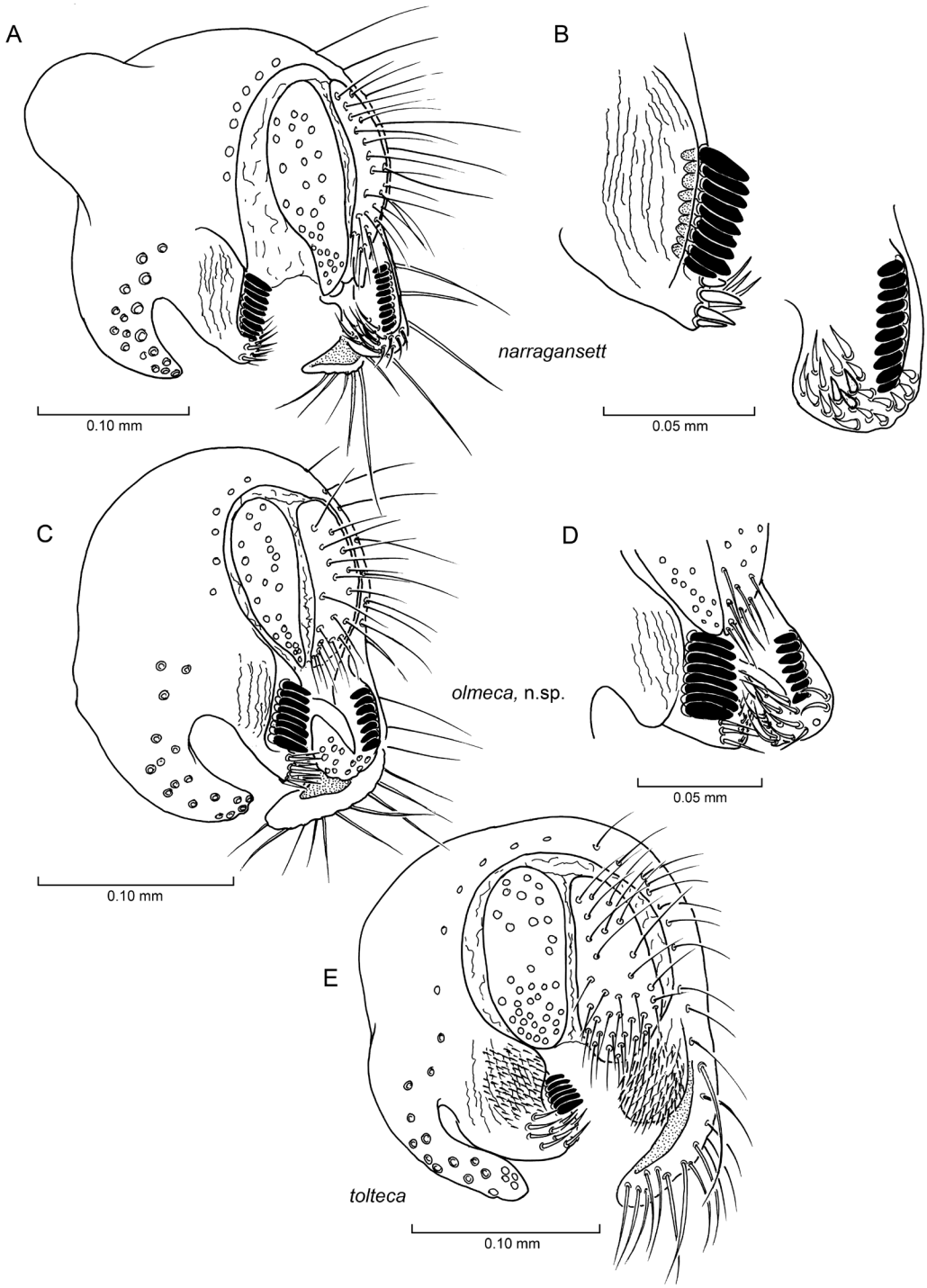

FIG. 12. Epandria and associated structures in representative species of the *affinis* subgroup. **A**. *D. narragansett* (ASG 10); **B.** Details of A; **C.** *D. olmeca*, n. sp. (ASG 25); **D.** Detail of C; **E.** *D. tolteca* (ASG 23).

Comments: The most unusual host record in the *obscura* group are the specimens cited above of *azteca* collected in San Francisco by Kelson in 1962, from spittlebugs. This was based on research of *Aphrophora* spittlebugs (Aphrophoridae: Cercopoidea) by Kelson for his M.Sc. thesis (Kelson, 1964a), then soon published (Kelson, 1964b). The host record was not reported in the journal publication. The spittlebugs were studied on Monterey pine (*Pinus radiata* D. Don) and Knobcone pine (*Pinus attenuata* Lemmon) in the San Francisco area. The immediate assumption would be that the larvae were grazing in the spittle masses, except that Kelson in his thesis specified the puparia were found "in the spittle mass and *on the nymphs* of *A. canadensis*" (Kelson 1964a: 17) (italics mine). Vinton Thompson, who has extensively studied the spittlebugs in this area (e.g., Thompson, 2021) informed me Oct. 24, 2023, that "I have collected lots of *A. canadensis* spittles near Monterey but have seen no larvae or pupae [of Drosophilidae] myself. On the other hand, I was not specifically looking." *Drosophila azteca* almost certainly does not have an obligatory relationship with spittlebugs as does *Cladochaeta* (Grimaldi and Nguyen, 1999), which makes it very unusual that *D. azteca* pupated on the spittlebug nymphs.

Drosophila* (*Sophophora*) *chibcha, new species

Figures 2A, 4B, 7D, 9F–I, 11D, 14D

Diagnosis: Facial carina very thin, small; notum and pleuron light brown; acrostichal setulae in 6 rows; sex comb with 3 slender teeth on ta_1, 2 on ta_2 (specimen from Peru with 1 tooth also on the left ta_3), teeth protrude away from tarsal segments. Inner lobe of ventral epandrial lobe lacking furrows at base; surstylus with row of 9–10 prensisetae; valves of aedeagus unique among New World species, having coarse scales on ventral surface (dorsally with finer ones). Costa Rica to Peru and Venezuela.

Description: Coloration: Frons dark brown, lighter on ptilinal margin; frontal vittae blackish brown, dull; fronto-orbital plates and ocellar triangle faintly shiny, lighter brown; antennal pedicel, flagellomere 1, face, clypeus, cheek light brown, palp dark yellow-tan. Scutum light brown, grading to slightly darker brown posteriad and on scutellum; notum with slight shine; postpronotal lobe, notopleural area, anepisternum, and anepimeron slightly darker, katepisternum same to slightly lighter. Legs tan; halter bulb light (whitish to yellow); abdomen uniformly brown in both sexes, darker in ♂.

Head: Arista with 3–4 dorsal, 2 ventral branches, plus terminal fork; pedicel with 1 stout, longer seta, 3 smaller ones. HD/HW 0.76 (mean of 4♂). Anterior reclinate orbital seta directly lateral to slightly posterolateral of the proclinate orbital; posterior reclinate midway between proclinate and inner vertical setae or slightly closer to proclinate; proclinate 1.7× length of anterior reclinate, posterior reclinate 1.20× length of anterior reclinate. Ipsilateral vertical setae separated only by distance approximately 2× the socket diameter; inner vertical in line with proclinate and posterior reclinate, IV/OV 0.87. Ocellar setae sockets on tangent between median and posterolateral ocelli; postocellars parallel to slightly convergent, length slightly less than ocellars, OC/POC 1.24; 5–6 small setulae in ocellar triangle. Frons with 10–12 setulae

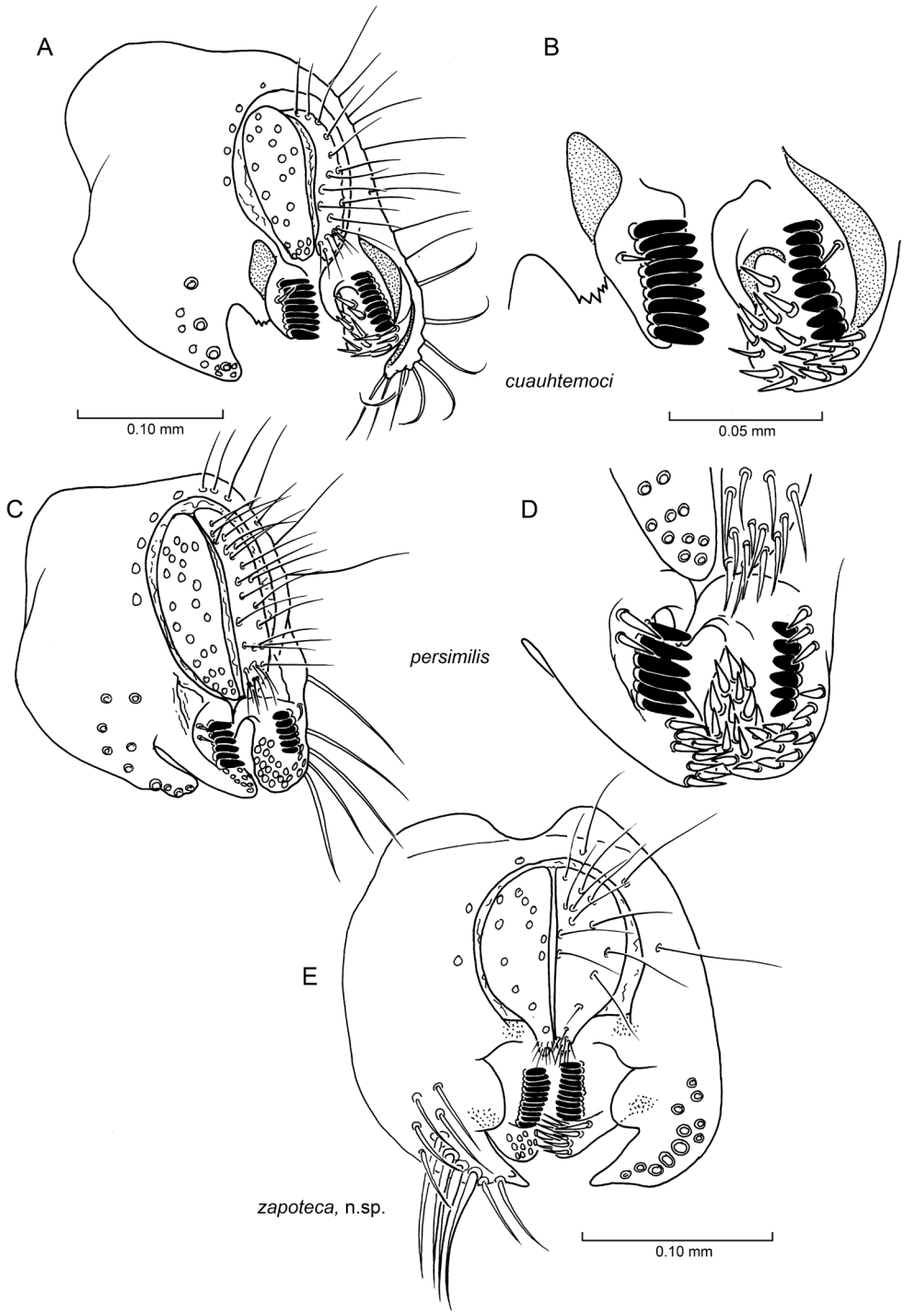

FIG. 13. Epandria and associated structures in representative species of the *pseudoobscura* subgroup. **A.** *D. cuauhtemoci* (ASG 38); **B.** Detail of A; **C.** *D. persimilis* (ASG 36); **D.** Detail of C; **E.** *D. zapoteca*, n. sp. (ASG 20).

near anterior margin. FL/LFW 0.98, UFW/LFW 1.61. Face slightly deeper than wide, frontal W-index 2.89; carina small, narrow, short (0.3–0.4× length of face); vibrissa long, 1st genal seta small, GS1/VL 0.30, gena with row ~7 setae, increasing in length posteriad. Cheek of moderate depth, ED/CD 8.65. Palp with 1 long apical seta, 2–3 shorter setae in middle of ventral margin. Eye broadly oval in lateral view, EW/ED 1.21.

Thorax: Length 0.77 mm (mean of 4♂). Acrostichals in 6 rows between anterior dorsocentrals, lengths slightly increasing posteriad; acrostichals in front of scutellum or anterior dorsocentrals not enlarged. Anterior dorsocentrals 0.61× length of posterior ones; distance between ipsilateral dorsocentrals less than that between contralateral ones. Postpronotum with 2 strong setae, UPS/LHS 0.75; 2 strong notopleural setae near notopleural suture, plus 1 longer one dorsally, another postsutural; katepisternum with 2 large setae, posterior one larger (S-index 0.65), sclerite with 4–5 small setulae. Anterior scutellar setae approximately parallel, posterior ones crossed for about 0.3× their length, anterior pair 0.85× length of posterior pair. Legs: profemur with 3 longer ventral setae (lengths approximately equal to femur width); mid and hind tibiae with stout, ventroapical setae, thinner dorsal-preapical seta; ♂ protarsus with length of ta_1 1.07–1.38× that of ta_2; ta_1 with 3 teeth, ta_2 with 2; teeth long, slender, not touching, projecting away from tarsomeres, tooth lengths 0.1.5–2× width of tarsomeres. Wing of moderate length and width, ThL/WL 0.45, WL/WW 2.33, C-index 1.84, hb-index 3.61, 4V-index 2.49, 5X-index 2.51.

Abdomen: Male terminalia: epandrium height approximately equal to width; cerci somewhat flattened, ventral portion tapered, with small tuft of fine setulae; outer lobes of ventral epandrial lobe broad in lateral view, relatively short; margin of inner lobe of ventral epandrial lobe faintly defined from surstylus; surstylus with row of 10–11 prensisetae; aedeagus and valves very slightly shorter than postgonites; valves uniquely with irregular row ~10–12 coarse scales on ventral margin, additional scales on dorsolateral surface; aedeagal membrane with sparse, finer scales, no microtrichia; hypandrium length ~1.3× the width. Female terminalia: spermathecsa cup shaped, width 1.5× the height; sleeve broad and funnellike, no apical indentation. Oviscapt broad in lateral view, apically blunt, with ~12 small ovisensilla pegs along margins.

Type: Holotype, ♂: COSTA RICA: Punatarenas, Las Alturas, 20 km NE San Vito de Hava, 1500 m, 20/VIII/91, Grimaldi and Stark, sweeping forest floor. Dissected (ASG 05), in AMNH.

Etymology: In keeping with a tradition of naming American species of the *obscura* group for indigenous cultures, this species is named for the Chibcha people, as a noun in apposition. The Chibcha (pronounced *cheeb'-ka*) inhabited Colombia since at least the fifth century BCE; they also settled in Panama, both countries centered within the distribution of this species.

Specimens Examined: Paratypes: COSTA RICA, Prov. San José , Moravia, Zurquí de Moravia, 1600 m, 5–8 Sep 2012, W. Porras, Tp. Malaise #1, ZADBI-1, -84:00:57 10:02:58 #104987, ♂ (dissected, ASG 04); 22 Sep 2012 pan light trap, #105059,♀ (dissected, ASG 17), 24 Sep 2012 Dry MT, ZADBI-60 #165076 ♀ (dissected, ASG 09); San José, Zurqui de Moravia, 1600 m, VII/92, Paul Hanson, Malaise trap ♀ (dissected, ASG18) (AMNH, MNCR). PERU: Cusco, Est. Biol. Wayqecha, 13.1845°S 71.58459°W, 2806 m, malaise trap 6, WP532, 8–11/XII/11, Steck, Norrbom, Sutton, Nolazco, 1 ♂ (dissected, ASG 08), 1♀ same data, except:

WP583, 4–12/VI/12 (USNM). VENEZUELA: Aragua, Rancho Grande, 26/II/89, D.A. Grimaldi, 1♂ (dissected, ASG 07) (AMNH)♀.

Distribution: Costa Rica, Venezuela, Peru.

Comments: The Peru specimen has some differences with other specimens of this species: frontal-index 0.81 (vs. 1.00–1.09), cheek deeper (ED/CD 6.66 (vs. 9.2–9.5), frontal-W index 2.6 (vs. 2.85–3.10), but which may not be statistically significant. Most notable is the unique occurrence of a "tooth" on male protarsomere-3. This tooth does not occur on its right ta_3, suggesting that the left one is teratological. Slight asymmetries in tooth counts of the sex combs of individual flies is not unusual in various species of the *obscura* group (e.g., Crumpacker, 1973). For these reasons, and the fact that the male genitalia are identical, I am considering the Peru specimen to be the same species.

All the specimens were collected without bait traps, instead captured in Malaise and light traps, or (in Venezuela) by net sweeping the forest floor. All the collecting localities are cloud forest; a detailed description of the Zurqui, Costa Rica, site is given in Borkent et al. (2018).

Drosophila (*Sophophora*) *dobzhanskii* Patterson

Figure 7E

Drosophila (*Sophophora*) *dobzhanskii* Patterson 1943: 82.

Diagnosis: Distinctive for the large ♂ sex comb, having ~18 teeth on ta_1, on ta_2 a "single tooth...little more than enlarged bristle" (Patterson, 1943: 82). Notum and pleuron coffee brown, acrostichals in 6 rows; oviscapt with ovisensilla along ventral margin setiform, not pegs; spermatheca without apical indentation.

Types: Holotype, ♂: Mexico: "collected July 1942, just west of Mexico City by G.B. Mainland" (Patterson, 1943: 82). In USNM; examined but not dissected.

Specimens Examined: Besides type (above): 2♀♀: MEXICO: Desietrode de los Leones, Distrito Federal IV/29/42, G.B. Mainland 1342.1/PARATYPE dobzhanskii (in AMNH), 1 ♀ dissected (ASG33).

Distribution: Known only from the type series.

Comments: I have not dissected a male specimen, but the female has a distinctive oviscapt, as described above.

Drosophila (*Sophophora*) *narragansett* Sturtevant and Dobzhansky

Figures 2C, D; 5A–C, 7F, 9J; 12A, B; 15A, D

Drosophila (*Sophophora*) *narragansett* Sturtevant and Dobzhansky, 1936: 577.
Drosophila (*Sophophora*) *seminole* Sturtevant and Dobzhansky, 1936: 577. NEW SYNONYMY.

Diagnosis: Males immediately recognized among North American species of the group by the silvery frons, best seen in frontal view in dried/fresh specimens. Distinguished from *D.*

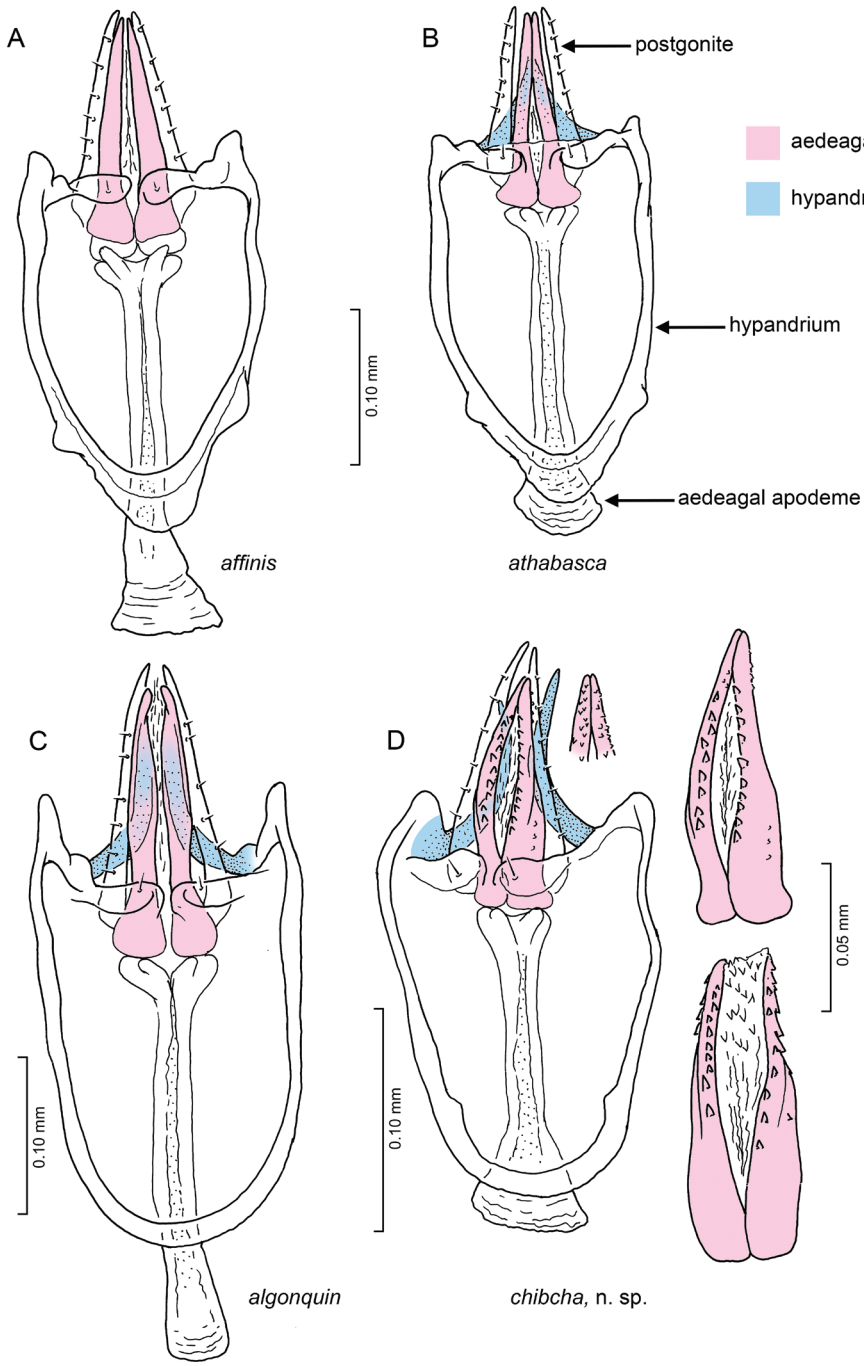

FIG. 14. Hypandrium, aedeagus and other appendages of representative species of the *affinis* subgroup (ventral views). The valves of the aedeagal sheath and the pair of hypandrial lobes are highlighted in color; the postgonites are not. **A.** *D. affinis* (ASG 29) (hypandrial lobes hidden); **B.** *D. athabasca* (ASG 31); **C.** *D. algonquin* (ASG 32); **D.** *D. chibcha*, n. sp. (ASG 05), with detail of aedeagal valves of ASG 05 (above), and ASG 08 (below). All to the same scale except details of *D. chibcha*.

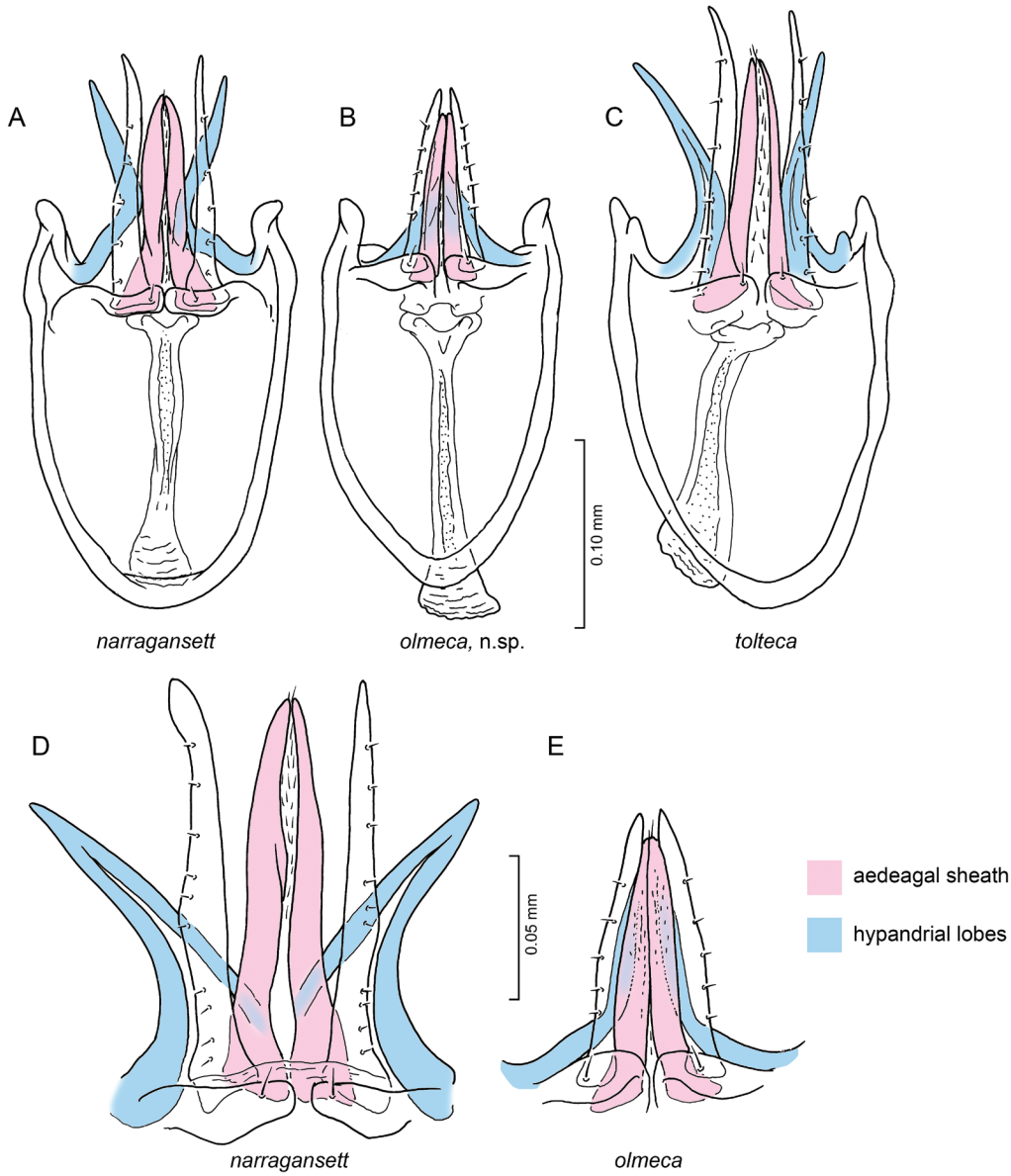

FIG. 15. Hypandrium, aedeagus and other appendages of representative species of the *affinis* subgroup (ventral views). **A.** *D. narragansett* (ASG 10: paralectotype, Massachusetts); **B.** *D. olmeca* (ASG 25: holotype); **C.** *D. tolteca* (ASG 23); **D.** *D. narragansett* (ASG: Virginia); **E.** *D. olmeca* (ASG 25: holotype, detail of B). A–C to same scale; D and E to same scale

olmeca, n. sp. (Chiapas Mexico), also with a silvery male frons, as discussed under that species below. *D. narragansett* further distinguished by the following: male ta_1 with 4–5 teeth and ta_2 with 1; ta_1 1.3× length of ta_2; base of inner ventral epandrial lobe with furrows, no microtrichia; surstylus with 9–10 prensisetae. Spermatheca distinctive, roughly cup-shaped, apical indentation short; sleeve large, conical, with fine annulations.

Redescription: Coloration: Frons in ♂ silvery in frontal view, especially frontal vittae (fronto-orbital plates and ocellar triangle slightly less so); in dorsal view of ♂ this silvery shagreenation diminished; ♀ frons pollinose, slightly olive but not silvery, ocellar triangle and pair of spots at vertex lateral to ocelli without pollinosity; portion of frons near ptilinal suture dull, dark yellow. Antenna with pedicel light brown, flagellomere 1 darker brown; face, cheeks, and palps dull, tan; clypeus light brown. Scutum, scutellum, postpronotal lobe very light brown, dull, with dusting of pruinescence; notopleural area, anepisternum and anepimeron slightly darker brown, katepisternum lighter. Legs and halter knob dark yellowish tan; abdomen uniformly brown in both sexes, darker in ♂.

Head: Arista with 4 dorsal, 2 ventral branches, plus terminal fork; pedicel with 4 larger setae. HD/HW 0.74 (mean of 4♂). Anterior reclinate orbital seta slightly posterolateral to the proclinate orbital; posterior reclinate slightly closer to proclinate than to inner vertical seta; proclinate 1.65× length of anterior reclinate, posterior reclinate 1.14× length of anterior reclinate. Ipsilateral vertical setae close together, sockets separated by distance ~2× their diameter; inner vertical in line with proclinate and posterior reclinate; vertical setae long, IV/OV 0.96. Ocellar seta socket on tangent between median and posterolateral ocelli; postocellars of medium length, parallel to convergent, pointing backward, shorter than ocellars (OC/POC 1.30); ~6 small setulae in ocellar triangle. Frons with 2–8 minute setulae near anterior margin. FL/LFW 0.94, UFW/LFW 1.47. Frontal W-index 2.85; carina very small, thin, short (half the length of face); vibrissa long, 1st genal seta small, GS1/VL 0.56, gena with 5–6 setae, decreasing in length posteriad. Cheek fairly narrow, ED/CD 7.5. Palp with 1 long preapical seta. Eye broadly oval in lateral view, EW/ED 0.81.

Thorax: Length 0.88 mm (mean of 4♂). Acrostichals in 6 even rows between anterior dorsocentrals, lengths slightly increasing posteriad; acrostichals in front of scutellum or anterior dorsocentrals not enlarged. Anterior dorsocentrals 0.72× length of posterior ones; distance between ipsilateral dorsocentrals less than that between contralateral ones. Postpronotum with 2 strong setae, h-index 0.77; 2 strong notopleural setae near notopleural suture, plus 1 dorsally, another, short postsutural; katepisternum with 2 large setae, posterior one about 2× the size of other (S-index 0.57), sclerite with 5–7 small setulae. Anterior scutellar setae convergent, posterior ones crossing for about 0.2× their length, both pairs approximately equal in length (scut-index 0.96). Legs: Profemur with ventral row of 3–4 long setae on distal half (lengths approximately equal to femur width); mid and hind tibiae each with stout, ventroapical seta, thinner dorsal-preapical seta; ♂ protarsus ta_1 1.3× length of ta_2; ta_1 with 4–5 teeth, ta_2 with 1; teeth stout, touching, length 1.3× tarsomere width. Wing of moderate length and width, ThL/WL 0.44, WL/WW 2.28, C-index 2.65, hb-index 2.49, 4V-index 2.23, 5X-index 2.15.

Abdomen: Male terminalia: epandrium height slightly greater than width; cercus relatively narrow, with narrowed ventral lobe; outer lobes of ventral epandrial lobe relatively short (tips reaching to level of about midway to surstylus); margin of inner lobe of ventral epandrial lobe not well defined from surstylus, base of inner lobe with furrows; surstylus with row of 9–10 prensisetae; aedeagus and valves slightly shorter than (0.9× the length of) postgonites; gonites with faint elbow near middle of lateral margin. Aedeagal valves without ornamentation; membrane of aedeagus with very fine microtrichia. Hypandrium length 1.3× the width. Female terminalia: spermatheca distinct, width 1.5× the height; sleeve very large, funnel shaped, with fine annulations, extended into capsule 0.9× the capsule height, with small apical indentation protruding into end of sleeve. Oviscapt of moderate depth in lateral view, apex slightly narrowed; with ~13 ovisensilla pegs along margins.

Type: Lectotype, ♂, selected by myself from a series of 9♂, 14♀ specimens, all labeled as: "WoodsHole, Mass [printed]/stock 25 [written]/A.H. Sturtevant Collection, 1970 [printed." Steyskal did not apply a note to any specimen as the type. 1 ♂, 1♀ paralectotype dissected. In the USNM.

Specimens Examined: Besides the lectotype and the paralectotype series (above), the holotype of *seminole* and several specimens identified as *seminole* (see in Comments below).

Distribution: Currently a very rare species that historically extends from southern Alabama (Hartsell, Kushla), Mississippi (Corinth), and mid-Florida (St. Petersburg) north to Massachusetts (Amherst, Woods Hole), northern Michigan (University of Michigan Biological Station), and in the west to Nebraska (Lincoln, Chadron St. Forest), Missouri (St. Louis) (Miller, 1958), as well as Indiana (locality not specified) and Texas (Bastrop St. Park) (Barrio et al., 1992). The record and figures in M. Miller et al. (2017) of *D. narragansett* from Maine are incorrect. These are based on a series of specimens in the AMNH: "SE Guarette Maine, July 1948 / M.R. Wheeler collector," which were misidentified by Marshall Wheeler as *narragansett*. The specimens are actually *D. athabasca*, with a spermathecal capsule that is especially flat and broad.

In a study of abundances of *D. affinis*, *D. algonquin*, *D. athabasca*, and *D. narragansett* (Miller, 1958), the last one was not found at most of the localities, and when present was less than 1% of the abundance of these four species, except at two sites: Corinth, Mississippi (3%) and Hartshell, Alabama (7%). Astonishingly, *narragansett* has to my knowledge been collected only once within the past 60 years, despite its broad range: a male swept from over compost in May 2017 in Rochester New York (Werner et al., 2020a, 2020b). I have never collected it, nor have many other drosophilists.

Comments: The holotype of *seminole*, a male, is labeled: "Kushla, Ala[bama], My.14.22, oak trunk [in Sturtevant's writing] / A.H. Sturtevant collection, 1970 [printed]." In USNM. This is the sole specimen from the type locality (Kushla), it has a penciled note by Steyskal (in his writing) "seminole type"; it was labeled 12 June 2023 by myself as the holotype; glue on the tip of the abdomen prevented it from being dissected for the genitalia. The glue also embedded the foretarsi, but fortunately it is clear and four long teeth are visible on protarsomere-1. The type of *D. seminole* is darker than specimens in the type series of D. *narragansett* and the specimen from Virginia, but in all other respects it is identical to those others, including measured proportions

of body structures and setae. The putative differences between *D. narragansett* and *D. seminole* in the silvery frons, reported by Sturtevant and Dobzhansky (1936) and cited by Sulerud and Miller (1966), are incorrect and one basis for confusion that *D. seminole* could be a separate species. The silvery male frons may not be apparent in specimens preserved in alcohol.

Two other specimens in the USNM collection identified as *D. seminole* are the following: one mentioned in the original publication (Sturtevant and Dobzhansky, 1936) labeled as: "Whistler Ala[bama] Oc[t.].20.24 [written in Sturtevant's hand] / A.H. Sturtevant Collection 1970 [printed]/*Drosophila seminole* [written]." This specimen, a male with the genitalia everted, is not *D. seminole* (i.e., *D. narragansett*); it lacks the distinctive silvery frons. A third specimen is a male with a silvery frons, labeled: "Mountain L[ake], Va., 22-VII-'40 W.H. #2, L.J. & M.J. Milne / *Drosophila seminole* det. Steyskal '[19]44." This specimen is *D. narragansett*, although it has some interesting distinctions from other measured specimens of *D. narragansett*: upper seta of postpronotal lobe smaller than lower one (h-index 0.62, vs. 0.80–0.87 for others), smaller anterior scutellars (Scut-index 0.88, vs. 0.97–1.02 for others), C-index smaller (2.48, vs. 2.65–2.71), and hb-index smaller (2.18, vs. 2.42–2.75). The male genitalia of the type series of *D. narragansett* and the Virginia specimen are identical.

Drosophila (*Sophophora*) *novitskii* Sulerud and Miller

Drosophila novitskii Sulerud and Miller, 1966: 470.

Diagnosis: Males very distinctive, sex comb on ta_1 having 6–8 teeth and ta_2 having none, length of ta_1 1.2× that of ta_2; surstylus unique among New World species in lacking row of prensisetae; testes short and elliptical (vs. coiled).

Type: Sulerud and Miller (1966) reported the only specimens, from the Rocky Mountain Biological Laboratory, in Gothic, Gunnison Co., Colorado, which is at an elevation of ca. 2900 m. I am unaware of any specimens that exist for this species, including the ones reported by these authors.

Specimens Examined: None.

Distribution: Known only from the type locality in Colorado.

Comments: *Drosophila alpina* Burla, a Palearctic boreal-alpine species that was beautifully redescribed by Baechli et al. (2004), is another member of the *obscura* group that lacks a row of prensisetae on the surstylus. *Drosophila alpina*, however, has sex combs typical of the *obscura* subgroup, with ta_1 and ta_2 each having more than 10 teeth. Despite the unusual surstyli, *D. novitskii* and *D. alpina* are clearly unrelated.

Drosophila* (*Sophophora*) *olmeca, new species

Figures 5D, 9K; 12C, D; 15B, E

Diagnosis: Facial carina very thin, small; acrostichal setae in 6 rows; sex comb with 4 teeth on ta_1, 1 on ta_2. Known only from male. Like *D. narragansett*, male with silvery frons and rela-

tively small body size (0.74 for *D. olmeca* type, mean of 0.88 mm thorax length for *narragansett*), *D. olmeca* distinguished by the distinctively longer outer lobes of ventral epandrial lobe, whose tips nearly touch ventrally; postgonites shorter, length 0.60× that of hypandrium (vs. 0.77–0.80× in *D. narragansett*). Further distinguished from *D. narragansett* by several wing indices, as given in the description below.

Description: Coloration (♂ only): Frons with silvery pollinosity over entire front, including frontal vittae, fronto-orbital plates, and ocellar triangle (most obvious in frontal view, in dorsal view frontal vittae are darker); antennae, face, ventral margin of cheek light brown (cheek dorsally lighter); clypeus and palps light brown. Scutum and scutellum medium brown, dull, with dusting of pruinescence; postpronotal lobe, notopleural area, anepisternum similarly brown; katepisternum lighter. Legs light yellow; halter knob light brown; abdomen uniformly brown in ♂.

Head: Arista with 4 dorsal, 2 ventral branches, plus terminal fork; pedicel with 3 longer setae. HD/HW 0.80. Anterior reclinate orbital seta slightly posterolateral to proclinate orbital; posterior reclinate slightly closer to proclinate than to inner vertical setae; proclinate 1.7× length of anterior reclinate, posterior reclinate 1.07× length of anterior reclinate. Ipsilateral vertical setae close; inner vertical in line with proclinate and posterior reclinate, IV/OV 0.95. Ocellar setae sockets on tangent between median and posterolateral ocelli; postocellars of moderate length, shorter than ocellars, OC/POC 1.33, parallel, pointing backward; 4 small setulae in ocellar triangle. Frons with 5 setulae near anterior margin. FL/LFW 1.00, UFW/LFW 1.50. Face relatively short, FD/FW 1.15, frontal W-index 2.95; facial carina very narrow, short (0.3× length of face); vibrissa well developed, 1st genal seta small, GS1/VL 0.38, gena with ~6 rather short setae. Cheek of moderate depth, ED/CD 8.2. Palp with 1 long apical seta. Eye broadly oval in lateral view, EW/ED 0.75.

Thorax: Length 0.74 mm. Acrostichals in 6 even rows between anterior dorsocentrals, lengths slightly increasing posteriad; acrostichals in front of scutellum or anterior dorsocentrals not enlarged. Anterior dorsocentrals 0.67× length of posterior ones; distance between ipsilateral dorsocentrals less than that between contralateral ones. Postpronotum with 2 strong setae, UPS/LHS 0.77; 2 strong notopleural setae near notopleural suture, plus longer seta dorsally, another, long postsutural seta; katepisternum with 2 large setae, posterior one nearly 2× the length (S-index 0.57), sclerite with 4–5 small setulae. All scutellar setae parallel, posterior scutellars longer, ASC/PSC 0.82. Legs: profemur with short, ventral row of 3 setae (lengths slightly less than femur width); mid and hind tibiae with stout, ventroapical setae, thinner dorsal-preapical seta; lengths of ♂ protarsus ta_1 and ta_2 nearly equal; ta_1 with 4 teeth, ta_2 with 1; ta_1 teeth touching, greatest length of teeth 1.3× the width of tarsomere. Wing: C-index 2.44 (vs. 2.65 in *D. narragansett*), hb-index 2.86 (vs. 2.49), 4V-index 2.23, 5X-index 2.50 (vs. 2.15).

Abdomen: Male terminalia: epandrium slightly higher than wide; cerci relatively flat, without distinct ventral lobe, ventrally with tuft of ~8 setulae; outer lobe of ventral epandrial lobe long, curved inward such that distal tips almost touch; margin of inner lobe of ventral epandrial lobe hardly defined from surstylus, base of inner lobe with fine furrows; surstylus with row of 7–8 prensisetae; aedeagus and valves only slightly shorter than postgonites; [presence

of microtrichia on aedeagus not observable]; aedeagal valves without micropapillae. hypandrium length 1.45× the width. Female terminalia: unknown.

Type: Holotype ♂: San Cristobal, Chiap[as], MEX[ICO] / May 1959, M. Wasserman. Dissected (ASG25), in AMNH.

Etymology: Derived from the Olmec people, who lived 1200–400 BCE in southeastern Mexico and are well known for their carvings of monumental stone heads.

Specimens Examined: Known only from the type specimen.

Distribution: Chiapas, Mexico.

Drosophila (*Sophophora*) *tolteca* Patterson and Mainland

Figures 4C, 7G, 9L, 12E, 15C

Drosophila tolteca Patterson and Mainland, in Mainland and Patterson, 1944: 32.

Diagnosis: Recognizable for the large ♂ sex comb on ta_1, with generally 7–8 teeth (range of 5–9: Sulerud and Miller, 1966); ta_2 with one very small, thin "tooth" barely distinguishable from adjacent setae; male ta_1 short, length ~0.80× length of ta_2. Male genitalia with base of inner ventral epandrial lobe with furrows and dense microtrichia. Female: apex of oviscapt blunt, ovisensilla all short pegs; spermatheca squat, width 2× the height, with apical indentation.

Type: Types not found. Mainland and Patterson (1944) did not specify a type specimen, merely stating (p. 33) that "The stock upon which the description is based originated from specimens collected near Cordoba [Veracruz]."

Specimens Examined: All in AMNH: Mexico: Desietrode de los Leones, Distrito Federal, VII/29/42, G.B. Mainland 1342.1, 1♂, 1♀. EL SALVADOR: San Salvador / Jan. 21, 1954, W.B. Heed, 1♂; Volcan Santa Ana, 5670 ft., 20.7a / Nov. 1953, W.B. Heed, 1♂; Volcan Boqueron, 4500 feet, 91.16 / Feb 25, 1954, W.B. Heed, 1♂. NICARAGUA: 11 klm N Matagalpa 57.22 / Santa Maria de Ostuma / June 1954, W.B. Heed, 1♂. From culture 14012-0210.0, DNA seq publ by V. Schawaroch, 2002, 5♂♂ (ASG 23), 1♀ (ASG 24).

Distribution: Reported from Colombia (near Bogotá: Hunter, 1964, 1966; Villamizar and Alvarez, 2010), Ecuador (Cotopaxi and Pinchincha: Acurio and Rafael, 2009), El Salvador (Heed, 1957), and Mexico (Mainland and Patterson, 1944). It is also reported from Coroico (near La Paz) Bolivia, based on a strain studied by Barrio et al. (1992). I am unaware of any material from Bolivia. The Coroico strain was the only one of *D. tolteca* studied by Barrio et al. (1992), so comparisons with Central American strains and specimens have not been made, genetically or morphologically, and the identity of the Bolivia material has not been verified.

Drosophila pseudoobscura Subgroup

Diagnosis: Male with valves of aedeagus having micropapillae, protarsomere sex comb with ta_1 having generally 3–5 teeth and ta_2 with 3–5 teeth (fig. 10); both sexes with facial carina relatively broad, having flattened edge; acrostichal setulae in 6–8 rows depending on species (see fig. 6).

Drosophila (*Sophophora*) *cuauhtemoci* Felix and Dozhansky

Figures 2E, 3D, 8A, 10A; 13A, B; 16A

Drosophila (*Sophophora*) *cuauhtemoci* Felix and Dobzhansky, in Felix et al., 1976: 167.

Diagnosis: A very distinctive species from Mexico: ♂ with apical two-thirds of midtibia swollen, having two opposing, parallel combs of long setae (their lengths greater than the width of the tibia), one comb on the dorsal margin of the tibia and another on the ventral margin. Male protarsus with 4 (sometimes 5) teeth on ta_1, 3 teeth on ta_2. Acrostichals in 6 rows. Oviscapt broad in lateral view; spermatheca without apical indentation (Felix et al., 1976, mentioned that the spermatheca is "darker and less convex than in *D. pseudoobscura*," but it is actually more convex).

Types: Holotype, ♂, from original description: Mexico: 10 km N Cuernavaca along Highway 95 (between Cuernavaca and Mexico City), July 29, 1974, in mixed pine and oak forest. In UCDBM, originally reported to be in the CAS (Felix et al., 1976). The original description also mentions paratypes collected in the same locality but in 1975, as well as in Lago Patzcuara, Michoacan and Parque Nacional El Chico, near Pachuca, Hidalgo, Mexico. Felix et al. (1976) reported that paratypes were also deposited in the AMNH, but which were never here. All paratypes are in the UCDBM.

Specimens Examined: 2♂, 1♀: Mex[ico] Morelos, Cuernavaca, VII 29 1974, Th. Dobzhansky / PARATYPE Drosophila cuauhtemoci Felix & Dobzhansky (ASG38 ♂, ASG39♀). In UCDBM.

Distribution: Known only from south central Mexico.

Comments: It would be interesting to eventually observe how the male uses the midleg brushes, probably in courtship.

Drosophila (*Sophophora*) *lowei* Heed, Crumpacker and Ehrman

Figures 3A, 8B, 10B

Drosophila lowei Heed, Crumpacker, and Ehrman, 1969: 398.

Diagnosis: Very similar to sympatric *D. pseudoobscura*, but distinguished by the bronze-like sheen on the blackish notum (vs. without sheen in *D. pseudoobscura*); ♂ sex comb having fewer teeth on both tarsomeres: ta_1 with 4–6 teeth and ta_2 with 3–4 teeth (vs. generally 6–9 on ta_1 and 5–9 on ta_2 in *D. pseudoobscura* [Crumpacker, 1973]); wing distinctly longer than body (vs. shorter); surstylus with row of 9–11 prensisetae (vs. 6–7); posterior margin of hypandrium with pair of prominent, pointed lobes (in *D. pseudoobscura* this margin barely raised). Acrostichals in 8 rows. Female: Oviscapt with long ovisensilla, lengths ~2× the width (vs. length equal to width); spermatheca subspherical, with apical indentation reaching into internal sleeve (vs. oval, indentation not reaching apex of sleeve).

Type: Holotype, ♂: A19.2 / 78 Sept. 1960 / Santa Catalina Mts., Tucson, Ariz., TYPE [in red] [all handwritten by W.B. Heed, from publication: Arizona: Pima Co., Tucson, Santa Catalina Mtns., Mt. Lemmon, W.B. Heed]. In USNM. Examined, not dissected.

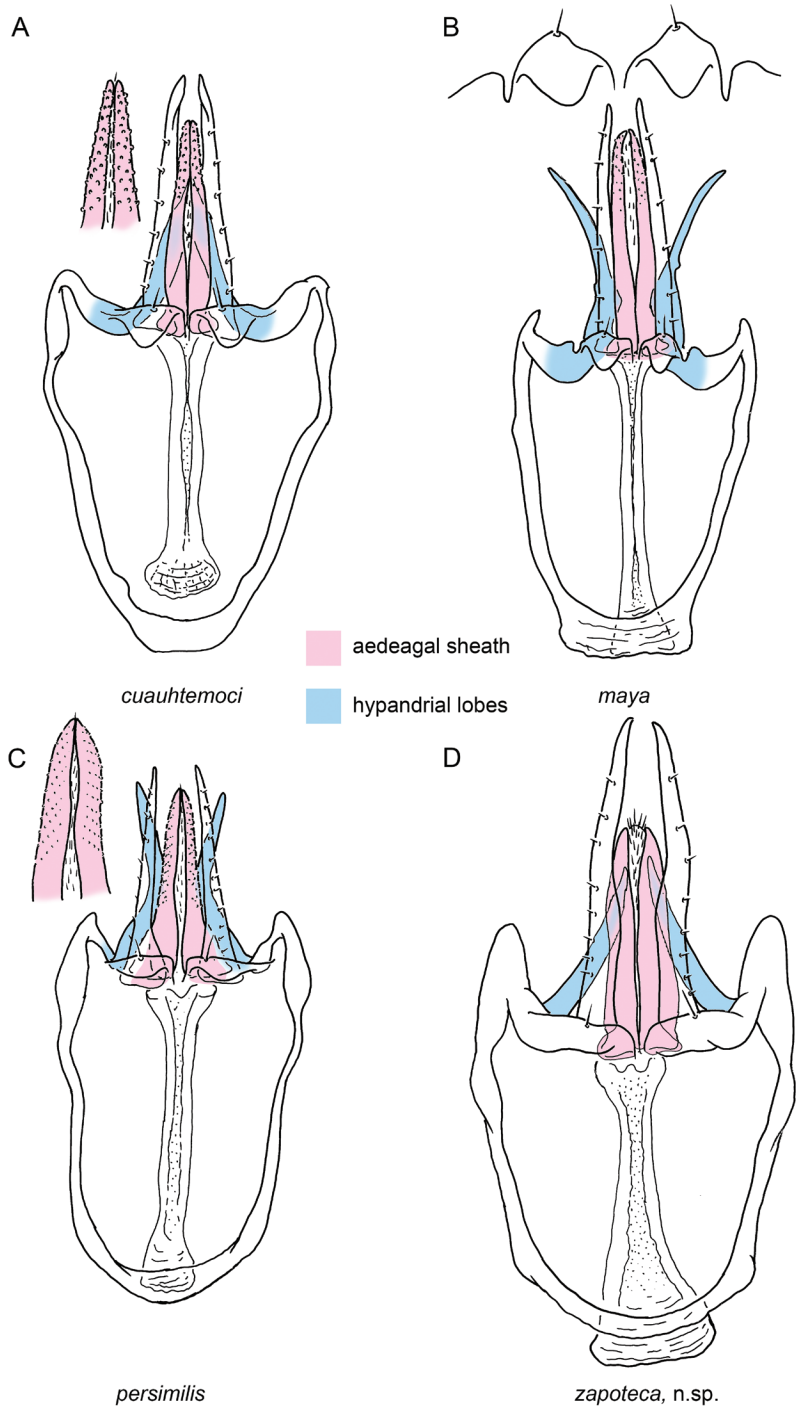

FIG. 16. Hypandrium, aedeagus and other appendages of representative species of the *pseudoobscura* subgroup. **A.** *D. cuauhtemoci* (ASG 38); **B.** *D. maya* (ASG 02: Guatemala), with details of pregonite lobes; **C.** *D. persimilis* (ASG 36); **D.** *D. zapoteca*, n. sp. (ASG 20: holotype)

Specimens Examined: 9 paratypes: 4 with same data as holotype, labels handwritten. One specimen with simply "A33.6" [handwritten by Heed; from publication: Arizona, Cochise Co., Rustler Park, near Portal, Chiricahua Mtns., VII/15/1961 W.B. Heed]. 5 specimens with simply "2056.1" [handwritten, not Heed's], 1 with Heed's writing: 38 mi W Heber, Ariz. VIII/8/50, M.R. Wheeler. All in AMNH, 2 dissected.

Distribution: Higher elevations in Arizona and Colorado, probably extending into Sierra Madre Occidental in Mexico. Heed et al. (1969) mentioned that *D. lowei* can be very common at 7000–9000 ft. (2100 to 2740 m) in pine (*Pinus*) and fir (*Abies*) forests in Arizona, and the species prefers rotting mushroom bait. In Colorado near the Colorado Springs area, *D. lowei* extended up to 11,400 ft. (3475 m) near Pike's Peak; it is abundant at higher elevations in Colorado (e.g., Crumpacker, 1973).

Drosophila (*Sophophora*) *maya* Heed and O'Grady

Figures 2B, 3B, 8C, 10C, 16B

Drosophila (*Sophophora*) *maya* Heed and O'Grady, 2000: 98.

Diagnosis: Acrostichals in 6 rows; carina narrow above, broadened at base; sex comb with ta_1 having 3–5 teeth and ta_2 having 2–4; ta_1 1.5× length of ta_2; surstylus with row of 7–9 prensisetae, inner "hook" short and blunt; posterior margin of hypandrium with small pair of raised, sclerotized lobes (height equal to width); anterior margin of hypandrium narrowed, flat. Oviscapt with small ovisensilla pegs; spermatheca unique in group: dome shaped, no apical indentation, basal sleeve very short (~1/4 length of capsule).

Type: Holotype, ♂ (point-mounted body): "Cerro Monte Cristo, 7000′ [ft] 44.12 / Rep. de EL SALVADOR / Feb. 5, 1954 WB Heed / Genitalia on slide 44.12A / Holotype Drosophila maya Heed & O'Grady. In AMNH. The holotype had been dissected by Heed and genitalia slide mounted (Heed no. 44.12A). Slide: 44.12A, Monte Cristo, El Salvador, 7000′, pseudolike, W.B. Heed, 1954, from pinned fly / sex comb = 4/3, c[lasper] 8 teeth, p(enis) index = 10.2 / TYPE ♂ (all labels handwritten by Heed), CUIC 88673.

Specimens Examined: Three paratypes (each with blue PARATYPE label): 1♂ (pinned body), Rep. de Honduras / Monte Vyuca, 10 km NW Zamorano, 5000′ 49.22 / Mar. 1954 W.B. Heed. In AMNH. 1♀, 1♂ (pinned bodies): Rep. de EL SALVADOR / Cerro Monte Cristo 7000′ 44.12 /Feb. 6, 1954 WB Heed / Paratype Drosophila maya / ♀ dissection ASG19; ♂ ibid., with also labels handwritten by Heed "genitalia 44.12B, sex combs 4/3, 3/3" / ASG41. In AMNH (also slide mounted dissections: in CUIC, no number). GUATEMALA: Zacapa, 10 km N San Lorenzo, 2200 m., 8-10/XI/86, M. Sharkey, FIT [flight intercept trap]. In AMNH; dissected by D.G. (no. ASG02).

Distribution: Reported by Heed and O'Grady (2000) from El Salvador and Honduras (above), with the new record reported here from Guatemala.

Comments: Slide-mounted dissections of the male genitalia of the type (44.12A) and a paratype (44.12B), in the Heed material housed in the CUIC, have the hypandrium distorted

by the weight of the coverslip. Regardless, the distinctive pair of small, paramedian lobes on the posterior margin of hypandrium, and the flat anterior margin are readily apparent. The proportions of the aedeagus and periphallic appendages also fully agree with the specimen from Guatemala. The slide mountant used by Heed, probably Hoyer's, has darkened to a medium brown.

Drosophila (*Sophophora*) *miranda* Dobzhansky

Drosophila miranda Dobzhansky, 1935: 377.

Diagnosis: Edge of facial carina slightly flattened; acrostichal setae in 8 rows; distinguished from sympatric species *D. pseudoobscura* and *D. persimilis* by body being larger (by 10%–15%), darker (especially the legs), and sex comb with more teeth: ta_1 with usually 8 teeth (ranging from 6–10), ta_2 with usually 6 (ranging from 5–8); acrostichals in 8 rows.

Type: Holotype, ♂: Olympic Mts. Washington [no collector or date, handwritten] / TYPE [red label, printed]. In AMNH.

Specimens Examined: Six paratypes, same label data as holotype; 9 specimens: Prairie Creek S.P. [State Park], Calif. July 1951 / M.R. Wheeler, W.B. Heed / 2179.2. In AMNH.

Distribution: This species has one of the narrowest distributions in the group north of Mexico; it is relatively rare compared to the sympatric *D. pseudoobscura* and *D. persimilis*, preferring cool, wet coastal and montane forests of the Pacific Northwest. Its northern extent is Vancouver Island, south in the Cascade Range to Mt. Whitney and to the Monterey Peninsula in California.

Comments: I have not studied the female terminalia.

Drosophila (*Sophophora*) *persimilis* Dobzhansky and Epling

Figures 8D, 10D; 13C, D; 16C

Drosophila persimilis Dobzhansky and Epling, 1944: 7.

Diagnosis: Facial carina with edge slightly flattened; acrostichal setae in 8 rows; sex comb with usually 6 teeth on ta_1 (range of 5–7), usually 5 on ta_2 (range of 4–6). Distinguished from sympatric *D. pseudoobscura* by tip of aedeagus not quite reaching to tips of closed, folded postgonites (Rizki, 1951) (but see below). Spermatheca with deep, conical, annulate sleeve; no apical indentation; ventral margin of oviscapt with fewer ovisensilla than in *D. pseudoobscura*.

Type: No types found; none are mentioned by Dobzhansky and Epling (1944: 7), although "Type locality: Reedsport, Oregon" was reported.

Specimens Examined: 1♂ (ASG36), 1♀ (ASG38): *Drosophila persimilis*, culture 14011-0111.0, DNA seq publ by V. Schawaroch, 2002 [specimens from voucher series].

Distribution: Along the west coast of North America from British Columbia and Vancouver Island in the north to Santa Barbara, California in the south. It prefers wet, cool, coastal

climate in the northern parts of its range, and high elevations in the Cascades and Sierra Nevadas (Dobzhansky and Epling, 1944).

Comments: The figures of the male genitalia by Rizki (1951) show the postgonites as if they were turned laterally (perhaps these spread out under the coverslip); the apices curve dorsally, so in a full ventral view of the genitalia the apical curvature is not seen. Relative lengths of the aedeagus and postgonites are doubtfully a reliable character to separate *D. persimilis* and *D. pseudoobscura*.

Drosophila (*Sophophora*) *pseudoobscura* Frolova

Figures 3C, 8E, 10E

Drosophila pseudoobscura Frolova, in Frolova and Astaurov, 1929: 212.
Drosophila pseudoobscura bogotana Ayala and Dobzhansky, 1974: 216.

Diagnosis: Facial carina broad, edge flat; acrostichal setae in 8 rows; sex comb with usually 6–7 teeth on ta_1 (range of 5–8), usually 5 on ta_2 (range of 4–7); tip of aedeagus extending slightly past tips of closed, folded postgonites (Rizki, 1951) (which may not be a reliable feature). Spermatheca with sleeve extending 0.6× the height of bulb, with apical indentation.

Type: Frolova and Astaurov (1929) did not report any type specimens and no type is known to exist in any North American institution. Type holdings of Diptera in the Zoological Institute of the Russian Academy of Sciences in St. Petersburg are provided online, but no *Drosophila* are listed (ZIN, 2023). Perhaps types are in another Russian institution.

Specimens Examined: 1♂ (ASG35), 1F (ASG34): *Drosophila pseudoobscura* culture 14011-0121.0, DNA seq. publ. by V. Schawaroch, 2002 [specimens from voucher series]. ♀♀.

Distribution: This species has the broadest distribution of all New World species, except perhaps for *D. athabasca*, occurring in North America throughout the Rocky Mountains west to the Pacific coast, from northern British Columbia to western Texas, and throughout Mexico (including Baja California), to northern Honduras. An isolated population that is genetically but not morphologically distinct occurs in northern Colombia, named as subspecies *D. pseudoobscura bogotana* (type in the California Academy of Sciences). The species is very common in western North America; it does not occur in the Great Plains.

Drosophila* (*Sophophora*) *zapoteca, new species

Figures 4D, 8F, 10F, 13E, 16D

Diagnosis: Facial carina thin, small; acrostichals in 6 rows; sex comb with 4–5 teeth on ta_1, 3–4 on ta_2; ♂ ta_1 and ta_2 of approximately equal length. Male genitalia distinctive: cercus with small, nipplelike ventral lobe; outer lobes of ventral epandrial lobe with pointed tips (projecting mediad), plus row of 4 very thick, large setae; surstylus with row of 11 prensisetae; aedeagus and valves much shorter than (0.65× length of) postgonites. Males distinguished externally from the sympatric *D. maya*, which has protarsomere ta_1 approximately 1.5× the length of ta_2.

Description: Coloration: Frons dark brown, frontal vittae flat, blackish; fronto-orbital plates and ocellar triangle lighter, slightly shiny; antennae, face, ventral margin of cheek dark brown (most of cheek light); palps light brown. Scutum and scutellum dark brown, dull, with dusting of pruinescence; postpronotal lobe, notopleural area slightly lighter; anepisternum dark brown, anepimeron and katepisternum same to slightly lighter. Legs light, tan; halter whitish cream; abdomen uniformly brown in both sexes, darker in ♂.

Head: Arista with 3 dorsal, 2 ventral branches, plus terminal fork; pedicel with 1 longer, 2 shorter setae. HD/HW 0.76 (mean of 4♂). Anterior reclinate orbital seta lateral to posterolateral of the proclinate orbital; posterior reclinate nearly equidistant between proclinate and inner vertical setae; proclinate 1.5× length of anterior reclinate, posterior reclinate 2.3× length of anterior reclinate. Ipsilateral vertical setae close; inner vertical in line with proclinate and posterior reclinate, IV/OV 0.88. Ocellar setae sockets on tangent between median and posterolateral ocelli; postocellars long, convergent to tips crossing, length slightly less than ocellars OC/POC 1.07; 4–5 small setulae in ocellar triangle. Frons with 6–7 setulae near anterior margin. FL/LFW 0.87, UFW/LFW 1.56. Face relatively short, FD/FW 1.0, frontal W-index 2.87; carina very small, narrow, short (0.3× length of face), low; vibrissa long, 1st genal seta small, GS1/VL 0.30, gena wit 6–7 setae, increasing in length posteriad. Cheek of moderate depth, ED/CD 7.5. Palp with 1 long apical seta, shorter seta in middle of ventral margin. Eye broadly oval in lateral view, EW/ED 0.78.

Thorax: Length 0.84 mm (mean of 4♂). Acrostichals in 6 rows between anterior dorsocentrals, lengths increasing posteriad; acrostichals in front of scutellum or anterior dorsocentrals not enlarged. Anterior dorsocentrals 0.67× length of posterior ones; distance between ipsilateral dorsocentrals less than that between contralateral ones. Postpronotum with 2 strong setae, equal in length; 2 strong notopleural setae near notopleural suture, plus 1 more dorsally, another postsutural; katepisternum with 2 large setae, posterior one larger (S-index 0.46), sclerite with several small setulae. Anterior scutellar setae slightly convergent, posterior ones convergent to cruciate (up to 0.4× their length), both pairs approximately equal in length. Legs: profemur with ventral row of 5–6 long setae (lengths approximately equal to femur width); mid and hind tibiae with stout, ventroapical setae, thinner dorsal-preapical seta; ♂ protarsus with ta_1 and ta_2 approximately equal length; ta_1 with 4–5 teeth, ta_2 with 3–4; teeth fairly stout, touching, lengths 1.2–1.3× width of tarsomeres. Wing of moderate length and width, ThL/WL 0.40, WL/WW 2.2, C-index 2.54, hb-index 3.16, 4V-index 2.21, 5X-index 2.36.

Abdomen: Male terminalia: epandrium height approximately equal to width; cercus with small, abruptly narrowed, nipplelike ventral lobe bearing small tuft of fine setulae; outer lobes of ventral epandrial lobe with abruptly pointed tips that point inward, plus row of 4 thick, large setae (and 6–7 smaller ones); margin of inner lobe of ventral epandrial lobe well defined from surstylus; surstylus with row of 11 prensisetae; aedeagus and valves much shorter than (0.65× the length of) postgonites; aedeagus with very fine microtrichia. Hypandrium relatively short, length 1.3× the width. Female terminalia: spermatheca short, wide, width 1.7× height; sleeve broad, annulate, extended into capsule 0.8× capsule height, lacks apical indentation. Oviscapt of moderate depth in lateral view, with 12–13 small ovisensilla along margins.

Type: Holotype, ♂: GUATEMALA: Zacapa, 10 km N San Lorenzo, 2200 m., 8-10/XI/86, M. Sharkey, FIT [flight intercept trap]. Dissected by D.G. (no. ASG20). In AMNH.

Etymology: Taken from the Zapotec, a people who lived 700 BCE–1521 CE, in the Valley of Oaxaca, southern Mexico, and well known for their elaborate ceramic figures.

Specimens Examined: Series of 9♂♂ and 6♀♀ (all paratypes) with same data as holotype, in AMNH. Dissections: ♀♀: ASG 03, ASG21; ♂♂: ASG 01, 20, 42, 43, 44, 45, 46.

Distribution: Known thus far only from the type locality in Guatemala.

Comments: Despite the obviously different spermathecae and male genitalia, there are very few external differences in body and setal proportions between the two species: D. *zaptoca* is only about 90% the size of *D. maya* and it has a slightly deeper cheek (ED/CD 7.5, vs. 9.6 in *D. maya*), and smaller genal seta-1 (vibrissa-index 0.30, vs. 0.52 in D. *maya*).

Obscura Subgroup

Drosophila (*Sophophora*) *frolovae* Wheeler

Drosophila frolovae Wheeler, 1949: 175.

Diagnosis: Unique among *obscura*-group species in the Americas for the large male sex combs on both basal protarsomeres: ta_1 with 14–16 teeth and ta_2 with 10–11. Also distinctive for the 8 rows of acrostichals, which occur in four New World species in the *D. pseudoobscura* subgroup.

Types: Holotype, ♂: 19 mi E Morelia, Michoacan de Ocampo, Mexico, F.A. Cowan, M.R. Wheeler, 8-30-47. In USNM.

Specimens Examined**:** Only the holotype, not dissected.

Comments: Wheeler (1949: 176) mentioned 2 males and "an unknown number of females" were collected "in a forest high in the mountains," but I am unaware of any specimens of this species other than the holotype. The acrostichal rows and large combs on both tarsomeres strongly suggests this species is more closely related to Old World species of the *obscura* subgroup, but confirming this will need to await the discovery of more characters and specimens.

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rare and interesting specimens reported here. Three colleagues at the AMNH checked historical records for Sturtevant's types: Melody Doering and Christine Lebeau in the Division of Invertebrate Zoology, who pored over the old card catalog of the former Department of Insects and Spiders; and Rebecca Morgan, AMNH Archivist, who consulted the Sturtevant and Dobzhansky correspondence. Vinton Thompson, AMNH, alerted me to the breeding record from spittlebugs, provided the references and additional observations. Lubomir Masner, now retired from the CNC in Ottawa, donated MT/FIT samples years ago, one of which contained specimens reported here. Specimens from the Zurquí site in Costa Rica came from the ZADBI project, spearheaded by Brian Brown and Art Borkent and funded by NSF grant DEB 1145890. Steve Gaimari and Tom Werner provided very helpful reviews, corrections, and commentary on the manuscript.

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