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Genus *Flexamia*: new species, phylogeny, and ecology

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GENUS *FLEXAMIA*: NEW SPECIES, PHYLOGENY, AND ECOLOGY

Robert F. Whitcomb[1] and Andrew L. Hicks[1]

ABSTRACT.—Eight new species of *Flexamia* DeLong are described, and two Mexican species previously synonymized are reinstated. Species are assigned to 13 species groups; keys are presented for the groups and for the 44 recognized species. Host data, in many cases with oligophagy coefficients, are presented for 37 of the species. Many species specialize on native, dominant, perennial, choridoid or panicoid grasses; some are monophagous. Seven sister species pairs specialize on the same (or a closely related) grass species; in addition, four closely related species appear to be restricted to *Bouteloua curtipendula*. Few if any specialists colonize their host throughout its entire range. Ecological factors such as phenology and/or host patchiness strongly influence geographic distribution. An intuitive phylogeny is proposed and is used as a basis for constructing 18 character transformations. The genus *Flexamia* probably originated in Mexico by division of an ancestral lineage from which the modern genus *Spartopyge* also diverged.

The first specimen of the genus *Flexamia* DeLong was apparently collected at Jacksonville, Florida, in the height of the Linnaean explosion; it was deposited in the British Museum (Natural History) and named *Jassus productus* by Walker (1851). In their studies of Iowa prairies in the latter part of the nineteenth century, Osborn and Ball encountered other species, which they referred to the genus *Deltocephalus*. DeLong (1926) erected a subgenus *Flexamia* DeLong within *Deltocephalus* Burmeister. DeLong and Sleesman (1929) recognized that *Deltocephalus* was an unworkably large assemblage of distantly related species and divided the genus into several genera (e.g., *Laevicephalus* DeLong & Sleesman, *Polyamia* DeLong & Sleesman, and *Flexamia*). The genus concept for *Flexamia* was refined by Oman (1949) in his revision of North American cicadellid genera, but the modern generic concept was established by Young and Beirne (1958). These authors segregated *Spartopyge* Young & Beirne, synonymized *Secopennis* Oman, described genitalic characters of males and females (the first use of genitalic characters for *Flexamia* females), and presented a species key. The 30 species they described included all of the widely distributed and commonly collected representatives of the genus, and their key proved to be accurate and easy to use. Young and Beirne also described possible relationships among species

and, without specifying an explicit phylogeny, proposed broad outlines of hypothetical evolutionary events in the genus. The genus was incorrectly synonymized with *Acurhinus* Osborn by Linnavuori (1959). Comparison of the specimens (all females) of *Acurhinus* (= *Dorydium*) *maculatum* Osborn in the Ohio State University collection led Linnavuori and DeLong (1978) to synonymize *Acurhinus* with the African stirelline genus *Hododoecus* Jacoli. The genus *Flexamia* as defined herein is an entirely North American taxon related to *Spartopyge*, to *Alapus* DeLong & Sleesman, and, perhaps distantly, to *Aflexia* Oman. The closest Old World relative may be *Enantiocephalus* Haupt.

Although the taxonomic status of *Flexamia* has been generally adequate since 1958, host data have been difficult to obtain. Earlier collectors were not knowledgeable agrostologists and often reported only that deltocephaline species, including *Flexamia*, resided on "grasses." Astute collectors such as Osborn and Ball recognized the importance of biological data, and their notes contain some host records. In 1967, H. H. Ross encouraged the senior author to ascertain the hosts of *Flexamia* species, in large part to test his intuitive belief that host relationships, especially host transfers, could be invoked to explain speciation of phytophagous insects. Accordingly, we sought to determine hosts of the species described by Young and Beirne. Much to our
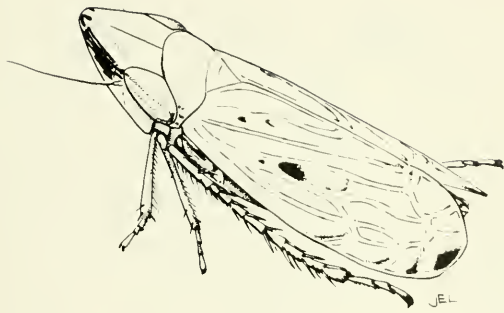
Fig. 1. *Flexamia serrata.*

surprise, in the course of this search, unde-
scribed species emerged, particularly when
we examined dominant, perennial *Muhlen-
bergia* or *Bouteloua* species (Whitcomb et al.
1986, 1987). Under these circumstances, it
seems appropriate to review the species con-
cept and to emend the generic concept,
which, although basically intact in its essential
aspects, must accommodate the new species.

Genus *Flexamia* DeLong

Deltocephalus subgenus *Flexamia* DeLong 1926:20, 22.
      Type species: *Deltocephalus reflexus* Osborn &
      Ball 1897, by original designation.
Flexamius, DeLong and Sleesman 1929:82.
Flexamius subgenus *Secopennis* DeLong & Sleesman
      1929:85. Type species: *Deltocephalus slossoni*
      Ball.
Acurhinus Osborn, Linnavuori 1959:89.
Flexamia DeLong, Young and Beirne 1958; Linnavuori
      and DeLong 1978:208.

Small deltocephaline leafhoppers. Length
of male 2.4–5.0 mm, of female 2.6–5.0 mm.
Head produced, median length of crown usu-
ally greater than interocular width; clypellus
broader at base than at apex; forewing with
reflexed veinlets to costal margin in vicinity of
small, outer anteapical cell.

Dried specimens yellowish brown or gray,
with ferruginous to black markings; live in-
sects in some cases with green pigmentation
changing to orange or stramineous when
dried. Apical area of crown partly or com-
pletely surrounded by darker markings, in
latter case with clearly defined, apical areolet.
Crown often with pair of oblique, dark mark-
ings at base; pair of transverse, dark markings
at about midlength; pair of darker markings
parallel to lateral margins near apex. Face
color varying from pale to black, often useful

in species discrimination. Pronotum of some
species with conspicuous, longitudinal
stripes, but many species with faint, wider
stripes. Veins of forewings usually dark-mar-
gined; distinct, dark-margined areole fre-
quently near center of corium.

MALE.—Plates usually shorter than pygo-
fer, frequently fused along mesal margins;
pygofer usually with pronounced posterior
lobe in lateral aspect; style with longitudinally
grooved, preapical lobe, which is usually not
pronounced; connective linear, arms contigu-
ous basally, sometimes fused to aedeagus.
Connective with upper portion less heavily
sclerotized than lower portion, often thinner
and extended dorsad in thin keel that varies in
width interspecifically; dorsal aedeagal apo-
deme with pair of conspicuous appendages
directed caudoventrad or caudad. Aedeagus
interspecifically variable, of great value in
species discrimination.

FEMALE.—Sternum VII nearly always
longer than VI, often 2X or more; hind margin
with 2–4 teeth and usually small, median
notch. Pygofer with well-dispersed setae;
ovipositor barely reaching pygofer apex.

Flexamia Species Groups

In the following discussion, we describe 13
species groups and provide keys to species.
We describe 8 new species and reinstate 2
species previously synonymized. We also re-
view important characteristics of previously
described species, emphasizing diagnostic
morphology, ecology, and biogeography. Our
brief descriptions of previously described spe-
cies complement the descriptions of Young
and Beirne (1958).

Key to *Flexamia* Species Groups

1.   Dorsum with pair of stripes extending from hind
      portion of disc of crown across pronotum and
      scutellum (Figs. 2A–D) 2
—   Dorsum without such stripes (Figs. 2E,F) 4
2(1). Individuals large, at least 4.5 mm . . . .
      . . . . IV. *grammica* group
—   Individuals smaller 3
3(2). Forewing broadly truncate (Fig. 2D); Arizona
      . . . . VIII. *ritana* group
—   Forewing obliquely truncate (Fig. 2B) or not
      truncate (Fig. 2A) (prairie); Florida . . . .
      . . . . VII. *albida* group
4(1). Face entirely black, genae at most with oblique,
      pale streak; crown without midlength transverse
      lines 5
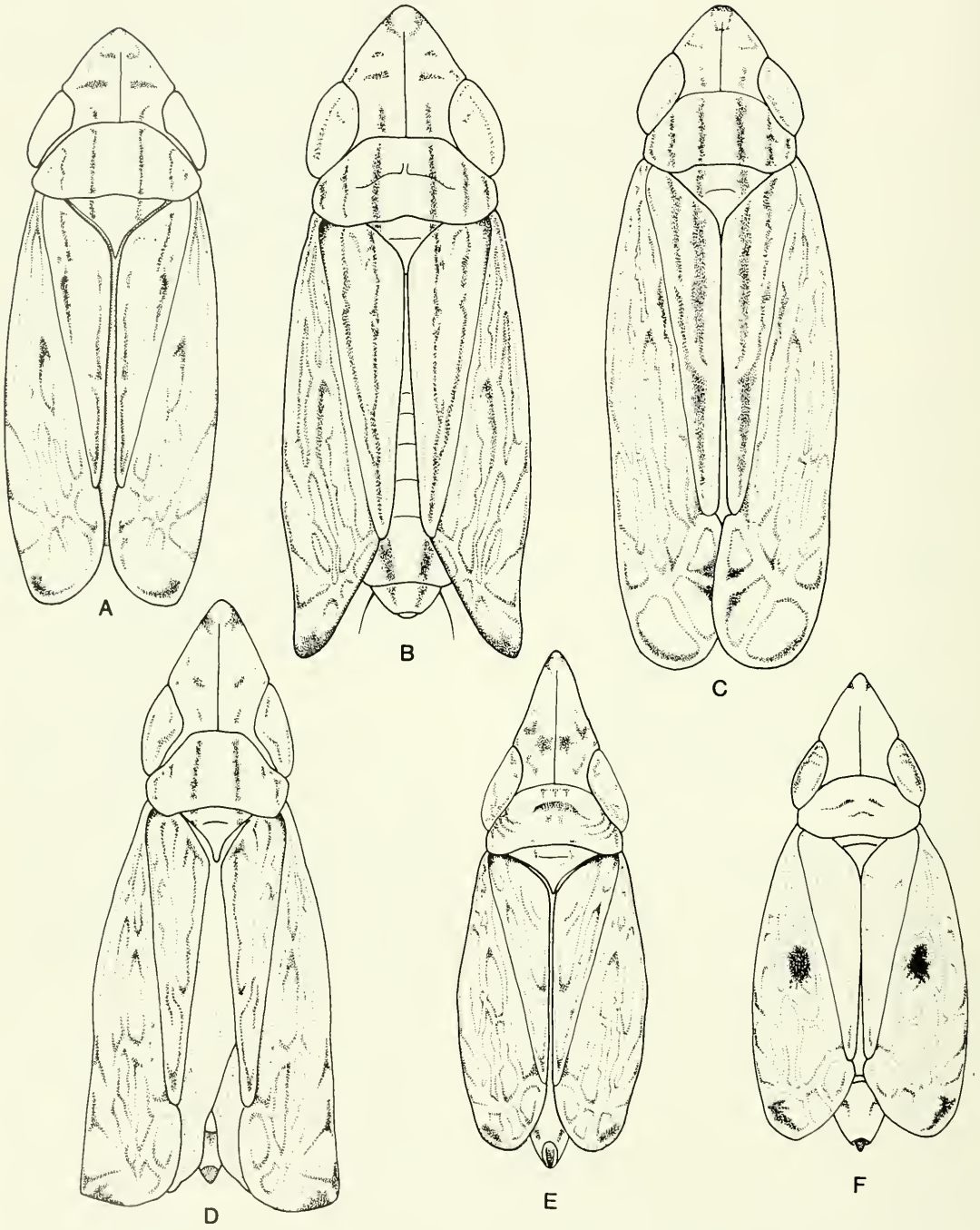
Fig. 2. Habitus of *Flexamia* species: A, *albida*; B, *slossonae*; C, *grammica*; D, *ritana*; E, *pyrops*; F, *areolata*.
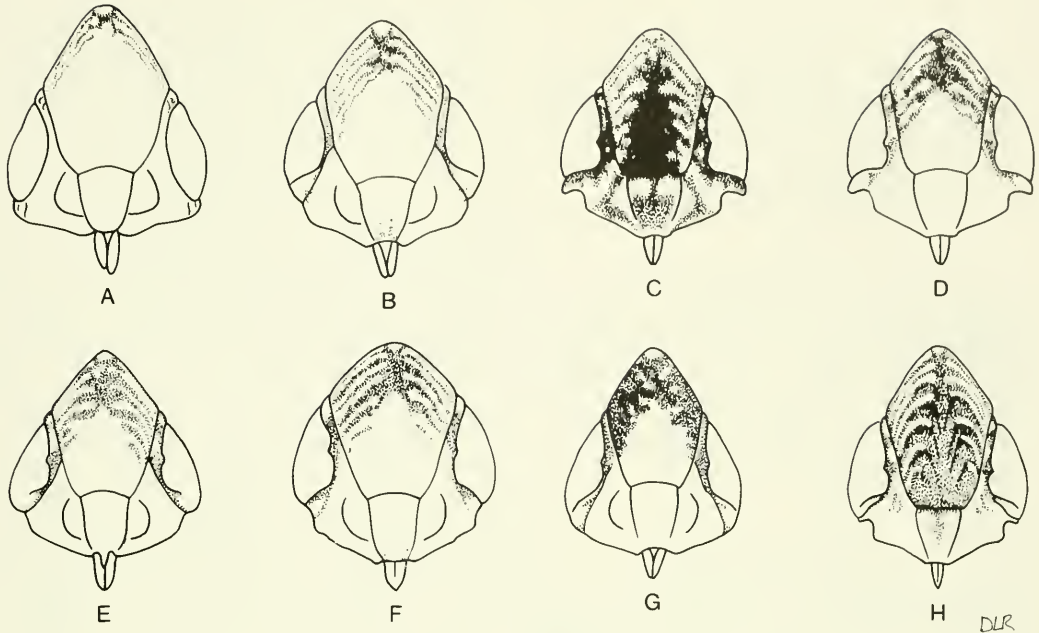
Fig. 3. Faces of *Flexamia* species: A, *serrata*; B, *stylata*; C, *prairiana*; D, *prairiana*; E, *picta*; F, *decora*; G, *flexulosa*; H, *sandersi*.

—	Face black basally, pale apically, or brownish in part; at least genae pale, crown usually with midlength transverse lines 6
5(4).	Forewing with conspicuous black spot (Fig. 2F) in corium; crown with median length more than one-half greater than interocular width .... XII. *areolata* group
—	Forewing without conspicuous black spot in corium; crown with median length less than one-half greater than interocular width .... XI. *imputans* group
6(4).	Face pale with several narrow, parallel, fuscous, interocular lines interrupted at middle (Fig. 3A); northwestern (Fig. 30) .... XI. *serrata* group
—	Face with (Figs. 3B, D–G) or without (Figs. 3C, H) interocular lines but not as above 7
7(6).	Either with crown more than twice interocular width (Fig. 2E) (*pyrops* Crumb), or with conspicuous, dark, apical wing blotch (Fig. 4C) *and* sordid yellow face with black interocular band (*picta* [Osborn]); viewed laterally, male pygofer with conspicuous, acutely angulate, ventral lobe (Figs. 5A,B); aedeagus (Fig. 6D) with pair of anteapical processes and apical, flangelike processes .... VI. *picta* group
	Habitus not as above; male pygofer with posterior lobe rounded ventrally; aedeagus not as above 8
8(7).	Males 9
—	Females 14
9(8).	Aedeagus and connective fused (Figs. 6F,G) .... XIII. *prairiana* group

|		
—	Aedeagus and connective distinctly articulated (Figs. 6A–C, E)	10
10(9).	Aedeagus without apical processes (Fig. 6C)	11
—	Aedeagus with (at least minute) apical ...... processes	12
11(10).	Male plates broad, not tapered (Figs. 11A–I) .... I. *pectinata* group	
—	Male plates more elongate and tapered (Figs. 9C,F) .... III. *zacate* group	
12(10).	Aedeagus (Figs. 7F,G) with 2 pairs of processes .... V. *curvata* group	
—	Aedeagus not so	13
13(12).	Aedeagus with 2 processes on shaft (Fig. 7H) .... II. *abbreviata* group	
—	Aedeagus with 3 processes on shaft (Figs. 6E, 31A, D–M) .... X. *flexulosa* group	
14(8).	Face white, ivory, or very pale yellow, sharply contrasting with black interocular line (Figs. 3B,F,G) ..... X. *flexulosa* group (in part)	
—	Face with lower part not white or pale (Fig. 3H), or if pale, not contrasting sharply with interocular band, or interocular band brown, not black (Fig. 3D)	15
15(14).	Body color stramineous	16
—	Body color not stramineous	17
16(15).	Hind margin of sternum VII with medial projection (Fig. 10O)........................ ....X. *flexulosa* group (*inflata* subgroup)	
—	Hind margin of sternum VII without projection	20
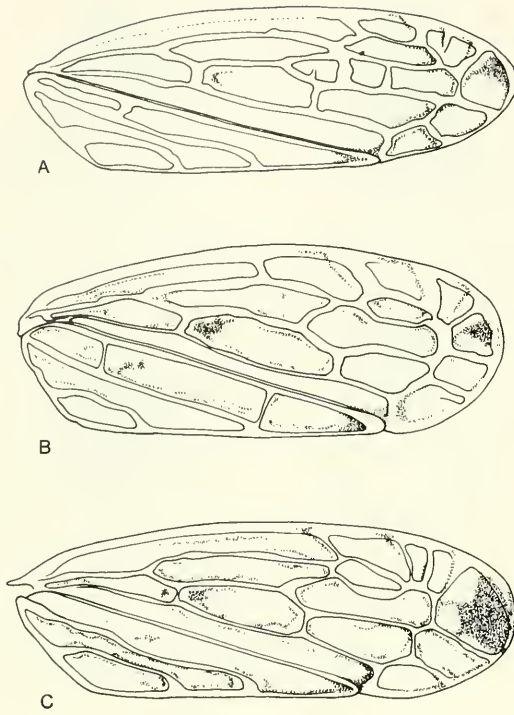
Fig. 4. Wings of *Flexamia* species: A, *inflata*; B, *curvata*; C, *picta*.

17(15). Sternum VII (Fig. 10E) with median, trape-
zoidal projection, with a medial notch, usu-
ally with smaller, shallower notches on either
side . . . . II. *abbreviata* group

— Sternum VII not as above 18

18(17). Sternum VII produced medially in a distinct
lobe or projection (Figs. 10S,T) . . . .
. . . . XIII. *prairiana* group

— Sternum VII not produced medially in dis-
tinct lobe, or if produced, with deep, median
incision 19

19(18). Hind margin of sternum VII incised to form
pattern of four teeth; hind margin usually
heavily infuscated on hind margin in vicinity
of teeth (Figs. 14A–H) . . . . . I. *pectinata* group

— Hind margin of sternum VII not so 20

20(19). Hind margin of sternum VII slightly concave
on each side of median excision; infuscated
notches usually contrasting sharply with
stramineous color of sternum (Figs. 10J,K)
. . . . V. *curvata* group

— Hind margin of sternum VII not so (Figs.
10I,L) . . . . III. *zacate* group

I. The *pectinata* Group

The greatest proposed changes in *Flexamia*

species concepts are in the *pectinata* species
group to which we add five new species and
reinstate two others. All species of the group
have aedeagal shafts without apical processes.
Although aedeagal characters are not as useful
for species discrimination in this group as in
other groups, the male plates and female ster-
num VII provide useful apomorphies that de-
fine the group. The plates (except in *collo-
rum*) are broad and basally parallel-sided. The
hind margins of the female sternum VII of all
species possess four medial teeth with sur-
rounding infuscation (but note the extensive
modification in *mescalero* [Fig. 21H]). The
size and shape of the teeth vary interspecifi-
cally. The species are largely southwestern
and/or Mexican, and many appear to have
small ranges. The nominate species *F. pecti-
nata*, however, has a wide geographic range.
As defined by Young and Beirne (1958), this
species ranges from western Mexico (*zamora*
DeLong & Hershberger) through the eastern
highlands (Valles and Monterrey [*minima*
DeLong & Hershberger]), the Davis Moun-
tains of west Texas, Otero and Guadalupe
counties of New Mexico north to North Da-
kota, and as far east as Akron, Ohio, in the
prairie peninsula. However, our studies indi-
cate that *zamora* and *minima* should be rein-
stated. Recognition herein of the new species
bandarita, *gila*, *collorum*, *jacala*, and *mesca-
lero* makes it clear that this group is diverse
and has speciated frequently. The host of
pectinata is side-oats grama (*Bouteloua cur-
tipendula*), a widespread prairie species. In
addition to *pectinata*, there are three south-
western side-oats grama specialists of the
pectinata group. *Flexamia doeringae* and *F.
gila* reside in the southeastern Arizona moun-
tains and Mogollon Rim region and extended
conifer-oak savanna of Mexico, respectively.
Flexamia bandarita, as far as known, is con-
fined to the Chisos Mountains and Marathon
Basin of Trans-Pecos Texas. We suspect that
side-oats grama, which also has a wide range
in Mexico, will prove to be the host of some
Mexican species of the *pectinata* group. The
most distinctive species of the group (*mesca-
lero*), however, appears to specialize on *Muh-
lenbergia pauciflora*.

Several factors may account for speciation
in the *pectinata* group. Side-oats grama is it-
self a complex of ecotypes that vary greatly in
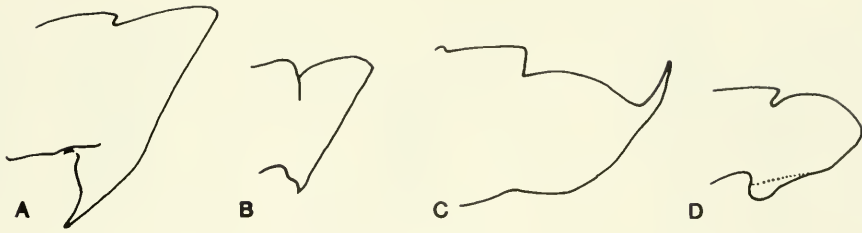structure and seasonality (Gould 1979). This

Fig. 5. Pygofers of *Flexamia* species: A, *picta*; B, *pyrops*; C, *stylata*; D, *producta*. Redrawn from Young and Beirne (1958).
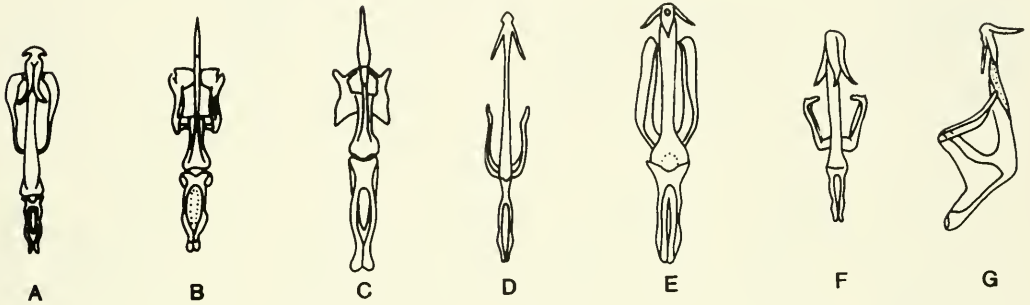

Fig. 6. Aedeagus and connective of *Flexamia* species: A, *curvata*; B, *abbreviata*; C, *canyonensis*; D, *picta*; E, *flexulosa*; F, *prairiana*; G, *graminea*. Redrawn from Young and Beirne (1958). Aspects: A-F, caudoventral; G, lateral.

chloridoid grass crosses many biome lines and is a dominant in mesic Sonoran and Chihuahuan grasslands and in montane systems within these semiarid grasslands. It is common through much of the prairie and occurs eastward on nonforested slopes in the Appalachian mountains. Like other major dominants of North American grasslands, therefore, side-oats grama has a much wider geographic range than any of the cicadellid species that exploit it.

The Chihuahuan desert system presents a major barrier to geographical continuity of prairie grasses, and side-oats grama is no exception. Many prairie cicadellid taxa occur west of this desert system, but, depending upon the case, the taxonomic results vary. For example, populations related to the buffalo-grass specialist *Athysanella* (*Gladionura*) *emarginata* occur in disjunct stands of *Buchloë* in New Mexico's Hidalgo County. This population, until very recently, had been regarded as a subspecies (*sobrina*) but will be elevated to a species in a forthcoming revision

of *Gladionura* (H. D. Blocker, personal communication). On the other hand, forms of *A.* (*Gladionura*) *argenteola* (a *Bouteloua gracilis* specialist) in southeastern Arizona are not distinguishable from short-grass prairie forms. The connecting link between the relatively mesic, temperate grasslands of the northern Mexican highlands and the prairie is tenuous at best, consisting of a small set of "stepping stone" montane islands within the Chihuahuan desert of Coahuila and Chihuahua, or of the relatively narrow grassland periphery surrounding the desert on the east and west and meeting at the south in the state of San Luis Potosí. Also, the mesquite-acacia savanna and Trans-Pecos shrub savanna of Texas are further barriers to geographic continuity of *B. curtipendula*. During full glaciations, these arid regions had climates that were much more moist than they are today (Van Devender and Burgess 1985).

One of the new species, *collorum,* from the Edwards Plateau of central Texas, is apparently a specialist on Nealley grama, *Bouteloua*
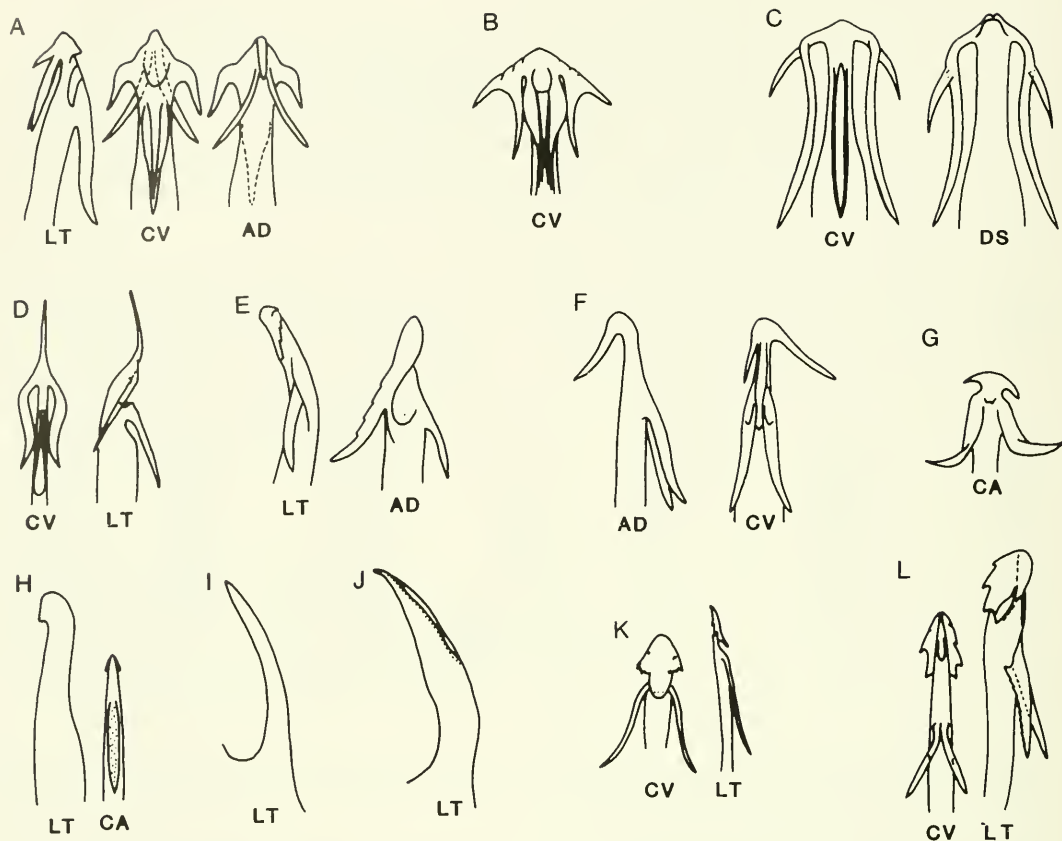
Fig. 7. Aedeagal apices of *Flexamia* species: A, *serrata*; B, *albida*; C, *slossonae*; D, *ritana*; E, *grammica*; F, *curvata*; G, *surcula*; H, *abbreviata*; I, *zacate*; J, *canyonensis*; K, *picta*; L, *pyrops*. Aspects: AD, anterodorsal; CA, caudal; CV, caudoventral; DS, dorsal; LT, lateral. Redrawn from Young and Beirne (1958).

uniflora. Flexamia collorum may be related to another new species, *jacala*, whose type locality in Mexico is close to the intersection of eastern and western montane Mexican grasslands. The latter species is represented by a single male specimen from the USNM, so nothing is known about its biology.

Finally, another new species, *mescalero*, discovered in a single location in southeastern New Mexico, presumably arose by host transfer to New Mexican muhly, *Muhlenbergia pauciflora.*

Description of the *pectinata* Group

Medium-sized to small deltocephaline leafhoppers. Length of ♂ 2.7–3.8 mm, of ♀ 2.8–4.2 mm. Species with general facies of genus; brown or in dark specimens, almost black. Crown variably produced. [♂] Plates (Figs. 11A–I) elongate, broad, parallel-sided basally (except *collorum*). Pygofer with distinct, posterior lobe, strongly constricted in lateral aspect, both dorsally and ventrally. Aedeagus and connective distinctly articulated. Aedeagus (Figs. 12A–I) with no apical processes, or at most slightly capitate (*mescalero*), often appearing flared in dorsal aspect. [Note: Caution must be exercised when using the aedeagal apex as a diagnostic character, since this structure is membranous and is subject to tearing and breaking during copulation or preparation of the specimen.] Styles variable interspecifically (Figs. 13A–I). Gonopore subapical on caudoventral surface. [♀] Sternum VII (Figs. 14A–H) with four medial teeth on hind margin; teeth varying interspecifically in length and shape, surrounded by infuscated region.
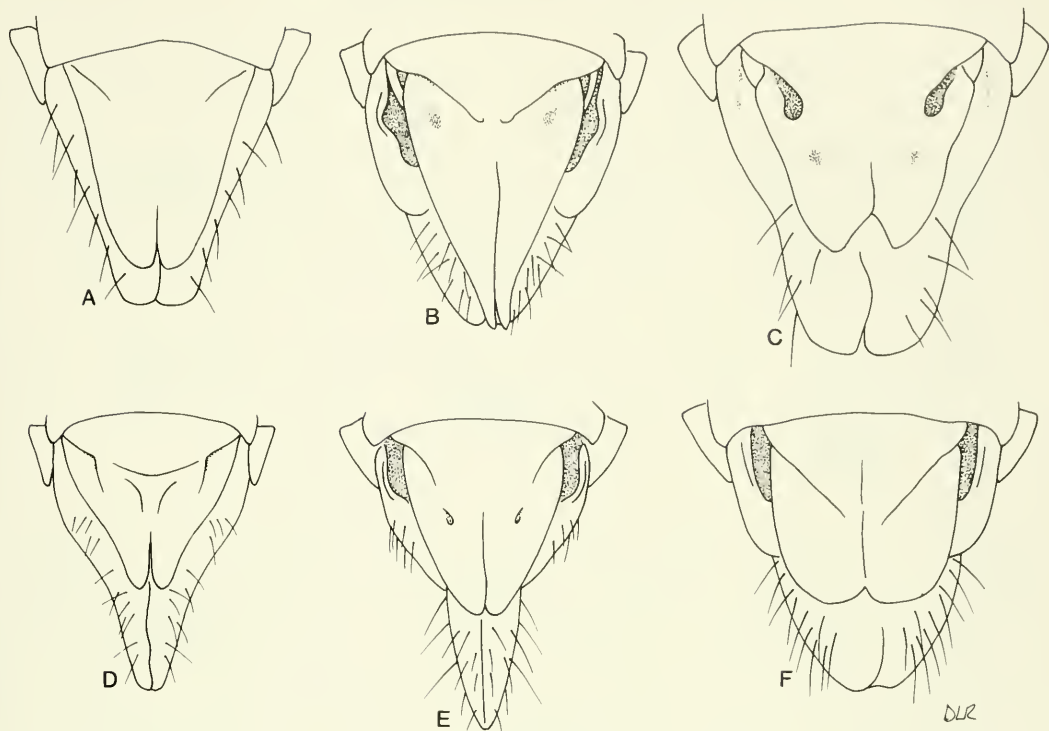
Fig. 8. Male plates and pygofers of *Flexamia* species: A, *albida*; B, *slossonae*; C, *serrata*; D, *ritana*; E, *abbreviata*; F, *grammica*.
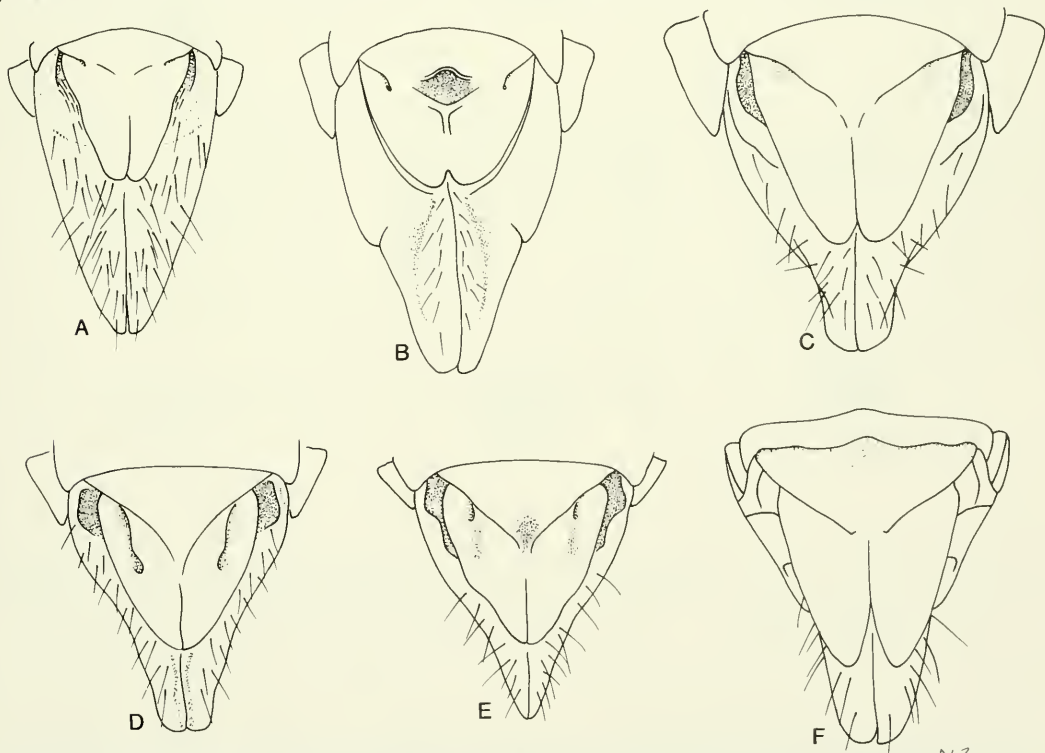

Fig. 9. Male plates and pygofers of *Flexamia* species: A, *picta*; B, *pyrops*; C, *canyonensis*; D, *curvata*; E, *surcula*; F, *zacate*.
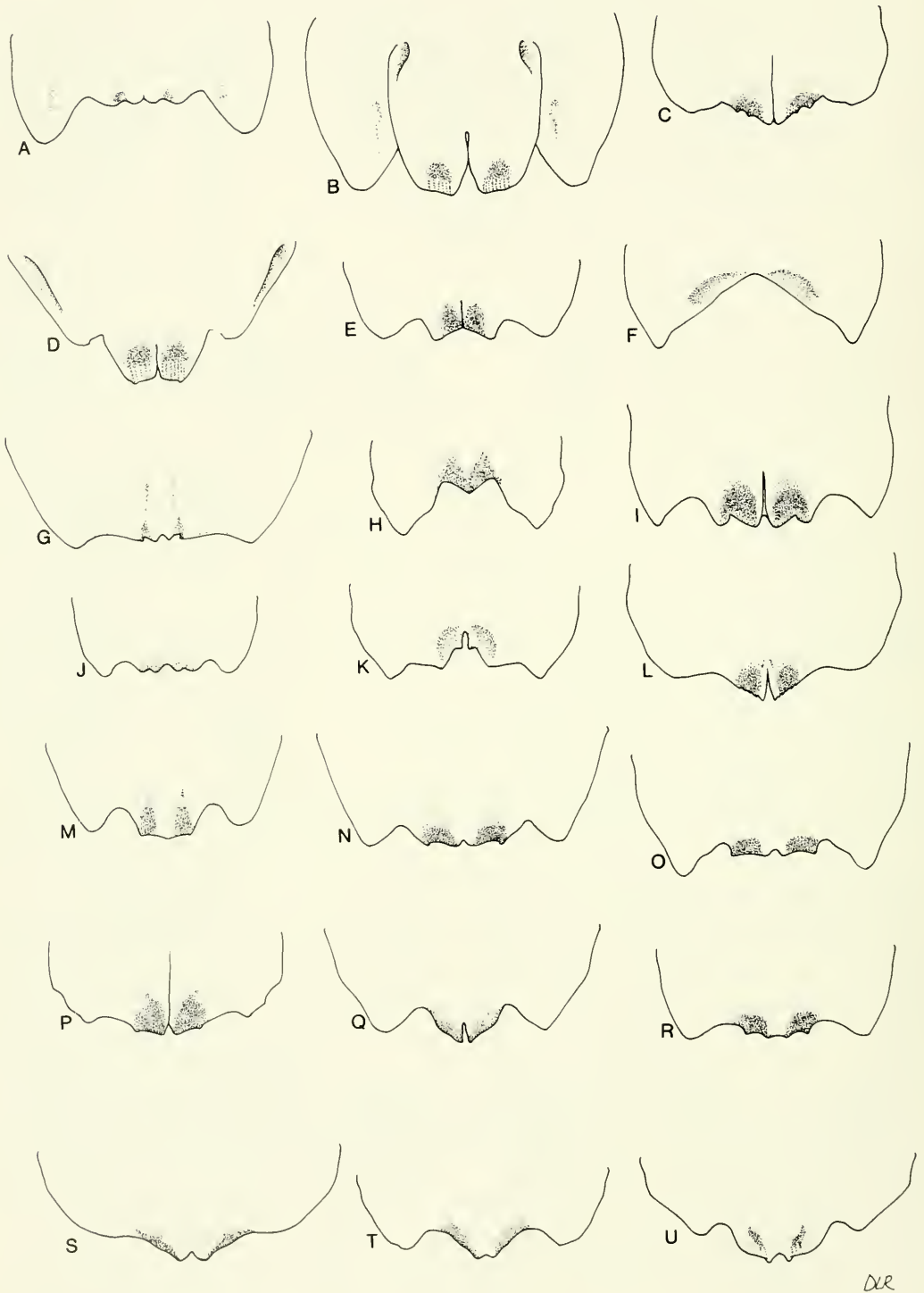
Fig. 10. Female sternum VII of *Flexamia* species: A, *albida*; B, *slossonae*; C, *serrata*; D, *ritana*; E, *abbreviata*; F, *grammica*; G, *picta*; H, *pyrops*; I, *canyonensis*; J, *surcula*; K, *curvata*; L, *zacate*; M, *flexulosa*; N, *decora*; O, *inflata*; P, *imputans*; Q, *areolata*; R, *stylata*; S, *prairiana*; T, *sandersi*; U, *graminea*.
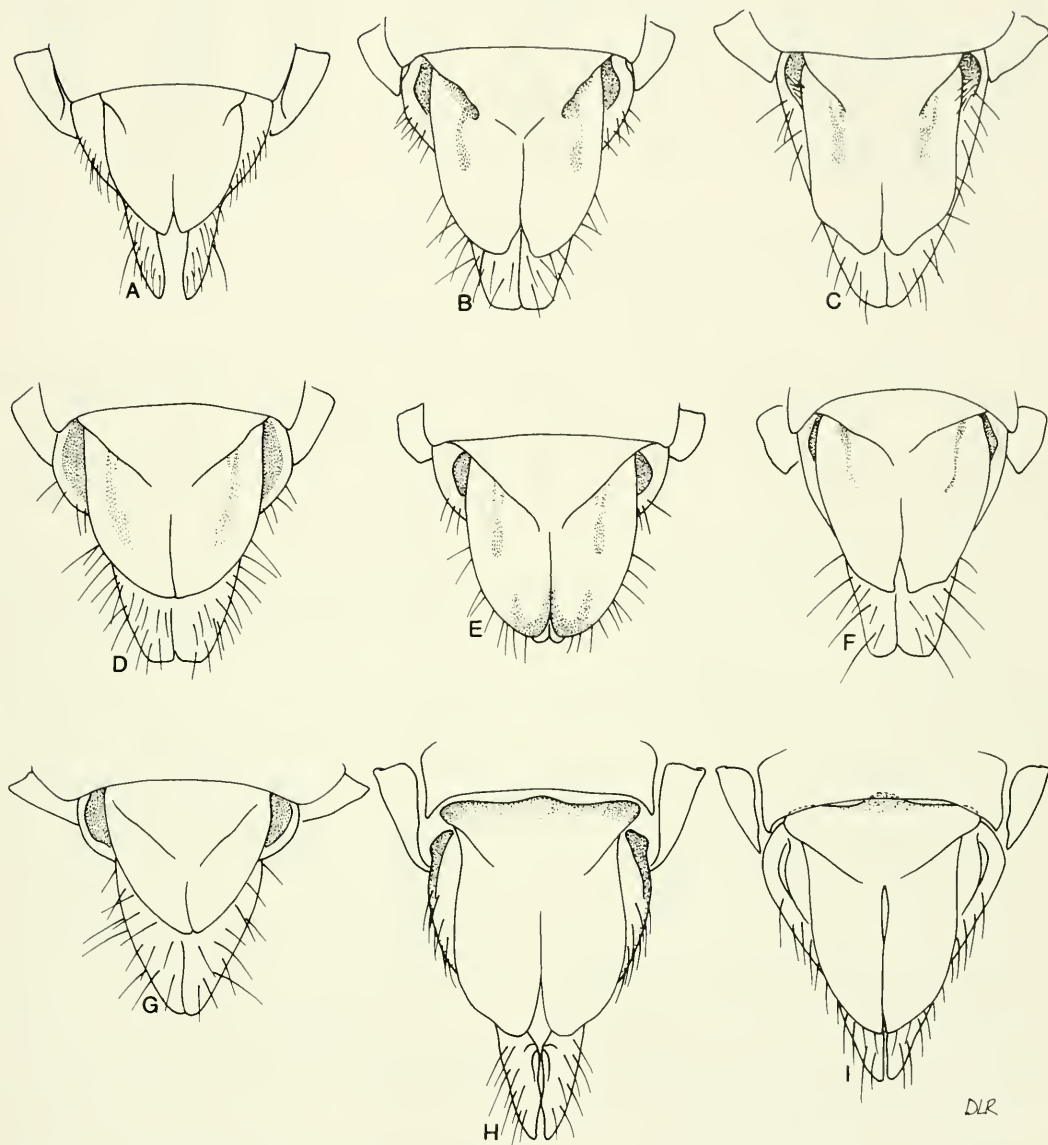
Fig. 11. Male plates and pygofers of *Flexamia pectinata* group, ventral aspect: A, *minima*; B, *zamora*; C, *pectinata*; D, *bandarita*; E, *gila*; F, *doeringae*; G, *collorum*; H, *jacala*; I, *mescalero*.
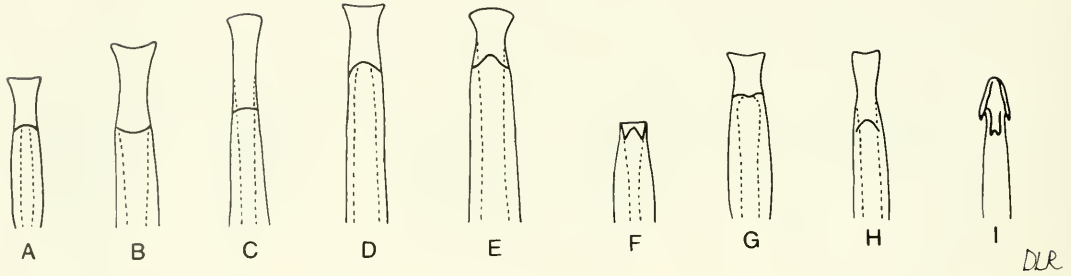
Fig. 12. Aedeagal apices of *Flexamia pectinata* group, caudoventral aspect: A, *minima*; B, *zamora*; C, *pectinata*; D, *bandarita*; E, *gila*; F, *doeringae*; G, *collorum*; H, *jacala*; 1, *mescalero*.

Key to Males of the *pectinata* Group

1. Plates long and parallel-sided at bases 2
— Plates short, not parallel-sided . . . .
. . . .*collorum* Whitcomb & Hicks

2(1). Plates subrectangular (Figs. 11C,F) 3
— Plates with apices rounded 4

3(2). Aedeagus in ventral aspect (Fig. 12F) with pro-
tuberance close to tip; face pale; Arizona . . . . .
. . . . *doeringae* Beamer & Tuthill
— Aedeagus in ventral aspect with protuberance
considerably removed from tip (Fig. 12C); face
brown; prairie . . . . *pectinata* (Osborn & Ball)

4(2). Plates (Fig. 11A) with apices acute; Mexico . . .
. . . .*minima* DeLong & Hershberger
— Plates with apices not acute 5

5(4). Plates almost as long as pygofer (Fig. 11E) . . . .
. . . .*gila*, n. sp.
— Plates no more than 3/4 length of pygofer 6

6(5). Aedeagus expanded apically in ventral aspect,
appearing bluntly saggitate (Figs. 121, 22) . . . .
. . . .*mescalero*, n. sp.
— Aedeagus not expanded apically 7

7(6). Style apex (Fig. 13H) avicephaliform in lateral
aspect . . . .*jacala*, n. sp.
— Style apex not avicephaliform 8

8(7). Style apex (Fig. 13D) ventrally directed, chelate
. . . . *bandarita*, n. sp.
— Style apex (Fig. 13B) not chelate . . . .
. . . .*zamora* DeLong & Hershberger

Key to Females of the *pectinata* Group

1. Sternum VII with 4 teeth of approximately equal
length and 3 relatively shallow incisions 2
— Sternum VII with deep incisions and/or teeth of
different length 4

2(1). Sternum VII with infuscations on either side of
middle incision (Fig. 14G); Texas, host *Boute-
loua uniflora* . . . . *collorum*, n. sp.
— Sternum VII not as above 3

3(2). Sternum VII with heavy infuscation around

teeth on hind margin (Fig. 14C); USA, prairie
. . . . *pectinata* (Osborn & Ball)
— Sternum VII with light infuscation on hind mar-
gin (Fig. 14A); Mexico . . . .
. . . .*minima* DeLong & Hershberger

4(1). Sternum VII with outer teeth longer than inner
teeth 5
— Sternum VII with inner teeth longer than outer
teeth 6

5(4). Sternum VII with outer teeth sharply pointed,
median incision shallow (Fig. 14B); Mexico . . .
. . . .*zamora* DeLong & Hershberger
— Sternum VII with outer teeth blunt, median
incision deep (Fig. 14H) . . . . *mescalero*, n. sp.

6(4). Inner teeth of sternum VII together forming
blunt, median projection (Fig. 14F) . . . .
. . . . *doeringae* Beamer & Tuthill
— Inner teeth of sternum VII separated, acute at
tip, separated by tapered incision 7

7(6). Sternum VII with three incisions of equal depth
(Fig. 14E) . . . . *gila*, n. sp.
— Sternum VII with median incision deeper than
lateral incisions (Fig. 14D) . . . . . *bandarita*, n. sp.

1. *Flexamia minima* DeLong & Hershberger, n. stat.

Flexamia minima DeLong & Hershberger 1947: 138.
Flexamia pectinata, Young & Beirne 1958: 46. (In part.)

Length of ♂ 2.9 (2.8–2.9) mm, ♀ 3.0 (2.7–3.2) mm; head width of ♂ 0.84 mm, ♀ 0.92 mm. Crown produced; median length of crown 0.74 x head width and 1.45 x interocular width (♂ n = 6; ♀ n = 3). Crown light brown to pale yellow with dark, circular spot around apex, pair of broken, transverse lines at midlength, two oblique markings at rear, appearing continuous with the medial pair of six pale brown, pronotal stripes. Face with broad, dark brown, interocular band, fading to pale yellowish. Brown basally, disc and
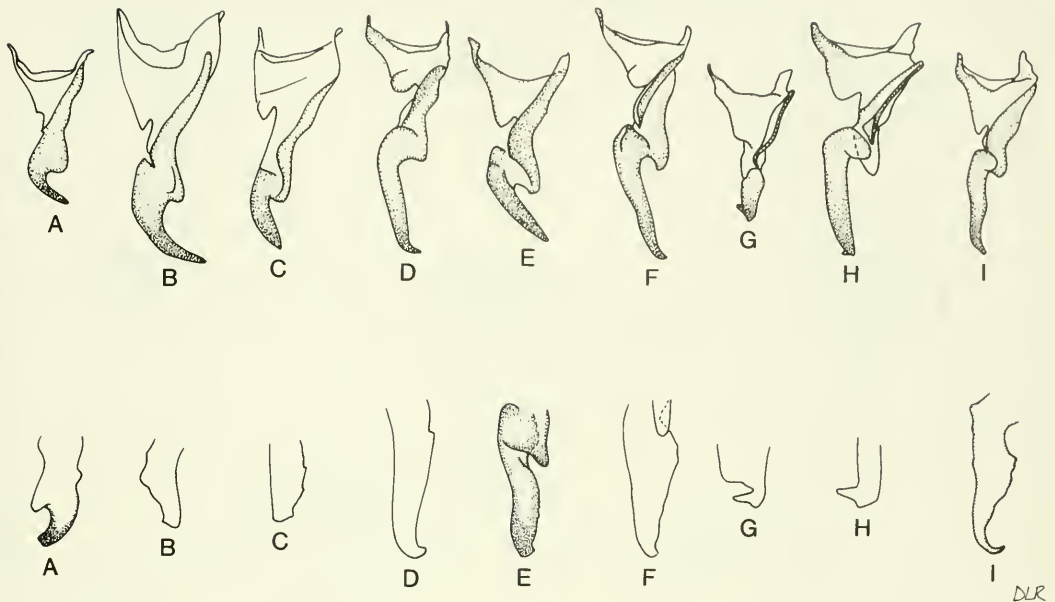
Fig. 13. Styles and style tips of *Flexamia pectinata* group: A, *minima*; B, *zamora*; C, *pectinata*; D, *bandarita*; E, *gila*; F, *doeringae*; G, *collorum*; H, *jacala*; I, *mescalero*.

apex of forewings usually with irregular, dark spot.

MALE.—Pygofer much like that of *pectinata* but shorter; plates (Fig. 11A) barely exceeding ventral lobe in lateral view or 2/3 length of pygofer, unevenly tapering to blunt apices. Genitalia similar to those of *pectinata* and *zamora*, but little more than half their size. In ventral aspect, apex of style not exceeding plane of well-developed, preapical lobe, angle formed between preapical lobe and style apex more acute than in *pectinata*. Connective similar to that of *pectinata*, but with a narrower, deeper, U-shaped incision at the joint with the aedeagus. Other characters as in *pectinata*.

FEMALE.—Sternum VII with posterior margin broadly, shallowly emarginate, hind margin with four teeth of approximately equal length (Fig. 14A), lightly infuscated. Ovipositor with bases of first valvulae as in *zamora*.

TYPES.—Holotype ♂: Valles, San Luis Potosí, Mexico, 1 December 1938, J. S. Caldwell.

REMARKS.—An additional series of *minima*, collected by E. D. Ball at Monterrey, Nuevo León (5♂, 3♀, 11 August 1936, USNM), has

been examined. On the basis of characters of the male plates, the styles, and the distinctiveness of the female sternum VII from that of *zamora*, we reinstate *minima*. Species problems in this group are discussed under "Species Concept." This species, like *zamora*, may be entirely Mexican in distribution and is represented by the two collections discussed above (Fig. 15). The host or hosts are unknown, but the closely related *pectinata* specializes on *Bouteloua curtipendula*. The grasslands of San Luis Potosí are extensive, and many other warm season grasses, including other *Bouteloua* spp., are present (Rzedowski 1966); further fieldwork is required to clarify the biology of *minima*.

2. *Flexamia zamora* DeLong & Hershberger, n. stat.

Flexamia zamora DeLong and Hershberger 1947: 137.
Flexamia pectinata, Young and Beirne 1958: 46. (In part.)

Length of ♂ 3.6 (3.5–3.7) mm, ♀ 3.9 (3.7–4.2) mm; head width of ♂ 1.08 mm, ♀ 1.15 mm. Crown not strongly produced; median length of crown 0.61 x head width and 1.27 x interocular width (♂ n = 7; ♀ n = 3).
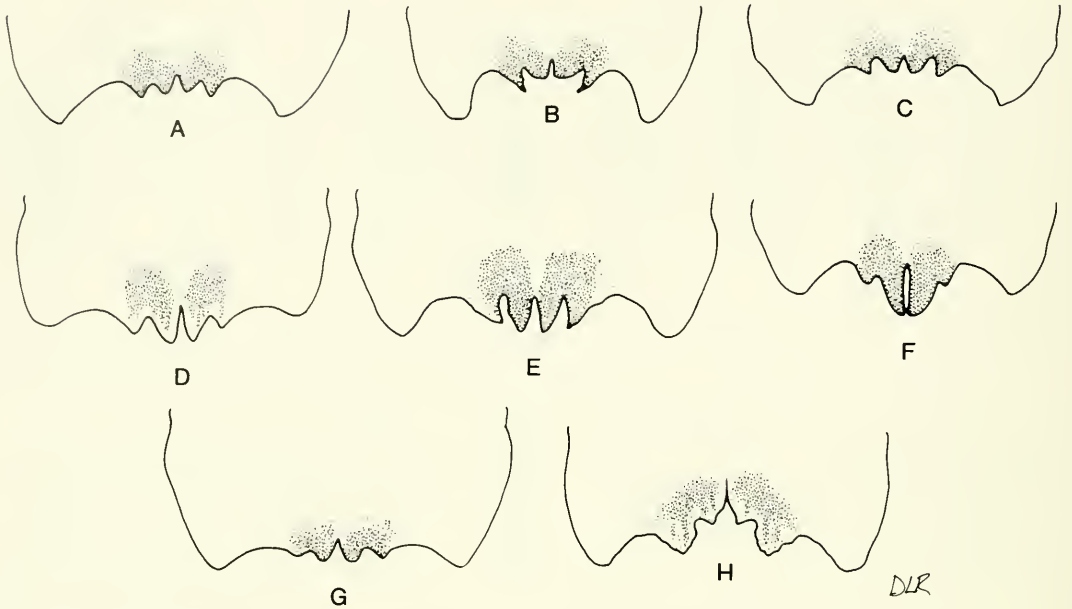
Fig. 14. Female sternum VII of *Flexamia pectinata* group: A, *minima;* B, *zamora;* C, *pectinata;* D, *bandarita;* E, *gila;* F, *doeringae;* G, *collorum;* H, *mescalero.*

Crown light brown with dark, circular spot around apex, pale brown, transverse line on either side at middle. Pronotum light brown, usually with traces of four wide longitudinal stripes. Elytra subhyaline, dark brown spot on disc; costal veinlets heavily margined with dark brown. Face black above, pale brown on lower portion.

MALE.—Pygofer as in *pectinata.* Plates (Fig. 11B) extending to approximately 3/4 length of pygofer, with apices less produced than in *pectinata,* bluntly rounded. Style apices exceeding the plane of the moderately developed, preapical lobe, forming an angle with it smaller than that in *pectinata.* Other characters as in *pectinata.*

FEMALE.—Sternum VII (Fig. 14B) with posterior margin shallowly emarginate; four produced teeth at middle; outer teeth longer, acute, curved inward. Ovipositor with basal processes of first valvulae similar to those of *pectinata,* but recurved portion not separated along the middle.

TYPES.—Holotype ♂: Zamora, Michoacán, Mexico, 2 October 1941, Plummer, Good, Caldwell and DeLong (OSU). Paratypes: 5 ♂, 3 ♀, same collection data (OSU and USNM).

REMARKS.—Although the male genitalia of

zamora are similar to those of *pectinata,* the styles of *zamora* differ in having a more acute angle between the apex and the less well-developed preapical lobe. Also, the plates are more evenly rounded than those of *pectinata* and longer than those of *minima.* The female sternum VII of *zamora* differs from that of *pectinata* in that the outer teeth of the hind margin are much longer than the inner teeth; in *pectinata* and *minima* the teeth are of equal length. This species, almost certainly entirely Mexican in distribution, is known only from its type locality (Fig. 15). The host or hosts are unknown, but other members of the complex feed on *Bouteloua curtipendula.*

3. *Flexamia pectinata* (Osborn & Ball)

Deltocephalus pectinatus Osborn & Ball 1897: 205.
Deltocephalus (Flexamia) pectinatus DeLong 1926: 32.
Flexamius pectinatus, DeLong and Sleesman 1929: 83.
Flexamius zamora, Young and Beirne 1958: 46. Incorrect synonymy.
Flexamia minima, Young and Beirne 1958: 46. Incorrect synonymy.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (2.9–3.8), of ♀ 3.6 (3.1–4.0). Head slightly produced (median crown length 1.40 x interocular width; 0.62 x head width) (♂ n = 37;
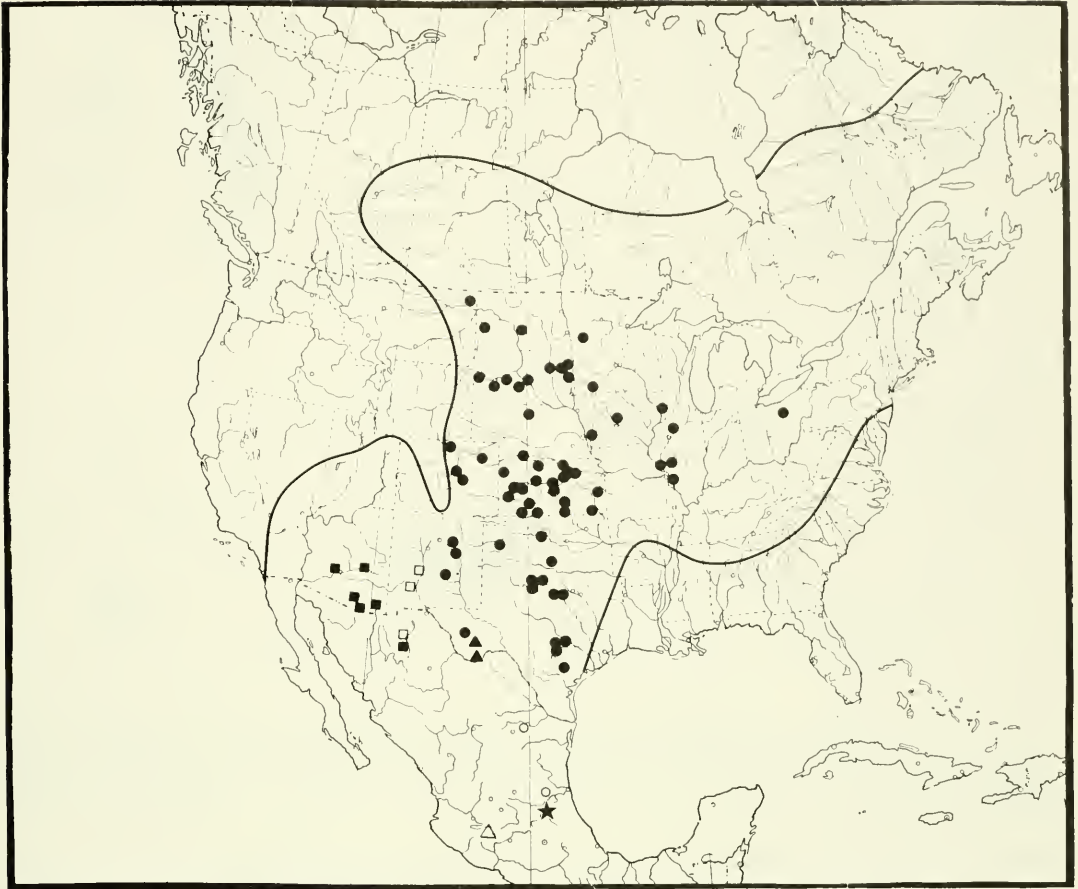
Fig. 15. Geographic distribution of *Flexamia pectinata* (●), *doeringae* (■), *bandarita* (▲), *gila* (□), *zamora* (△), *minima* (○), and *jacala* (★) with *Bouteloua curtipendula*.

♀ n = 29). [♂] Pygofer (Fig. 62F) strongly constricted both ventrally and dorsally; plates (Fig. 11C) wide and parallel-sided for much of their length, almost subrectangular, but with rounded tips. Aedeagus (Fig. 12C) symmetrical, without lateral processes; gonopore subapical on caudoventral surface. [♀] Sternum VII (Fig. 14C) with four teeth of approximately equal length. Ovipositor with bases of first valvulae recurved and calipterate (Fig. 63G).

GEOGRAPHIC DISTRIBUTION.—This species is a specialist of side-oats grama (*Bouteloua curtipendula*) in prairie and mesic grasslands; it occurs (Fig. 15) at higher elevations of the desert plains of eastern New Mexico east to Akron, Ohio, the eastern extension of the

prairie peninsula (Transeau 1935).

BIOLOGY.—Like other *Flexamia* species, *pectinata* is probably multivoltine and is present throughout the growing season. In New Mexico it is often absent from its host (*Bouteloua curtipendula*, side-oats grama) at lower elevations where host growth may be unpredictable because of sporadic drought. In Chihuahuan and Sonoran highlands it is replaced by *bandarita* and *doeringae*, respectively, and in the intervening mountains, by *gila*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.973; *Bouteloua* 0.926; *Bouteloua curtipendula* 0.825 (n = 57).

REMARKS AND DIAGNOSIS.—*Flexamia pectinata* can be recognized by a combination of its
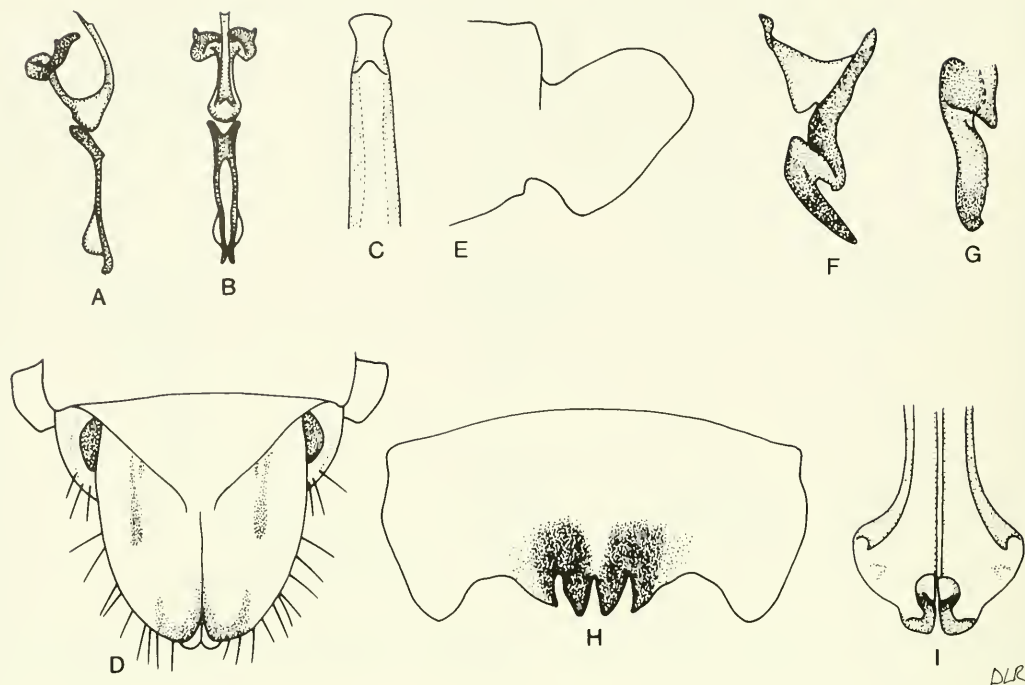
Fig. 16. *Flexamia gila*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, lateral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

external genitalic characters and its geographic range. Other species (*doeringae, jacala*) of the *pectinata* group with somewhat similar male plates do not occur with *pectinata* in its range. Of the nine members of the group, only *mescalero* (host: *Muhlenbergia pauciflora*) and *collorum* (host: *Bouteloua uniflora*) have ranges that overlap the range of *pectinata*. The male plates (Fig. 11I) and female sternum VII (Fig. 14H) of *mescalero* distinguish it from *pectinata* (Figs. 11C, 14C). The male plates of *collorum* (Fig. 11G) differ from those of *pectinata* in general aspect and in the absence of the sclerotized ridge on the inner plate surface that characterizes *collorum*. The female sternum VII of *collorum* is similar to that of *pectinata*. Although the characters discussed above permit tentative recognition of the commonly encountered *pectinata*, definitive identification requires examination of the genitalia.

4. *Flexamia gila*, n. sp.

Length of ♂ 3.4 (3.1–3.7) mm, ♀ 3.8

(3.6–4.0) mm; head width of ♂ 1.03 mm, ♀ 1.08 mm. Crown not strongly produced; median length of crown approximately 0.63 x head width and 1.32 x interocular width (♂ n = 6; ♀ n = 4).

Crown light brown with dark, circular spot around apex, pale brown, transverse line on either side at middle. Pronotum light brown, usually with traces of four wide, longitudinal stripes. Elytra subhyaline, dark brown spot on disc; costal veinlets heavily margined with dark brown. Face black above, pale brown on lower portion.

MALE.—Pygofer (Fig. 16E) much as in *bandarita*; posterior margin slightly more produced. Plates (Fig. 16D) broad, gradually rounded from base to apex, extending to approximately 4/5 length of pygofer. Connective in lateral view with dorsal keels narrow (or rarely absent), approximately 1/4 height of dorsal apodeme; apodemal processes as in *bandarita*; styles (Fig. 16F) long, diverging apically in ventral aspect, preapical lobe rounded, produced ventrad and laterad; style

portion distad from preapical lobe gradually narrowing to embrowned, strongly divergent, acute apex in ventral aspect, or, in lateral aspect (Fig. 16G), appearing bladelike, produced ventrally and flattened, bearing minute teeth along the irregularly curved ventral margin of style ending in a truncate apex that is slightly curved ventrad. Aedeagus (Figs. 16B,C) symmetrical, short, slender. Apical margin flared and convex, much as in *pectinata*. Distance between gonopore and apex less than in *pectinata*. Gonopore subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 16H) with posterior margin broadly but shallowly emarginate, with four produced teeth; middle teeth broad. Ovipositor with basal processes of first valvulae (Fig. 16I) recurved; recurved portion constricted above proximal margin, expanded slightly mesad and distad into differentially sclerotized lobes.

TYPES.—Holotype ♂: New Mexico, Sierra Co., Kingston, 17 August 1985, R. F. Whitcomb (6,300 ft, IPL 001875, *Bouteloua curtipendula*). Paratypes: 3 ♂ and 1 ♀, same collection data; 2 ♂ and 2 ♀, Mexico, 5 km S Casas Grandes, Chihuahua (5,600 ft, *Bouteloua curtipendula*, 3 September 1987, A. L. Hicks, IPL 001774); 2 ♂ and 1 ♀, New Mexico, Socorro Co., Magdalena Mtns., Water Canyon, 7,000 ft., 16 August 1987, IPL 001756, A. L. Hicks. Deposited BARC, CNC, KSU, KU, OSU, and USNM.

REMARKS.—The aedeagal characters of *gila* are intermediate between those of *doeringae* and *pectinata*. The styles in *gila* are less produced ventrally than in *doeringae*. The longer, bladelike styles of *gila* differentiate males of *gila* from those of *pectinata*; females can be readily differentiated on the basis of the morphology of the female sternum VII and the bases of the first valvulae. The host of *gila* is *B. curtipendula*. The name *gila*, a noun in apposition, denotes the New Mexican mountains where the holotype was collected.

5. *Flexamia bandarita*, n. sp.

Length of ♂ 3.4 (3.3–3.5) mm, ♀ 3.7 (3.4–4.0) mm; head width of ♂ 1.09 mm, ♀ 1.04 mm; head not strongly produced; median length of crown 0.64 x head width and 1.33 x interocular width (n = 8 ♂, 3 ♀).

Color variable, ranging from very dark gray to pale, with irregular, dark markings on dorsum and forewings; face very dark with pale arcs on upper half; variable in lower half. Head stramineous in lighter specimens with paired, transverse lines at midpoint of crown and oblique markings at rear; venter and legs with irregular, fuscous markings.

MALE.—Pygofer strongly produced ventrally in rounded lobe; plates (Fig. 17D) contiguous on basal half, diverging apically into narrow V; extending to approximately 3/4 length of pygofer; style (Fig. 17F) heavily sclerotized, sinuate in ventral aspect, extending almost to the apex of the aedeagus, gradually narrowing to acute, ventrally directed, chelate apex (Fig. 17G) that is closely associated with sclerotized ridge on inner surface of each plate; connective in lateral aspect with dorsal keels narrow; aedeagus (Figs. 17B,C) symmetrical with slender shaft, straight in ventral aspect, without apical processes. Apex flared in caudoventral aspect, but varying from concave to convex. Dorsal apodemal process small, not attaining the plane of the shaft of the aedeagus, appearing suboval in caudodorsal aspect, with lobelike, converging, ventral apices. Gonopore minute, subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 17H) with inner teeth of the hind margin longer than outer pair. Ovipositor with basal processes of first valvulae (Fig. 17I) recurved.

TYPES.—Holotype ♂: Brewster County, Texas, Chisos Mountains, Big Bend National Park, Texas, 7 August 1987, R. F. Whitcomb (5,200 ft, *Bouteloua curtipendula*, IPL 003262). Deposited in USNM. Paratypes: 2 ♂, 1 ♀, same collection data; 1 ♂, Texas, Marathon Basin, 8 August 1984, deposited USNM, BARC, KSU, KU; 5 ♂, 1 ♀, Chisos Mountains, D. J. and J. N. Knull, 17 July 1946, deposited OSU.

REMARKS.—*Flexamia bandarita* resembles *pectinata*, *gila*, and *doeringae*, but the sinuate styles of *bandarita* separate it from these species. The middle teeth of the female sternum VII are longer than the outer pair, suggesting an intermediate stage in development of the median process that is present in *doeringae*. Like *pectinata* and *doeringae*, *bandarita* is a specialist of side-oats grama and, so far as known, is restricted to that host. Its known geographic range (Fig. 15) includes the higher, more mesic grasslands of the Chisos Mountains in Big Bend National Park and the
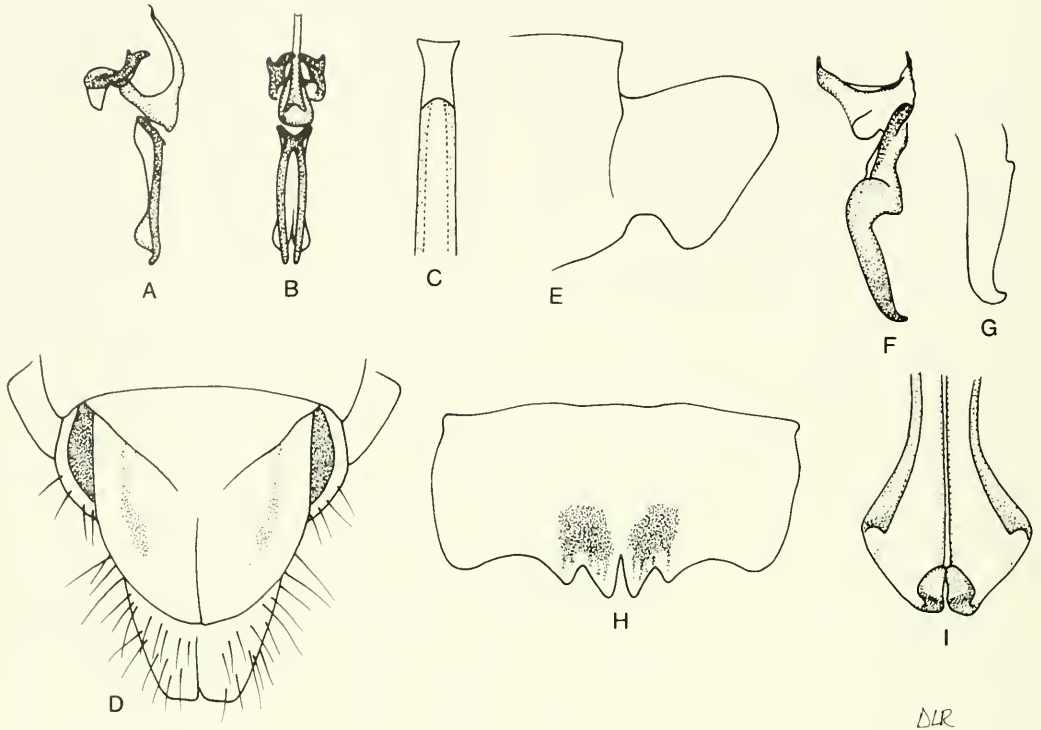
Fig. 17. *Flexamia bandarita*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, lateral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

Marathon Basin north of the park. This region is rich in endemism presumably derived by insularization of high grasslands by desertification in the surrounding true Chihuahuan desert. All insects in our recent series, taken August 1987, are extremely dark; the season had been one of record rainfall, and vegetative growth of all plants in the Chisos Mountains was very lush.

The name *bandarita*, a noun in apposition, is one of the common names for side-oats grama in Mexico.

6. *Flexamia doeringae* Beamer & Tuthill

Flexamia doeringae Beamer & Tuthill 1934: 3.

IMPORTANT CHARACTERS.—Length of ♂ 3.5 (3.2–3.7) mm, of ♀ 3.7 (3.3–4.1) mm. Head produced (median crown length 1.40 x interocular width; 0.70 x head width) (♂ n = 20; ♀ n = 20). Face ivory with broad, black, basal, interocular line, occasional dark markings be-

low. [♂] Plates (Fig. 11F) broad through most of their length, then narrowing sharply to rounded apices. Style with preapical lobe strongly developed, flattened and produced posteriorly; aedeagus (Fig. 12F) with protuberance near shaft apex close to tip in ventral aspect. [♀] Sternum VII (Fig. 14F) with inner teeth strongly produced and closely associated to form median process; ovipositor with each first valvula (Fig. 63A) recurved at base; recurved portion with transverse lobe cephalad of basal extremity.

GEOGRAPHIC DISTRIBUTION.—This species is known primarily from the mountains (Baboquivari, Catalina, Chiricahua, Huachuca, and Santa Rita ranges) of southeastern Arizona, but it also occurs in the Mexican highlands of Sonora and Chihuahua (Fig. 15). There is one record from Yavapai Co., Arizona (1 ♂, Granite Dell, 10 July 1933, R. H. Beamer).

BIOLOGY.—This species is apparently a

specialist on side-oats grama, *Bouteloua cur-tipendula*. Because this grass is a dominant in the mountains of southeastern Arizona and because many collectors have visited this region, *doeringae* is a common component of large *Flexamia* collections (Appendix I). The climate of the southeastern Arizona mountains is similar to that of the Mexican highlands but shows a definite Sonoran influence. *Flexamia doeringae* may therefore be a Sonoran vicariant that separated from the Chihuahuan *bandarita* and the prairie *pectinata*, which are also specialists of *B. curtipendula*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Bouteloua* 1.000; *Bouteloua curtipendula* 0.943 (n = 35).

REMARKS AND DIAGNOSIS.—The range of *doeringae* does not overlap that of any other member of the *pectinata* species group. This species can be readily distinguished by its ivory face, the pair of transverse lines on a pale, well-produced crown, and the structure of the external genitalia. The female sternum VII (Fig. 14F) is particularly distinct in having a medially produced structure consisting of a pair of long, central lobes and much shorter lobes on each side. The middle pair of teeth, in their size and degree of fusion, are maximally developed in this species.

7. *Flexamia collorum*, n. sp.

Length of ♂ 2.9 (2.7–3.0) mm, ♀ 3.0 (2.8–3.2) mm; head width of ♂ 0.87 mm, ♀ 0.89 mm. Crown not strongly produced; median length of crown 1.53 x head width and 0.68 x interocular width (♂ n = 11; ♀ n = 20).

Crown stramineous to light brown, pronotum with four faint, wide, brown stripes, forewings gray with irregular, dark markings. Face color and markings variable, without interocular line, but usually black in interocular area and lower area. Usually at least lorae pale. Crown with pair of oblique markings at rear, pair of transverse lines at midlength. Venter usually predominantly dark.

MALE.—Pygofer produced ventrally into an angulate lobe; caudoventral margin sloping dorsally to a broadly rounded, caudal lobe. Plates (Fig. 18D) short, extending to 1/2 length of pygofer, fused basally, contiguous medially for 2/3 length, acute apically. Plates produced on inner surface at about midlength into well-developed, sclerotized ridge that interfaces with style apices. Connective

(Fig. 18A) in lateral view with dorsal keels narrow, approximately 1/3 height of dorsal apodeme; apodemal processes as in *bandarita*; style (Fig. 18F) short, abruptly narrowing beyond preapical lobe to avicephaliform, mesoventrally directed apices (Fig. 18G). Aedeagus (Figs. 18B,C) symmetrical, shaft slender, without processes, slightly flared apically in caudoventral aspect. Gonopore subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 18H) with four teeth on hind margin; outer pair not well developed, inner pair distinct, but short and rounded; ovipositor with basal processes of first valvulae (Fig. 18I) recurved.

TYPES.—Holotype ♂: Kimble Co., Texas, Junction, 14 September 1987, R. F. Whitcomb and R. C. Chambers (1,300 ft, IPL 003599, *Bouteloua uniflora*). Deposited USNM. Paratypes: 16 ♂, 19 ♀, same locality; Sutton Co., Texas, Roosevelt, 14 September 1987, 14 ♂, 31 ♀ (1,400 ft, IPL 003593, 003595, 003598). Deposited at KU, OSU, CNC, USNM, KSU, and BARC.

REMARKS.—*Flexamia collorum* is distinct from other members of the *pectinata* species group, from which it is readily separated by the short, avicephaliform style apices and by the extensively developed ridge on the inside of the male plates. It has been collected at several localities (Fig. 19) in the Texas hills (Edwards Plateau), where it appears to specialize on Nealley grama, *Bouteloua uniflora*. Nealley grama differs from side-oats grama in having single spikelets at the base of the rachis; it also has a narrow geographic distribution in Texas and Mexico. Although this species appears to intergrade with *curtipendula* in the Mexican state of Coahuila (Johnson 1943), it is readily distinguished from it in central Texas.

The name *collorum* is an adjective meaning "of the hills," in recognition of the Texas hills where it was discovered.

8. *Flexamia jacala*, n. sp.

Length of ♂ 3.5 mm; head width of ♂ 1.08 mm. Crown produced; length of crown 1.42 x interocular width, 0.75 x head width.

Color gray with irregular, dark markings on dorsum and forewings; face without black interocular band; crown with oblique, rear and transverse, midlength markings. Venter and legs dark with irregular, fuscous markings.
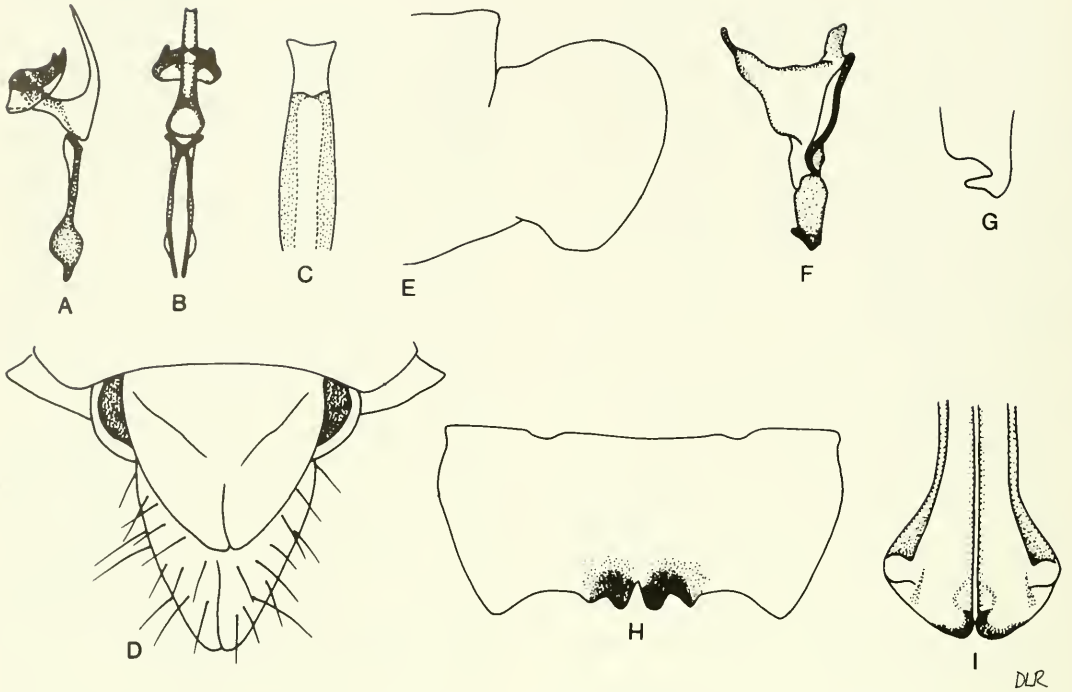
Fig. 18. *Flexamia collorum*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, lateral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

MALE.—Pygofer (Fig. 20D) as in *bandarita*. Plates (Fig. 20G) extend to approximately 2/3 length of pygofer, fused basally, contiguous medially for 2/3 of their length, converging to bluntly rounded apices; male genitalia similar to those of *bandarita*, but styles (Fig. 20E) straight in ventral aspect instead of sinuate, diverging apically; apices abruptly turning ventrad, appearing avicephaliform in lateral aspect (Fig. 20F), preapical lobe of style produced laterally and caudally. Connective (Fig. 20A) in lateral view with dorsal keels narrow; apodemal processes as in *bandarita*; aedeagal tip (Fig. 20C) slightly flared in ventral view. Gonopore subapical on caudoventral surface.

TYPES.—Holotype ♂: Mexico, Jacala, Hidalgo, 13 August 1936, E. D. Ball. Deposited in USNM.

REMARKS.—This species is known from a single male. Nothing is known of its biology. It is most closely related to *bandarita*, from which it can be distinguished by its styles,

which are straight in ventral aspect instead of sinuate; also, in lateral aspect the apices are avicephaliform instead of chelate. The name *jacala* is a noun in apposition denoting the type locality.

9. *Flexamia mescalero*, n. sp.

Length of ♂ 3.6 (3.5–3.9) mm, ♀ 3.8 (3.6–4.1) mm; head width of ♂ 1.07 mm, ♀ 1.12 mm. Crown moderately produced; median length of crown 1.42 x head width and 0.66 x interocular width (♂ n = 6; ♀ n = 16).

Color pale with brown markings. Crown ivory with pair of oblique markings on rear and pair of transverse lines at midlength; forewings pale gray with irregular, dark markings. Face variable, with or (more commonly) without black interocular band; specimens without band variably marked on face with brown or black.

MALE.—Pygofer (Fig. 21E) with posterior lobe angulate on ventral and caudal margins,
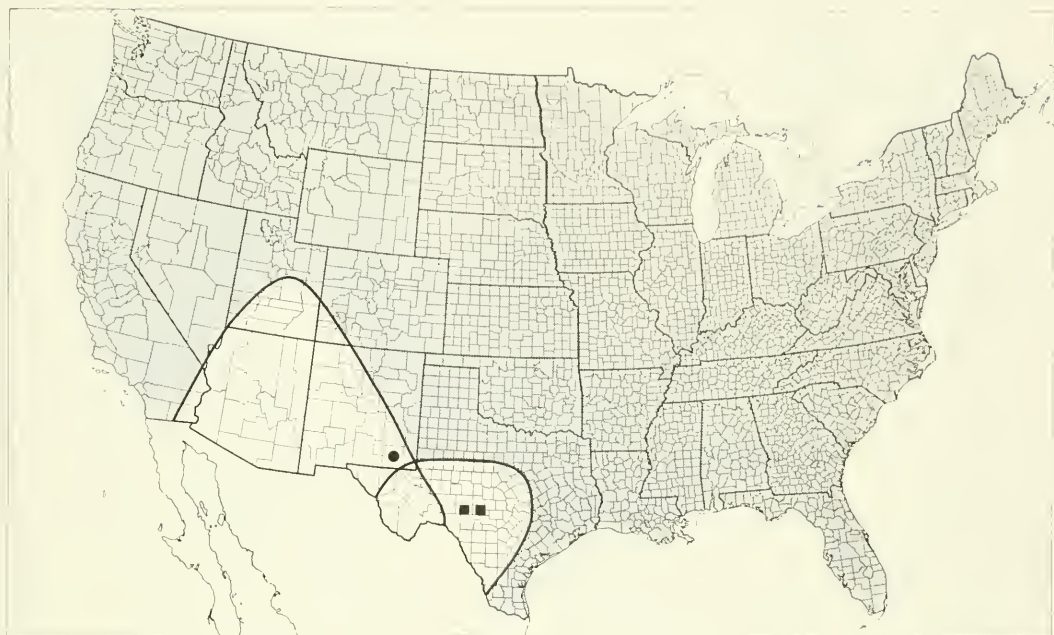
Fig. 19. Geographic distribution of *mescalero* (●) and *collorum* (■), with distribution of their hosts, *Muhlenbergia pauciflora* and *Bouteloua uniflora*, respectively.

slightly convex dorsally; plates (Fig. 21D) extending to approximately 4/5 length of pygofer, fused basally, diverging gradually along entire length; lateral margins tapering mesad to acute apices, inner surface with longitudinal groove and thickened mesal ridge along 3/4 of length, ending in small, embrowned tooth. Connective (Fig. 21A) in lateral view with dorsal keels narrow, approximately 1/4 height of dorsal apodeme; apodemal processes as in *bandarita*; styles (Fig. 21F) long in ventral aspect, slightly divergent distally, in lateral aspect with preapical lobe moderately produced and acute. Apical 1/2 of style flattened and minutely serrate basally, narrowing to ventromesally directed, calipterate apices (Fig. 21G), much as in *bandarita*. Aedeagus symmetrical, expanded apically in ventral aspect, appearing bluntly saggitate (Figs. 21C, 22), in lateral aspect slightly indented preapically; gonopore subapical on caudoventral surface.

FEMALE.—Sternum VII (Fig. 21H) with posterior margin notched deeply, middle teeth very short and deeply inset, median incision deep, in some specimens divergent at margin. Ovipositor with bases of first valvulae (Fig. 21I) with sinuate, recurved processes that converge medially.

TYPES.—Holotype ♂: Eddy Co., New Mexico, 23 August 1985. A. L. Hicks and R. F. Whitcomb, 4,600 ft, IPL 001977, *Muhlenbergia pauciflora*. Deposited in USNM. Paratypes: 9 ♂, 16 ♀, same locality as holotype. Deposited at KU, KSU, OSU, CNC, BARC, and USNM.

REMARKS.—*Flexamia mescalero* is the only member of the *pectinata* group that has not been collected on *Bouteloua*. The unique aedeagal apex (Figs. 21C, 22) and female sternum VII (Fig. 21H) are diagnostic for this species, give it unique status in the group, and could justify treatment as a distinct group (see cladogram of Fig. 58). The host of this species is New Mexican muhly, *Muhlenbergia pauciflora*. Attempts to find other localities for this species have been unsuccessful.

The name *mescalero* is a noun in apposition honoring the Native American Mescalero Apache nation, which inhabited the mountains of southeastern New Mexico in the pre-Columbian era and which is today
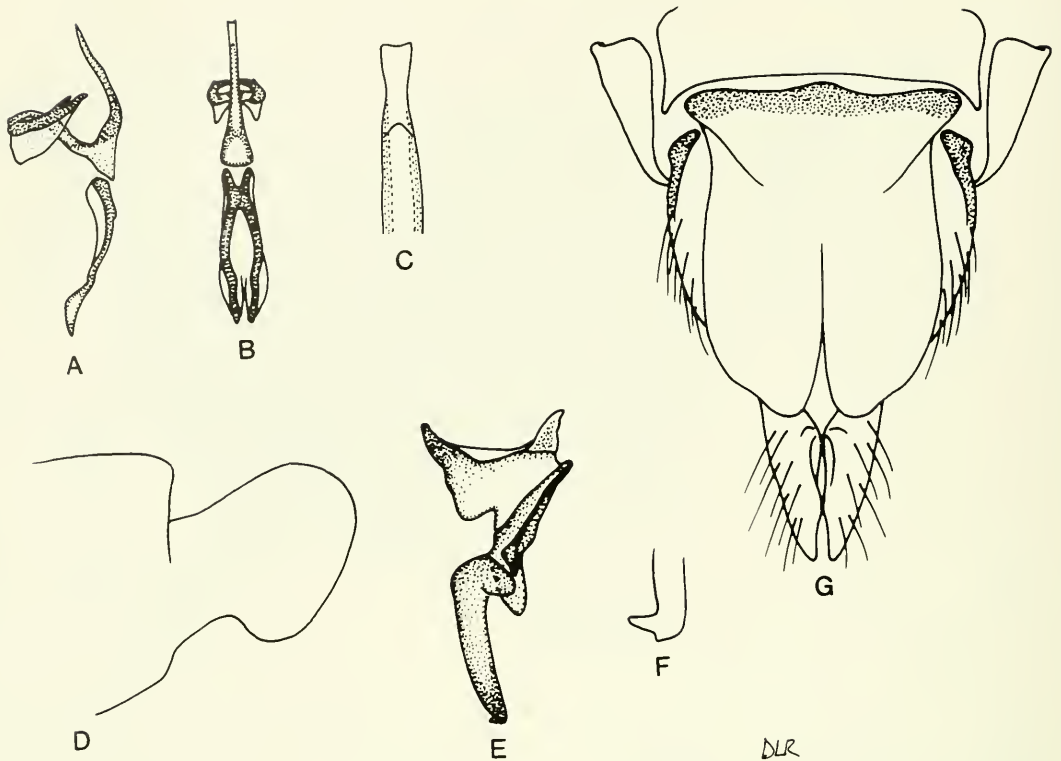
Fig. 20. *Flexamia jacala*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male pygofer, lateral aspect; E, right style, dorsal aspect; F, apex of right style, lateral aspect; G, male plates and pygofers, ventral aspect.

establishing high standards for judicious management of tribal lands.

II. The *abbreviata* Group

The *abbreviata* group consists of a single, widespread species that specializes on *Bouteloua* spp. The morphology of the aedeagal apex constitutes an autapomorphy that defines the monobasic group.

10. *Flexamia abbreviata* (Osborn & Ball)

Deltocephalus abbreviatus Osborn & Ball 1897: 206.
Deltocephalus (Flexamia) abbreviatus, DeLong 1926: 33.
Flexamius abbreviatus, DeLong and Sleesman 1929: 83.

IMPORTANT CHARACTERS.—Length of ♂ 3.1 (2.8–3.4) mm, of ♀ 3.2 (2.9–3.6) mm. Head moderately produced (mean crown length 1.26 x interocular width, 0.61 x head width) (♂ n = 20; ♀ n = 20). Face without distinct interocular line (but very rarely with a brown band contrasting with a pale face). Face often with parallel, sinuate, brown lines. [♂] pygo-

fer (Fig. 62H) strongly constricted, posterior lobe strongly produced on upper portion of posterior margin. Plates (Fig. 8E) shield-shaped, about 0.65 x pygofer length. Aedeagus (Fig. 7H) with elongate, anteapical gonopore on caudoventral surface, apex with pair of short, truncate processes curved cephalad, apodemal processes each with broad, membranous, apical expansion. [♀] Sternum VII (Fig. 10E) with a medial, truncate projection, which has a median incision that is almost always decorated on either side by a pair of infuscated spots.

GEOGRAPHIC DISTRIBUTION.—This species occurs (Fig. 23) from the Canadian prairie provinces to Montana, Utah, southwestern Nevada, Wisconsin, Illinois, Oklahoma, Texas, and Durango, Mexico (1 ♂, 27 mi N LaZarca, 27 October 1981, M. W. Nielson).

BIOLOGY.—Because of the dominance of its *Bouteloua* hosts, the densities it achieves on these hosts, and the accessibility of its hosts to
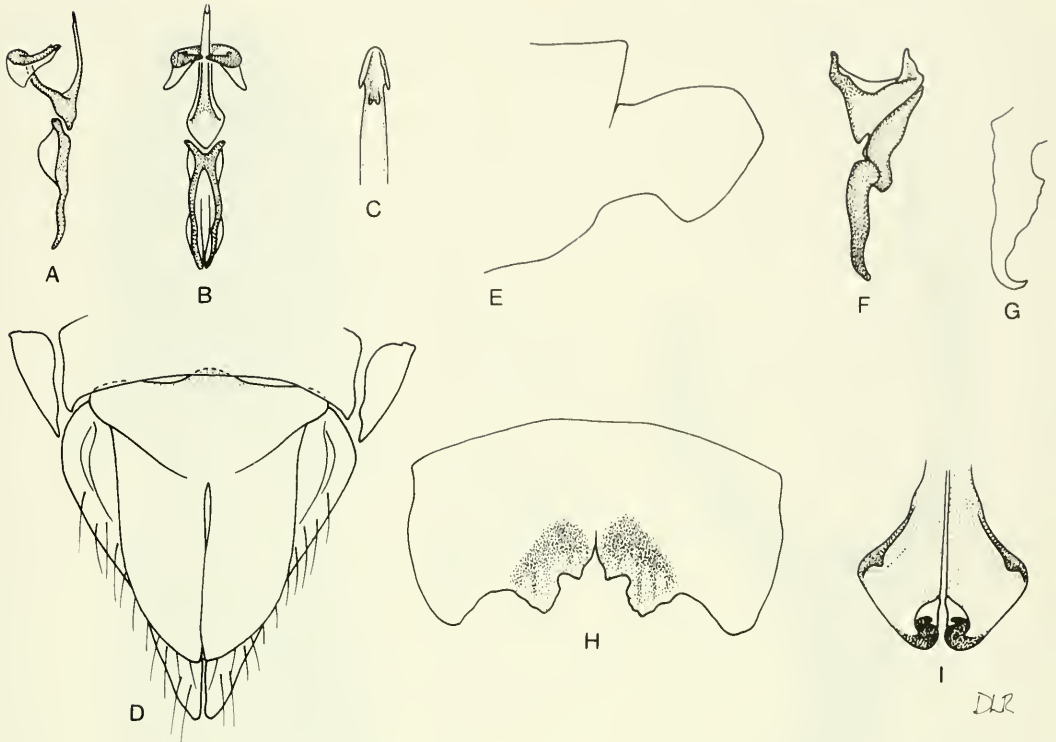
Fig. 21. *Flexamia mescalero*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, apex of right style, caudoventral aspect; H, female sternum VII; I, bases of first valvulae of female, dorsal aspect.

collectors, this is the most frequently collected *Flexamia* species (Appendix I). In the northern and western parts of its range it is a specialist on blue grama (*Bouteloua gracilis*), and the range of this grass limits its distribution (Fig. 23). In Chihuahuan grasslands and montane islands of southern Arizona and New Mexico, it is an inhabitant of mixed *Bouteloua* grasslands, where it may occur on blue, hairy (*B. hirsuta*), or, more rarely, black (*B. eriopoda*) grama. In the eastern prairie where the grasslands form a mosaic with patches of eastern deciduous forest, the only known host is hairy grama; the eastern boundary of the range of *abbreviata* is determined by this host. In the Edwards Plateau of Texas, *abbreviata* occurs on *B. hirsuta*, *B. pectinata*, *Muhlenbergia reverchonii* (seep muhly), and perhaps other chloridoid grasses.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.936; *Bouteloua* 0.836. Prairie: *Bouteloua* 0.780; *B. gracilis* 0.745

(n = 428); mixed *Bouteloua* grasslands: *B. gracilis* 0.317, *B. hirsuta* 0.568 (n = 347).

REMARKS AND DIAGNOSIS.—Males and females of this species can be recognized by the combination of their small size, brown face without interocular band, and unique morphologies of the sternum VII or male plates and pygofer (Fig. 8E). The hind margin of the female sternum VII (Fig. 10E) contains four teeth, a condition we believe to be homologous with similar structures in the *pectinata* group. *Flexamia abbreviata* occurs with *curvata* (host: *Buchloë dactyloides*) throughout much of the range of *Buchloë*. Dark male specimens of *curvata* are occasionally confused with *abbreviata* but can be tentatively recognized without dissection by characters of the plates and pygofers.

III. The *zacate* Group

The *zacate* group consists of two species that specialize on bush muhly (*Muhlenbergia*

Fig. 22. Scanning electron micrograph of aedeagus of *Flexamia mescalero:* A, lateral aspect (312X); B, ventral aspect of aedeagal apex (1680X).

porteri). These sister species are distinguished on the basis of their posteriorly produced male pygofers, curved aedeagus lacking apical processes, and elongate, but rounded male plates. No other *Flexamia* species has this combination of characters.

Description of the *zacate* Group

Medium-sized. Length of ♂ 3.2–4.1 mm, of ♀ 3.6–4.1 mm. Dorsum brown. Crown moderately produced. [♂] Plates elongate, but only about 2/3 length of pygofer, fused basally, narrowing continuously to apices. Pygofer (Figs. 25E, 62I) with posterior lobe strongly produced posteriorly. Aedeagus and connective (Fig. 6C) distinctly articulated. Aedeagus curved in lateral aspect, without apical processes (Fig. 25A). [♀] Sternum VII

(Figs. 10I, L) with deep, median incision.

Key to Species of *zacate* Group

1. Males 2
— Females 3

2(1). Aedeagus (Fig. 7I) narrow in ventral and lateral aspects; gonopore (Fig. 24) long and narrow, extending along apical third of shaft ....*zacate*, n. sp.

— Aedeagus (Figs. 6C, 7J) wide, scimitar-shaped in lateral aspect, diamond-shaped in ventral aspect. Gonopore not elongate, near midpoint of shaft .... *canyonensis* Young & Beirne

3(1). Hind margin of sternum VII (Fig. 10L) with outer pair of teeth essentially absent, fused with medial teeth to form median projection .... *zacate*, n. sp.

— Hind margin of sternum VII (Fig. 10I) with outer teeth distinct, rounded ....*canyonensis* Young & Beirne
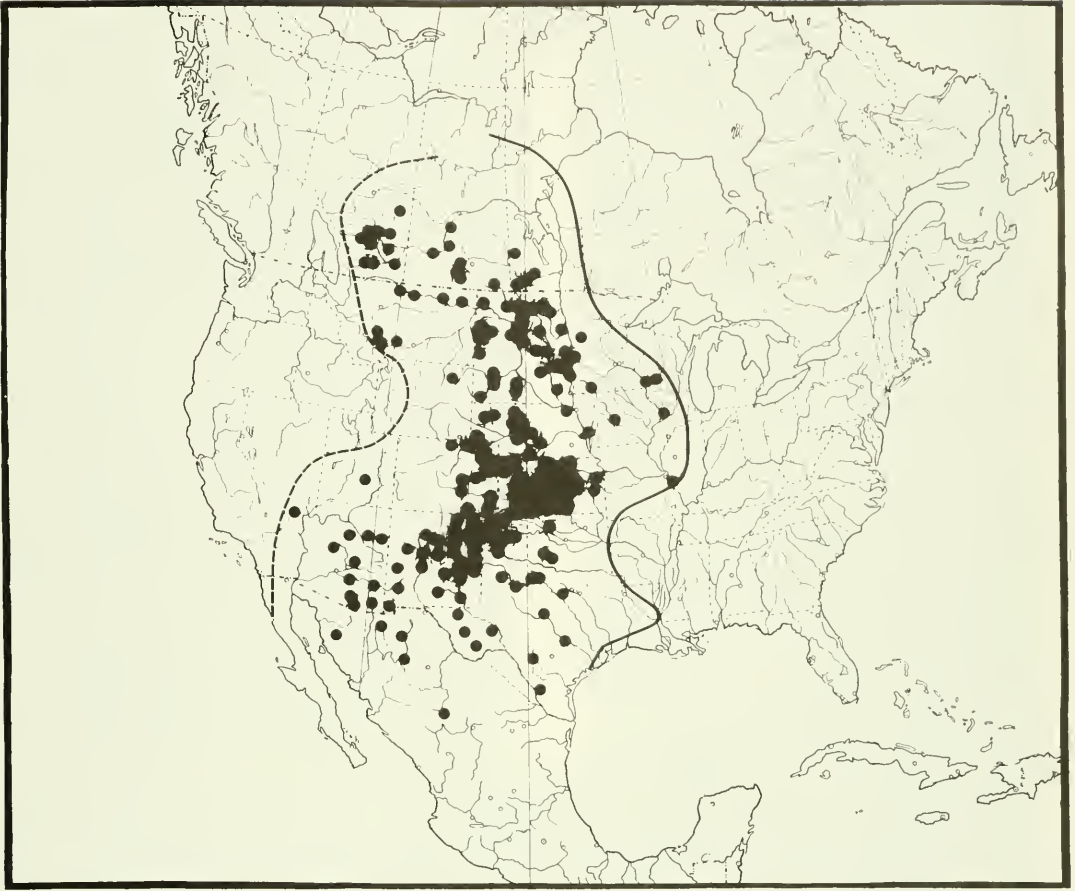
Fig. 23. Geographic distribution of *abbreviata*. Western limit is defined by the range of *Bouteloua gracilis*. Eastern limit is defined by the range of *Bouteloua hirsuta*. Host relationships in Mexico are unknown.

11. *Flexamia canyonensis* Young & Beirne

Flexamia canyonensis Young & Beirne 1958: 18.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.5–4.1) mm, of ♀ 3.9 (3.8–4.1) mm. Head moderately produced (1.29 x interocular width; 0.68 x head width) (♂ n = 4; ♀ n = 5). Face with clypeus and dorsal portion of genae black. Clypeus, lora, and lower part of genae pale yellow. [♂] Pygofer (Fig. 62I) as in *abbreviata*. Plates (Fig. 9C) gradually narrowing apically to rounded apices. Aedeagus symmetrical, scimitar-shaped in lateral aspect, diamond-shaped in ventral aspect. Gonopore on ventral surface of aedeagus, near midpoint of shaft. [♀] Sternum VII with deep, median incision on hind margin. Ovipositor with

bases of each first valvula (Fig. 63H) strongly recurved, processes sinuate in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—*Flexamia canyonensis* has been collected at Sabino Canyon, Arizona (E. D. Ball), and in our own studies at Kingman, Portal, and Santa Rita Experimental Range, Arizona (Fig. 26).

BIOLOGY.—Our collections of *canyonensis* are from bush muhly, *Muhlenbergia porteri*. This grass is common in the type locality, and we assume that it is the sole host. *Flexamia canyonensis* appears to be restricted to the highlands of the Sonoran Desert. This species and its Chihuahuan sister, *zacate,* are among the few *Flexamia* species to colonize semiarid habitats. Perhaps *canyonensis* is protected from desiccation by the microclimate

Fig. 24. Scanning electron micrograph of aedeagal apex of *Flexamia zacate*, ventral aspect (800X).

produced by its host, which grows within protective shrubs.

OLIGOPHAGY COEFFICIENTS.—*Muhlenbergia porteri* 1.00 (n = 9, 3 series).

REMARKS AND DIAGNOSIS.—Females can be easily recognized by their distinctive sternum VII (Fig. 10I), which bears a deep, median incision. Males can be tentatively recognized by their characteristic face pattern and produced, flattened pygofer. The aedeagus of *canyonensis* is unique.

12. *Flexamia zacate*, n. sp.

Length of ♂ 3.5 (3.2–3.9) mm, ♀ 3.8 (3.6–4.0) mm; head width of ♂ 1.04 mm, ♀ 1.08 mm. Crown produced; median length of crown 1.48 x head width and 0.71 x interocular width (♂ n = 37; ♀ n = 12).

Dorsum ivory. Crown with at least trace of oblique, basal and midlength, transverse lines. Face without black interocular line, black in interocular area with at most pale arcs, bottom of face brown, with irregular, pale markings. Venter stramineous with irregular markings.

MALE.—Pygofer (Fig. 25E) with weakly developed constriction before posterior lobe, ventral lobe small, caudoventral margin produced posteriorly, dorsal margin unevenly convex. Plates (Fig. 25D) extending to approximately 2/3 length of pygofer, fused basally, contiguous medially for 1/2 length, acute apically; connective in lateral view (Fig. 25A) with dorsal keels narrow, approximately
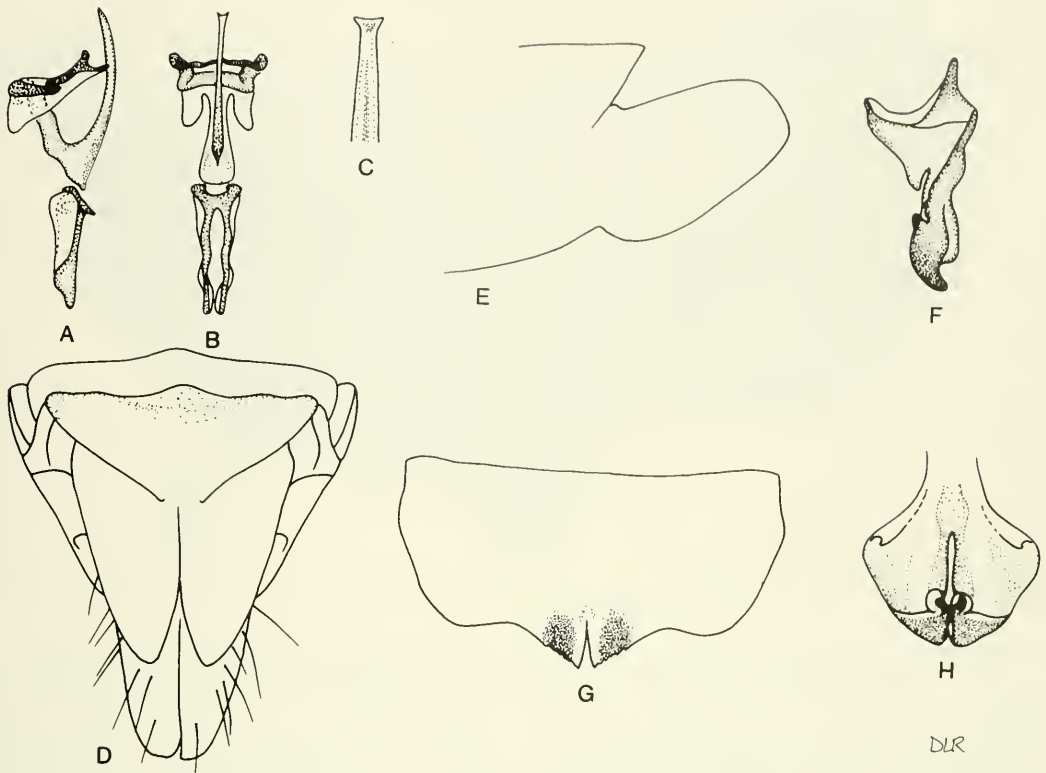
Fig. 25. *Flexamia zacate*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, apex of aedeagus, caudoventral aspect; D, male plates and pygofers, ventral aspect; E, male pygofer, lateral aspect; F, right style, dorsal aspect; G, female sternum VII; H, bases of first valvulae of female, dorsal aspect.

1/4 height of dorsal apodeme, with distinctive, minute tooth on ventral surface, anterior to distinct joint with the aedeagus; apodemal appendages campanulate in caudal aspect, with very slender, anteapical processes directed mesad; styles (Fig. 25F) with apex digitate, curving sharply ventrad, each bearing small preapical tooth on mesal surface; preapical lobe not produced. Aedeagus symmetrical, shaft slender and cylindrical without processes, curving gradually caudodorsad in lateral aspect, appearing straight in ventral aspect. Apex slightly flared in caudoventral aspect, flattened in lateral aspect, with apical margin concave. Gonopore (Figs. 24, 25C) long and narrow, extending along apical third of caudoventral surface of shaft.

FEMALE.—Sternum VII (Fig. 25G) with posterior margin produced medially, with deep, median incision; ovipositor with basal processes of first valvulae (Fig. 25H) with broad portions close to base.

TYPES.—Holotype ♂: Brewster County, Texas, Big Bend National Park (Panther Junction), 26 August 1985 (3,600 ft, R. F. Whitcomb and A. L. Hicks; IPL 002093). Deposited USNM. Paratypes: 33 ♂, 10 ♀, same locality and date, IPL 002057, 25 August 1985; 13 ♂, 4 ♀, same locality and date, deposited USNM, BARC, CNC, KU, KSU, and OSU. Thirty-five immature specimens (IPL 002057) have also been deposited with the paratypes.

REMARKS.—This species is a sister to *canyonensis* but can be distinguished from it by the shape of the aedeagus, which, though curved, is much narrower in lateral aspect and is not diamond-shaped in ventral aspect. The length of the gonopore of *zacate* also separates it from *canyonensis*. Both *canyonensis* and

Fig. 26. Geographic distribution of *canyonensis* (●) and *zacate* (■) and their host, *Muhlenbergia porteri*.

zacate are apparently specialists on bush muhly, *Muhlenbergia porteri*. This grass occurs chiefly in association with thorny shrubs such as *Acacia*, *Prosopis*, *Larrea*, or *Opuntia*, which defend it against large herbivores. The entire volume of the host shrub may be filled with the tangled culms of bush muhly; eventually the host shrub dies, presumably from competition. Because of its unique habitat, *zacate* is difficult to collect without a vacuum-collecting device. The name *zacate* is a noun in apposition denoting various grasses of the *Muhlenbergia* or *Sporobolus* types. Bush muhly is known in Mexico as "zacate arana" (spider grass).

IV. The *grammica* Group

The *grammica* group consists of a single, distinctive species. The morphology of the aedeagal apex and the female sternum VII provides autapomorphies that define the group.

13. *Flexamia grammica* (Ball)

Deltocephalus grammicus Ball 1900: 204.
Deltocephalus (Flexamia) grammicus), DeLong 1926: 37.
Flexamius grammicus, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 4.5

(4.1–5.0) mm, of ♀ 4.6 (4.3–5.0) mm. Head not strongly produced (mean crown length 1.08 x interocular width, 0.54 x head width) (♂ n = 20; ♀ n = 20). Dorsum (Fig. 2C) with three pairs of longitudinal, dark stripes, median pair extending from hind portion of the crown posteriorly through the scutellum and wings. Face stramineous with single, black interocular line. [♂] Pygofer (Fig. 62O) with narrow, posterior lobe, dorsal more prominent than ventral constriction in lateral aspect. Plates (Fig. 8F) broad, contiguous, parallel-sided for much of their length, broadly rounded apically. Aedeagus asymmetrical with anteapical gonopore on anterodorsal surface, with pair of recurved processes (Fig. 7E), one edentate on the side of shaft near gonopore, one at the shaft apex. [♀] Sternum VII (Fig. 10F) broadly and shallowly concave on posterior margin.

GEOGRAPHIC DISTRIBUTION.—*Flexamia grammica* occurs in southern Alberta and Saskatchewan south through the Great Plains to Texas (Fig. 27).

BIOLOGY.—In the northern part of its range, *grammica* is a specialist on prairie sandreed, *Calamovilfa longifolia*. In the southern part of its range, it specializes on *C. gigantea*.
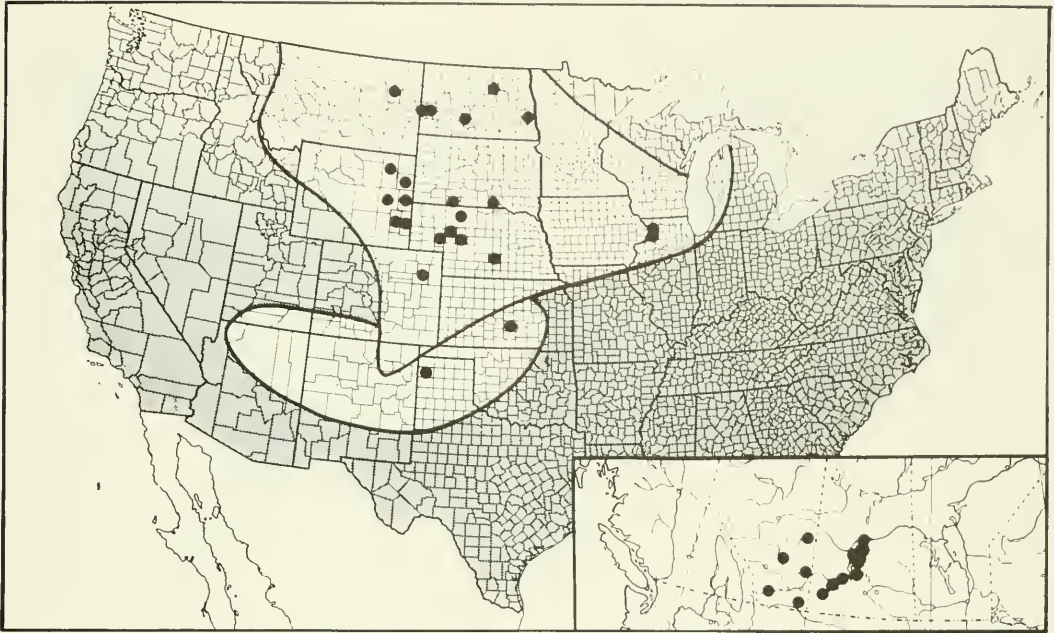
Fig. 27. Geographic distribution of *Flexamia grammica*, and two hosts, *Calamovilfa longifolia* (northern prairie) and *C. gigantea* (southern prairie and Southwest).

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Calamovilfa* spp. 0.872 (n = 47).

REMARKS AND DIAGNOSIS.—The habitus of *grammica* is distinctive, as is its size.

V. The *curvata* Group

The *curvata* group consists of two closely related sister species that specialize on buffalograss, *Buchloë dactyloides*. One (*curvata*) is adapted to temperate regions, whereas the other (*surcula*) is adapted to the subtropical climate of south Texas and Mexico. In the following description synapomorphies are designated [s].

Description of the *curvata* Group

Small, deltocephaline leafhoppers. Length of ♂ 2.4–3.5 mm, of ♀ 2.6–3.9 mm. Usually stramineous in color, but occasionally much darker. [♂] Pygofer (Figs. 62K, L) somewhat produced caudodorsally. Plates (Figs. 9D, E) short, shield-shaped, about half length of pygofer. Aedeagus (Figs. 7F, G) [s] with two pairs of apical processes; style apex [s] foot-shaped in broadest aspect. [♀] Female sternum VII (Figs. 10J, K) with median incision or notches, with infuscation surrounding or bordering notch or incision.

Key to Species of *curvata* Group

1. Males 2
— Females 3
2(1). Gonopore small, subcircular, opening near aedeagal apex; apical pair of processes short (Fig. 7G) .... *surcula* DeLong & Sleesman
— Gonopore elongate; apical pair of processes much longer (Fig. 7F) .... *curvata* DeLong
3(1). Female sternum VII (Fig. 10K) with completely infuscated, median incision .... *curvata* DeLong
— Female sternum VII (Fig. 10J) notched, but without median incision; infuscated on each side of notches .... *surcula* DeLong & Sleesman

14. *Elexamia surcula* DeLong & Sleesman

Flexamius [sic] *surculus* DeLong & Sleesman 1929: 99.

IMPORTANT CHARACTERS.—Length of ♂ 3.0 (2.6–3.4) mm, of ♀ 3.4 (2.9–3.7) mm. Head moderately produced (mean crown length 1.35 x interocular width; 0.68 x head width) (♂ n = 20; ♀ n = 20). Face stramineous, except for broad, brown, basal, interocular
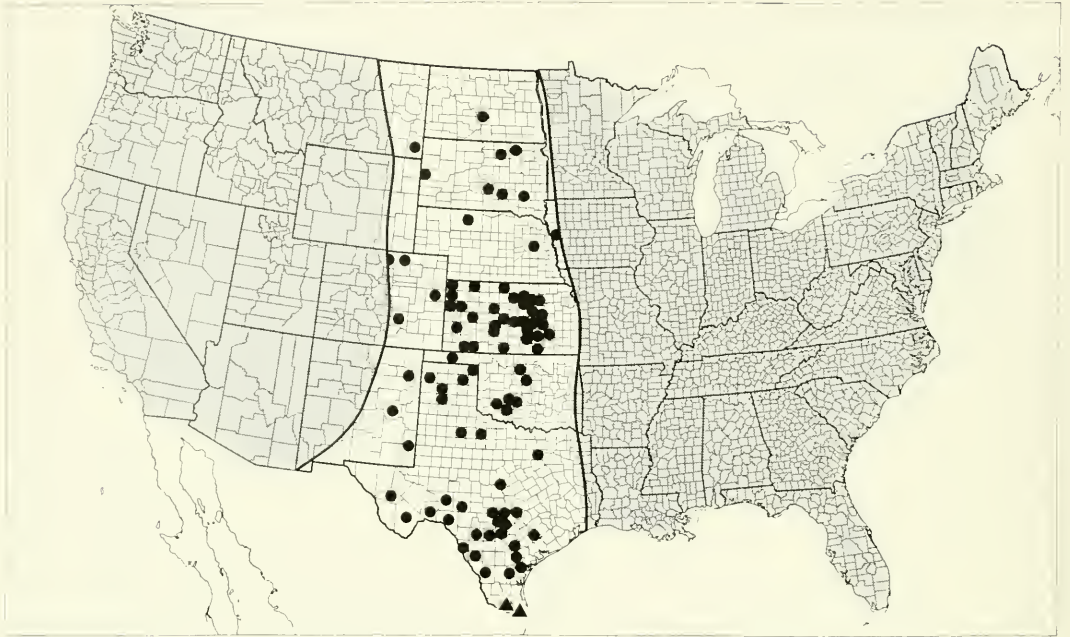
Fig. 28. Geographic distribution of *Flexamia curvata* (●) and *surcula* (▲) and their host, *Buchloë dactyloides*.

line. [♂] Pygofer (Fig. 62L) with posterior lobe strongly produced; style with apical portion foot-shaped, but longer than in *curvata*. Plates (Fig. 9E) as in *curvata*. Aedeagus (Fig. 7G) with pair of recurved, apical processes, shorter than in *curvata*, and pair of anteapical processes. [♀] Sternum VII (Fig. 10J) infuscated on either side of shallow notch. Ovipositor with each first valvula (Fig. 63I) with basal portion curved dorsad through more than 90 degrees, recurved portion oblique and crescentiform in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Subtropical Texas, and probably coastal prairies of northeastern Mexico (Fig. 28).

BIOLOGY.—*Flexamia surcula* is restricted to subtropical grasslands. We have collected it from *Buchloë* in the Rio Grande Valley in Cameron and Hidalgo counties of south Texas. Collection records from December, January, and February indicate that this species does not diapause and probably breeds more or less continuously throughout the season as host condition permits.

REMARKS AND DIAGNOSIS.—This species is closely related to *curvata*. We have referred a specimen labeled "paratype" from San Antonio, Texas, in the OSU collection to *curvata*.

The sternum VII of *surcula* females lacks the deep, median incision of *curvata*.

15. *Flexamia curvata* DeLong

Deltocephalus (Flexamia) curvatus DeLong 1926: 34.
Flexamius curvatus, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.1 (2.4–3.5) mm, of ♀ 3.4 (2.6–3.9) mm. Head moderately produced (mean crown length 1.33 x interocular width; 0.63 x head width) (♂ n = 21; ♀ n = 23). Face usually pale brown, often with traces of indistinct, brown interocular band. [♂] Pygofer (Fig. 62K) with posterior lobe simple, somewhat produced caudodorsally. Plates (Fig. 9D) short, shield-shaped. Style foot-shaped in broadest aspect. Aedeagus (Fig. 7F) subsymmetrical, recurved anterior processes extending basad almost to midlength of shaft, pair of shorter apical processes not in bilaterally symmetrical plane; gonopore an elongate channel on caudoventral surface. Recurved anteapical processes extending basad almost to middle of shaft; pair of shorter apical processes extending basad. [♀] Sternum VII (Fig. 10K) with hind margin concave on each side of median incision. Ovipositor with base of each first valvula

(Fig. 63F) bearing posteriorly directed, slender process.

GEOGRAPHIC DISTRIBUTION.—*Flexamia curvata* occurs throughout much of the temperate range of its host, *Buchloë dactyloides* (Fig. 28).

BIOLOGY.—This species often occurs in large populations on *Buchloë*, where it is a member of a guild that also includes *Athysanella, Polyamia, Laevicephalus,* and *Gillettiella* species (Whitcomb et al. 1987). In the subtropical part of the range of buffalograss (in south Texas and, presumably, Mexico), *curvata* is replaced by *surcula*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.986; *Buchloë dactyloides* 0.925 (n = 560).

REMARKS AND DIAGNOSIS.—This species is readily recognized by the combination of its small size and external genitalic characteristics. Most specimens are light stramineous, with conspicuous, black spots in the middle and apical cells of the forewing (Fig. 4B); these specimens are unmistakable. Very large male specimens of *curvata* might be confused with *inflata*, whose plates and pygofer are superficially similar. However, *inflata*, which like *curvata* is usually light stramineous in color, never has a dark spot in the center of the forewing. Dark specimens of *curvata* are occasionally referred erroneously to *abbreviata*.

VI. The *picta* Group

This group consists of two species, each with a distinctive habitus, which can be unambiguously designated as sister species on the basis of the morphology of the male aedeagus and pygofer, and the indistinct articulation between the aedeagus and connective. In addition, both species feed on *Aristida*. One (*pyrops*) has, perhaps, the most distinctive habitus in the genus (Fig. 2E), but *picta* can also be recognized without dissection. In the following description synapomorphies defining the group are designated [s].

Description of the *picta* Group

Medium-sized or large, deltocephaline leafhoppers. Length of ♂ 2.9–4.0 mm, of ♀ 2.9–4.9 mm. Crown variably produced (in *pyrops*, reaching more than 2 x interocular width). [♂] Pygofer [s] notched on dorsal margin, posterior lobe angulate, sharply produced. Plates small in relation to large pygo-

fers; [s] joint between aedeagus and connective indistinct. Aedeagus symmetrical, shaft elongate, [s] apex capitate, pair of slender, recurved, anteapical processes with entire edges. Gonopore subapical on caudoventral surface.

Key to Species of *picta* Group

1. Head produced, with crown more than twice interocular width (Fig. 2E) ...... *pyrops* (Crumb)

— Head only moderately produced .. *picta* (Osborn)

16. *Flexamia picta* (Osborn)

Deltocephalus pictus Osborn 1907: 165.
Deltocephalus funabulus Crumb 1915: 189.
Deltocephalus (Flexamia) pictus, DeLong 1926: 32.
Flexamius [sic] *pictus,* DeLong and Sleesman 1929: 83.

IMPORTANT CHARACTERS.—Length of ♂ 3.5 (2.9–4.0) mm, of ♀ 3.6 (2.9–4.2) mm. Head moderately produced (1.38 x interocular width; 0.64 x head width) (♂ n = 24; ♀ n = 20). Face pale yellow, with broad interocular band. Forewings usually dark gray, contrasting with lighter crown and pronotum, dark-pigmented spot in apex. [♂] Pygofer (Fig. 5A) similar to that of *pyrops*. Plates (Fig. 9A) very short, only about 1/3 length of pygofer, narrowed apically. Aedeagus and connective with indistinct joint with the connective, gonopore subapical on caudoventral surface. Aedeagal apex capitate; expanded portion with a few small teeth; pair of slender, recurved, anteapical processes with entire edges arising on each side of gonopore. [♀] Sternum VII with median projection. Ovipositor with base of each first valvula (Fig. 63J) curved through 180 degrees, obliquely bisinuate in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—This species occurs throughout much of the Southeast, from Massachusetts to Kansas, and south through the mixed prairie to Texas (Fig. 29).

BIOLOGY.—*Flexamia picta* appears to be associated with *Aristida* spp. Some of the colonized species are annuals. This is a unique situation in *Flexamia* hosts; all other known hosts are perennials.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.919; *Aristida* spp. 0.870 (n = 285).

REMARKS AND DIAGNOSIS.—It is important for students of the genus to learn the habitus of *picta*, which is very common throughout much of its range. This species can be recognized by the combination of a dark-pigmented
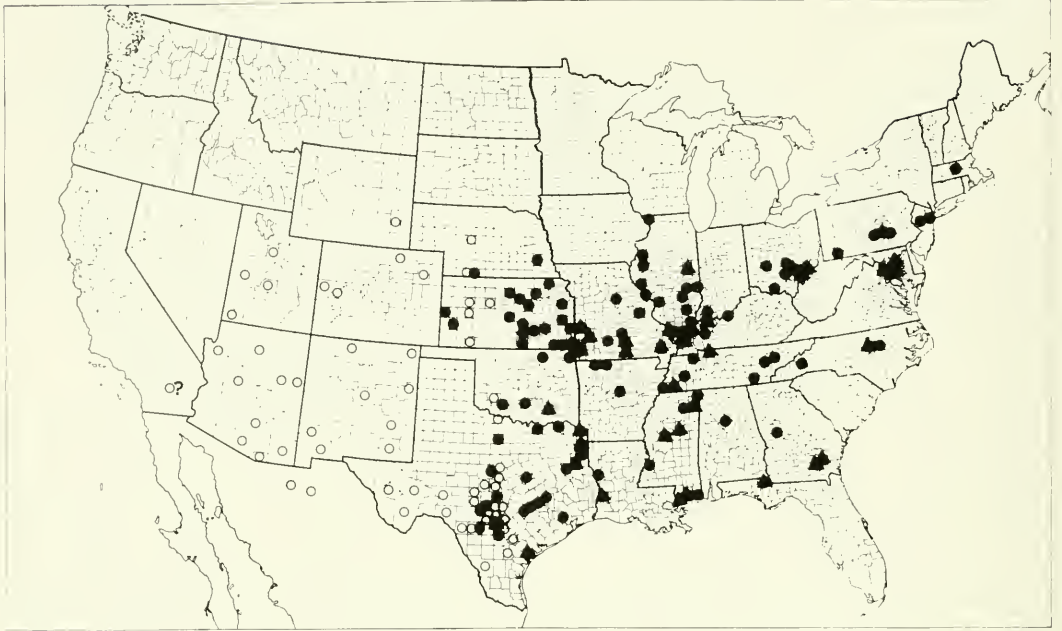
Fig. 29. Geographic distribution of three *Aristida* specialists: *Flexamia arizonensis* (○), *pyrops* (▲), and *picta* (●).

spot in the apex of the forewing (Fig. 4C) in combination with the face characteristics. The face is usually sordid yellow but occasionally is light gray or very pale brown. A few dark individuals of certain other species (e.g., *clayi*) may have a similar wing spot, but if so, the face is never pale. The geographical distribution of *picta* (southeastern) is also usually indicative. The range of *picta* overlaps the ranges of *flexulosa* and *arizonensis*, which have superficially similar faces, only in central Texas, Oklahoma, and Kansas. Finally, the small male plates, which contrast with very large pygofers, are diagnostic for *picta*. Thus, dissection is usually unnecessary for recognition of this species.

17. *Flexamia pyrops* (Crumb)

Deltocephalus pyrops Crumb 1915: 191.
Deltocephalus (Acurhinus) pyrops, DeLong 1926: 21.
Acurhinus pyrops, DeLong 1948: 226.
Flexamia pyrops, Oman 1949: 167.

IMPORTANT CHARACTERS.—Length of ♂ 3.8 (3.6–4.0) mm, of ♀ 4.2 (3.8–4.9) mm. Head very strongly produced (crown length 2.19 x interocular width, 1.00 x head width) (♂ n = 20; ♀ n = 20). Face stramineous, interocular line with three or more short, dentate projec-

tions from lower margin. [♂] Pygofer (Fig. 5B) with distinct notch on dorsal margin, posterior lobe produced ventrad in conspicuous, acute process; plates (Fig. 9B) very short, no more than 1/3 length of pygofer, rounded apically. Joint between connective and aedeagus not well developed. Aedeagus symmetrical, gonopore on caudoventral surface, pair of recurved, anteapical processes arising basad of gonopore. Apex of shaft (Fig. 7L) capitate, similar to that of *picta*, but with fewer, more distinct teeth. [♀] Sternum VII (Fig. 10H) with hind margin conspicuously concave at middle.

GEOGRAPHIC DISTRIBUTION.—Although this is a southeastern species, it occurs as far north as Pennsylvania, Ohio, Illinois, and Kansas (Fig. 29).

BIOLOGY.—*Flexamia pyrops*, like *F. picta*, is closely associated with *Aristida* spp., but the two species are seldom found together. The type of *pyrops* from Tennessee was taken on "*Aristida longespica.*" In Illinois the host was *A. dichotoma* var. *curtisii* (Whitcomb 1957).

REMARKS AND DIAGNOSIS.—The habitus of *pyrops* is unique and diagnostic.

VII. The *albida* Group

The *albida* group comprises two species that are very distinct in general facies and geographic distribution. Common characteristics of the species are their patterns of dorsal stripes, face patterns, and their bifurcate, apical, aedeagal processes (an apomorphy shared with *serrata*). The morphology of the male pygofers of the species may constitute a synapomorphy. The biology of *albida* and *slossonae* appears to be more complex than that of many other *Flexamia* species. The dorsal stripes, face patterns, and large size of these species suggest that they may have arisen from an ancestor related to *Spartopyge*.

Description of the *albida* Group

Medium-sized to large. Length of ♂ 3.4–4.2 mm, of ♀ 3.6–4.8 mm. Dorsum with distinctive pattern of stripes extending from head across pronotum, scutellum, and forewings. Face pale with black interocular band. Male pygofer with poorly differentiated posterior lobe. Aedeagus with pair of bifurcate, apical appendages, unpaired ventral process.

Key to Species of the *albida* Group

1. Forewings rounded, male plates (Fig. 8A) not exceeding pygofer, female sternum VII not trilobed; prairie . . . . *albida* (Osborn & Ball)

— Forewings obliquely truncate, male plates exceeding pygofer (Fig. 8B); female sternum VII trilobed (Fig. 10B); Florida . . . . . . *slossonae* (Ball)

18. *Flexamia albida* (Osborn & Ball)

Deltocephalus albidus Osborn & Ball 1897: 201.
Deltocephalus (Flexamia) albidus, DeLong 1926: 36.
Flexamius albidus, DeLong and Sleesman 1929: 83.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.4–3.9) mm, of ♀ 4.3 (3.6–4.8) mm. Crown not strongly produced (median crown length 1.08 x interocular width, 0.57 x head width) (♂ n = 12; ♀ n = 21). Face entirely pale. Pronotum (Fig. 2A) traversed by six longitudinal stripes, central pair extending to rear of crown, across scutellum, and as spots on base of forewing; pair of transverse lines midway on crown. Forewings subhyaline with several highly pigmented cells, conspicuously pigmented, costal cross-veins, and conspicuous pigmentation along the inner edge of the forewing. [♂] Pygofer (Fig. 62Q) with posterior lobe short, with small, rounded, ventrally

produced lobe. Plates (Fig. 8A) elongate, unnotched. Aedeagus symmetrical, gonopore subapical on caudoventral surface. Aedeagal apex (Fig. 7B) with pair of distinctive, bifurcate processes, each with few teeth on the dorsal margin. Apodemal processes greatly expanded at apex. [♀] Sternum VII (Fig. 10A) with posterior margin shallowly concave on each side of produced median portion. Ovipositor with base of each first valvula (Fig. 63O) recurved, basal extremity rounded and directed caudodorsad.

GEOGRAPHIC DISTRIBUTION.—This species occurs in the prairie of Minnesota and North Dakota, east to Illinois and south to the Blackland tall-grass prairie of Texas (Fig. 30).

BIOLOGY.—*Flexamia albida* is a resident of tall-grass and mixed prairies. Many records are from *Schizachyrium scoparium*. However, *albida* is not found in pure stands of *S. scoparium*, suggesting a life history more complex than that of other *Flexamia* species.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Panicoideae 0.674 (*Schizachyrium scoparium* 0.674); Chloridoideae 0.196 (*Bouteloua curtipendula* 0.196) (n = 46).

REMARKS AND DIAGNOSIS.—The habitus of *F. albida* is unique, and its geographic range does not overlap that of the other striped *Flexamia* species.

19. *Flexamia slossonae* (Ball)

Deltocephalus slossoni [sic] Ball 1905: 119.
Deltocephalus (Flexamia) slossoni, DeLong 1926: 36.
Deltocephalus (Secopennis) slossoni, DeLong and Sleesman 1929: 85.
Flexamia slossoni, DeLong and Caldwell 1937: 27.
Secopennis slossonae, Oman 1949: 168.

IMPORTANT CHARACTERS.—Length of ♂ 3.8 (3.5–4.2) mm, of ♀ 4.2 (3.8–4.5) mm. Crown produced (median crown length 1.38 x interocular width, 0.64 x head width) (♂ n = 20; ♀ n = 20). Face ivory with black interocular band at base. Dorsum with longitudinal lines extending from rear of the head across pronotum and scutellum to rear of forewings (Fig. 2B). Male plates (Fig. 8B) exceeding pygofer in length. [♂] Aedeagus (Fig. 7C) symmetrical, gonopore an elongate slit extending through most of length of unpaired ventral process; apical processes bifurcate, without teeth. [♀] Sternum VII (Fig. 10B) conspicuously tri-lobed.
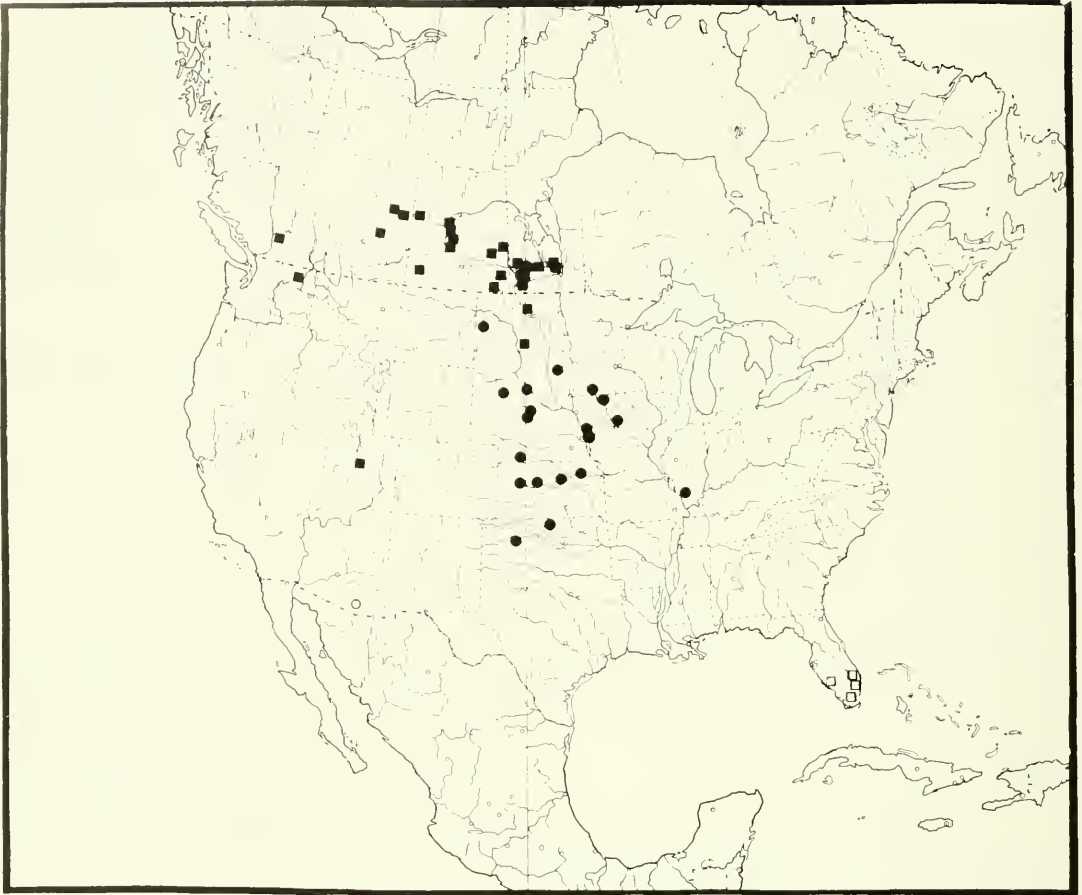
Fig. 30. Geographic distribution of *Flexamia serrata* (■), *albida* (●), *slossonae* (□), and *ritana* (○).

GEOGRAPHIC DISTRIBUTION.—*Flexamia slossonae* is restricted (Fig. 30) to subtropical grasslands of south Florida.

BIOLOGY.—DeLong (1926) reported finding adults and nymphs of *slossonae* on saltgrass (*Distichlis spicata*). We have found the species on the *Muhlenbergia* prairies of the Florida Everglades, in the absence of *Distichlis*. It seems likely that this species is a habitat rather than a host specialist.

REMARKS AND DIAGNOSIS.—Even if *slossonae* were not confined to the subtropical region of south Florida, its habitus would permit its unambiguous identification. The dorsal stripes of *albida* (Fig. 2A) are somewhat similar to those of *slossonae*, but in the latter species the stripes extend conspicuously to the rear of the forewings (Fig. 2B). Also, the

forewings (Fig. 2B) are obliquely truncate, exposing the terminal abdominal segment, which is also striped. The forewings of *ritana* (Fig. 2D) are broadly truncate.

VIII. The *ritana* Group

The *ritana* group consists of a single species. The monobasic group is defined by the bizarre aedeagal apex, which we designate as an autapomorphy.

20. *Flexamia ritana* Beamer

Flexamia ritana Beamer 1936: 257.

IMPORTANT CHARACTERS.—Length of ♂ 4.2 (3.9–4.4) mm, of ♀ 4.4 mm. Crown produced (mean crown length 1.67 x interocular width; 0.73 x head width) (♂ n = 4; ♀ n = 1). Dorsum

with stripes extending from head to forewings (Fig. 2D). Face pale white with broad, fuscous interocular band. [♂] Plates (Fig. 8D) about 1/2 length of pygofer, fused basally, tapering to bluntly acute apices. Aedeagus symmetrical, gonopore on caudoventral surface at base of unpaired processes (Fig. 7D); processes with entire edges, together lyriform; apodemal processes with anteapical protuberances. [♀] Sternum VII with conspicuous, median projection on hind margin.

GEOGRAPHIC DISTRIBUTION.—*Flexamia ritana* has been collected only in the Santa Rita Mountains of Arizona (Fig. 30).

BIOLOGY.—Despite many field hours expended in search, *ritana* has not been found since its collection in 1935. The original field notes of R. H. Beamer are not explicit in pinpointing the locality (see notes, Appendix III). Our field studies have emphasized collections on relatively pure patches of grass. Considering the accumulating evidence that primitive *Flexamia* species may be habitat specialists, future efforts should perhaps be directed at diverse habitats rather than single host species.

REMARKS AND DIAGNOSIS.—Superficially, *ritana* (Fig. 2D) resembles *albida* (Fig. 2A) but lacks transverse lines on the crown and has no darkly pigmented forewing cells. The forewings (Fig. 2D) are broadly truncate. The male plates and female sternum VII are entirely unlike those of either *slossonae* or *albida*.

IX. The *serrata* Group

This group consists of a single species. The defining autapomorphy of the group is the pair of dorsal, aedeagal processes.

21. *Flexamia serrata* Beamer & Tuthill

Flexamia serrata Beamer & Tuthill 1934: 4.

IMPORTANT CHARACTERS.—Length of ♂ 3.9 (3.6–4.3) mm, of ♀ 3.8 (3.2–4.4) mm. Crown moderately produced (mean crown length 1.26 x interocular width, 0.66 x head width) (♂ n = 20; ♀ n = 20). Face pale with interocular band consisting of parallel lines interrupted at middle. [♂] Pygofer (Fig. 62P) with posterior margin of lobe subangulate above midlength. Plates (Fig. 8C) short, broadly triangulate, about half length of pygofer, acute at apices. Aedeagus (Fig. 7A) subsymmetrical,

gonopore anteapical on caudoventral surface. Prominent, unpaired, ventral process basad of gonopore, extending basad along shaft, pair of shorter, recurved processes arising on each side of gonopore. Apodemal processes with mesal, anteapical protuberances. The unpaired aedeagal processes of some males from Linton, North Dakota (11 August 1977, 3 ♂, 3 ♀, R. F. Whitcomb, IPL 000351, and 24 July 1985, 34 ♂, 16 ♀, R. F. Whitcomb and E. A. Clark, IPL 001612) and Balta, North Dakota (1 ♂, 3 August 1985, K. G. A. Hamilton) are broken; such genitalia can be initially confusing. [♀] Sternum VII (Fig. 10C) with broad, median, posterior projection. Ovipositor with base of each first valvula very strongly recurved, recurved portion approximately parallel to axis of valvula (Fig. 63P).

GEOGRAPHIC DISTRIBUTION.—This species (Fig. 30) occurs from the southern tier of western Canadian provinces to Utah and North Dakota.

BIOLOGY.—*Flexamia serrata* is apparently associated with *Muhlenbergia richardsonis*, where it often occurs (especially in Canada) with *decora*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Muhlenbergia richardsonis* 1.000 (n = 57).

REMARKS AND DIAGNOSIS.—The face pattern of *serrata* (Fig. 3A) is unique. The range of this species overlaps considerably with that of *stylata*, which has superficially similar facial lines. However, in *stylata* the lines are not interrupted at the middle and contrast with a yellow rather than white face. The male plates of *stylata* (Fig. 34E) and the unique morphology of the male pygofer (Fig. 5C) also differentiate it from *serrata*. Whereas all individuals of *stylata* have at least a trace of a transverse line midlength on the crown, *serrata* has a completely unmarked crown.

X. The *flexulosa* Group

The *flexulosa* species group consists of 11 species. Evolution within this group has occurred on *Aristida*, *Bouteloua*, and, especially, *Muhlenbergia*. We have found no synapomorphy to define the group, but we have been able to define four subgroups. The nominate subgroup consists of two species. One of these, *arizonensis*, specializes on *Aristida purpurea* and/or other *Aristida* species. The other member of this subgroup is *flexulosa*, a

blue grama *(Bouteloua gracilis)* specialist. This species is designated as a sister to *arizonensis* on the basis of the extremely short, apically divergent plates, which are synapomorphic. The *decora* subgroup consists of three species. *F. decora* and *youngi* are identified as sisters on the basis of their ventral, aedeagal processes, which are much longer than the paired processes. Both are specialists on *Muhlenbergia richardsonis*. The current geographic distribution of these species suggests that they represent vicariant segregates of an ancestral *Muhlenbergia* specialist. The third species, *modica*, is a specialist on *Muhlenbergia repens* (a close relative of *M. richardsonis*) in more mesic grasslands of the eastern Desert Plains. This species is linked to the *decora* subgroup by the morphology of the male pygofer and female sternum VII. The third subgroup consists of three species: *arenicola*, a specialist on *Muhlenbergia pungens; stylata*, a specialist on *Muhlenbergia* species in uplands of the northern prairie and the eastern Rocky Mountains; and *celata*, a specialist of chloridoid grasses in sandhills, including sand blowout grass, *Redfieldia flexuosa*. The latter two species are designated sisters on the basis of their unique male pygofers, which are synapomorphic. A fourth subgroup consists of three species. One of these, *inflata*, a species of moist northern prairies, commonly occurs on *Muhlenbergia asperifolia*, which enables it to colonize riparian areas of the Southwest. *Flexamia texana*, a rare species from south central Texas whose biology is unknown, is designated sister to *beameri*, a species from New York whose biology is also unknown. The triangulate male plates and boat-shaped pygofers are synapomorphic for this subgroup.

Description of the *flexulosa* Group

Small to large. Length of ♂ 2.9–4.6 mm, of ♀ 3.0–4.7 mm. Gray to stramineous. Crown not strongly produced in some species *(decora, inflata)*, moderately produced in others. Face in many species *(flexulosa* and *decora* subgroups) white, ivory, or at the darkest, very pale yellow, contrasting sharply with dark, usually black interocular band. Face patterns in *stylata* subgroup similar, but with interocular band of parallel, discrete lines. In other species *(inflata* subgroup), face stramineous with no interocular band or at

most indistinct band not contrasting with lower face. Male plates triangulate, short or elongate, often apically divergent, in some species fused basally. Aedeagus and connective articulated. Aedeagus with paired apical processes and ventral unpaired process in sagittal plane, or displaced from sagittal plane *(inflata* subgroup). Gonopore apical or subapical on caudoventral surface. Female sternum VII with median projection.

Key to Males of the *flexulosa* Group

1. Pygofer produced caudally in spinelike process (Fig. 5C) 2
— Pygofer not so 3

2(1). Shaft of aedeagus thick, conspicuously curved, expanded apically with long, apical appendages (Fig. 31H) . . . . *stylata* (Ball)
— Shaft of aedeagus slender, not conspicuously curved or expanded apically, with shorter apical appendages (Fig. 31I) . . . *celata* Lowry & Blocker

3(1). Pygofer with posterior lobe produced, heavily sclerotized, and angled on ventral margin (Figs. 32E; 62MM) . . . . *arizonensis* Young & Beirne
— Pygofer with posterior lobe rounded ventrally . . 4

4(3). Aedeagus with greatly elongate, unpaired ventral process *and* with shaft straight or arched caudodorsally 5
— Aedeagus with paired and unpaired processes more or less same length *or* if one greatly elongate, then shaft sigmoidal 6

5(4). Aedeagal shaft (Fig. 31G) curved, unpaired process straight . . . . *decora* Beamer & Tuthill
— Aedeagal shaft (Figs. 31F, 38A,B) straight, unpaired process recurved . . . . *youngi*, n. sp.

6(4). Aedeagal shaft at least weakly sigmoidal in lateral aspect 7
— Aedeagal shaft arched caudodorsally, not sigmoidal 9

7(6). Aedeagus with paired processes less than 1/4 length of unpaired process, and not diverging from plane of shaft in lateral aspect (Fig. 31E) . . . . *inflata* (Osborn & Ball)
— Paired processes longer, and diverging from plane of shaft in lateral aspect 8

8(7). Aedeagal processes irregular, apex strongly asymmetrical (Fig. 31A); south central Texas . . . . *texana* Young & Beirne
— Aedeagal apex subsymmetrical (Fig. 31D), processes regular; New York . . . . *beameri*, n. sp.

9(6). Pygofer in lateral aspect with caudoventral margin from ventral lobe to caudal apex straight, not curved; paired processes of the aedeagus in lateral aspect diverging dorsally from the plane of the shaft; dorsal keels of the connective narrow; plates (Fig. 33A) small, short . . . . . *flexulosa* (Ball)
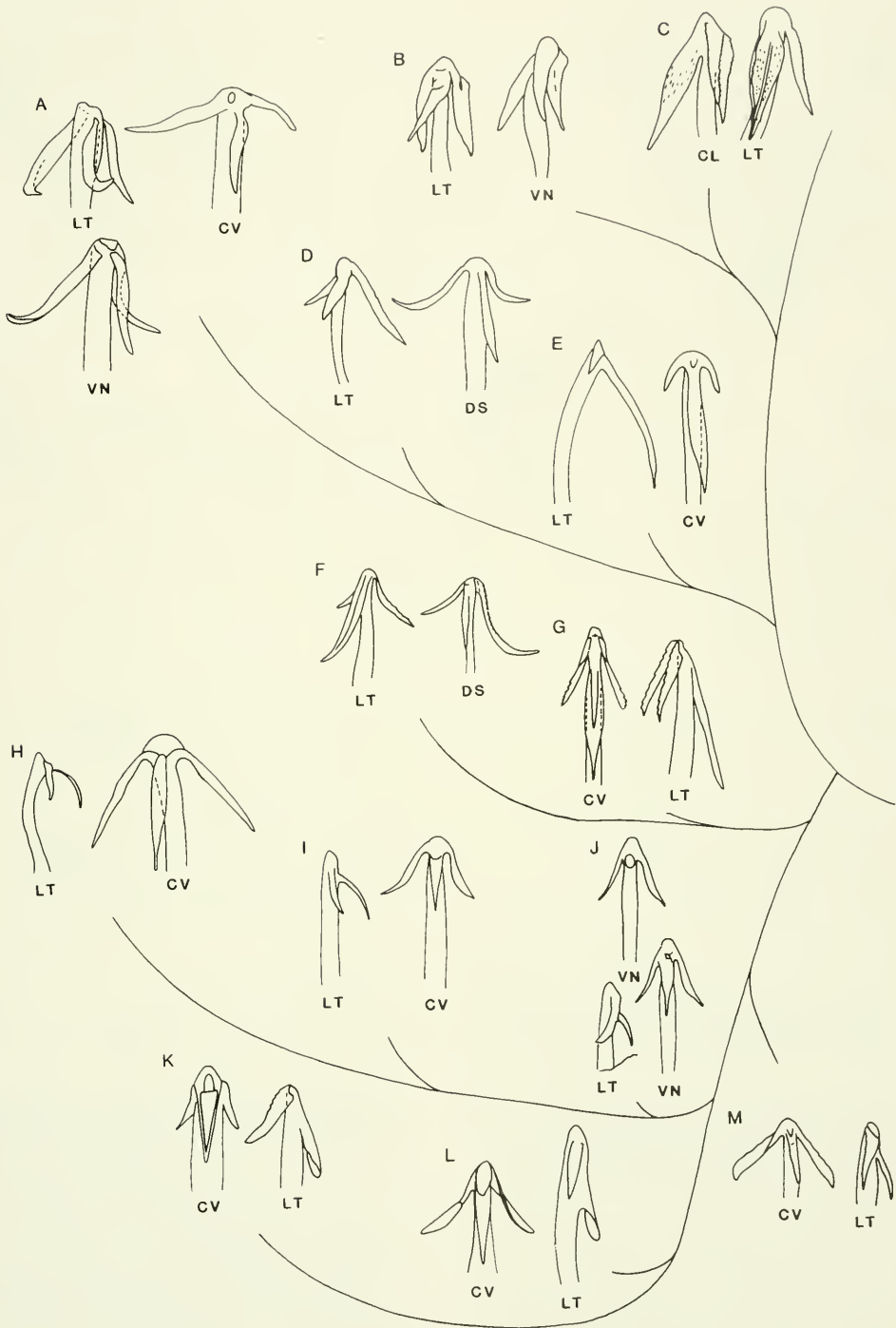
Fig. 31. Aedeagal apices of the *Flexamia flexulosa* group: A, *texana*; B, *imputans*; C, *areolata*; D, *beameri*; E, *inflata*; F, *youngi*; G, *decora*; H, *stylata*; I, *celata*; J, *arenicola*; K, *flexulosa*; L, *arizonensis*; M, *modica*. Aspects: CL, caudolateral; CV, caudoventral; DS, dorsal; LT, lateral; VN, ventral. Redrawn from Young and Beirne (1958).
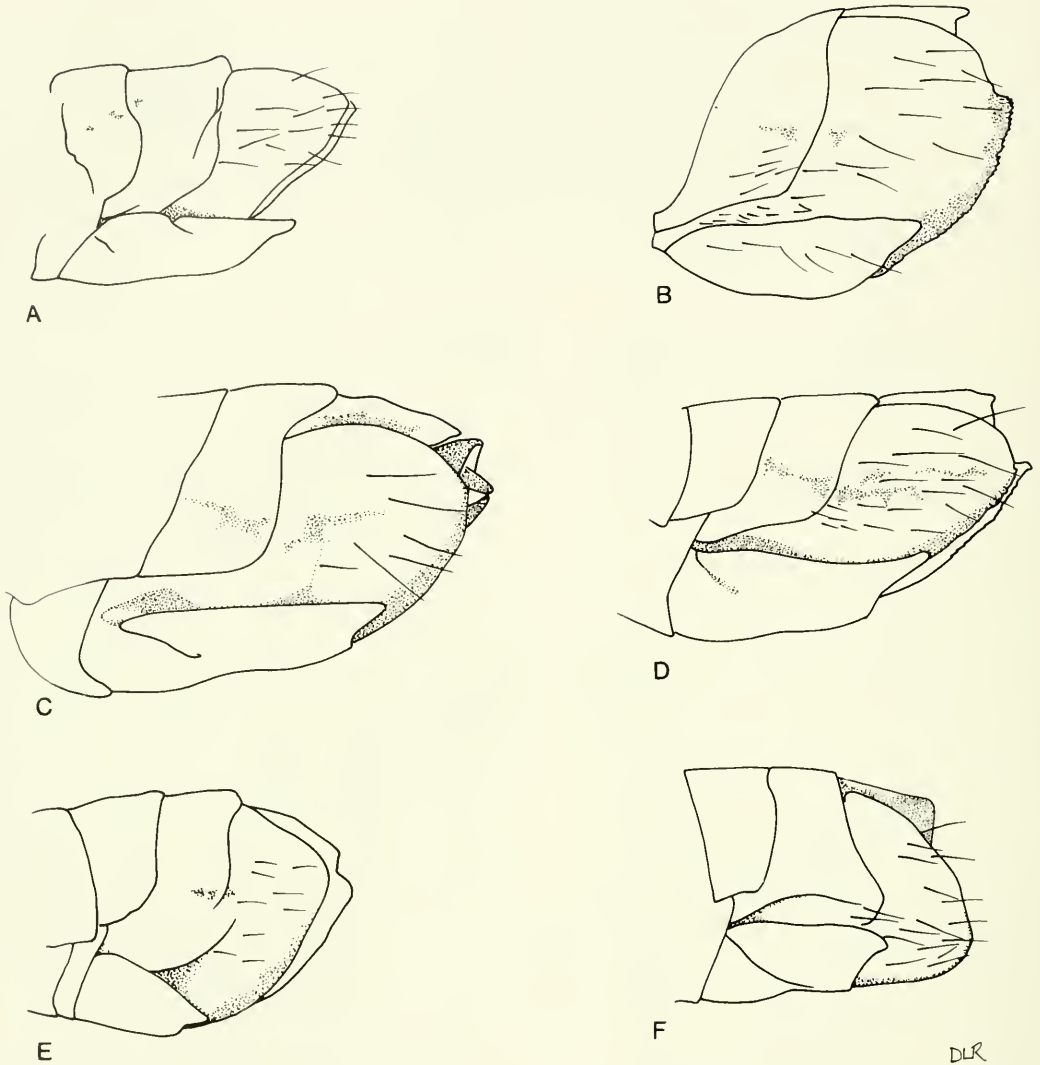
Fig. 32. Male plates and pygofers of some *flexulosa* group species, lateral aspect: A, *youngi*, B, *modica*, C, *arenicola*, D, *decora*, E, *arizonensis*, F, *flexulosa*.

—   Pygofer in lateral aspect with caudoventral margin curved from ventral lobe to caudal apex; paired processes of aedeagus in lateral aspect diverging weakly or not at all from the plane of the shaft; dorsal keels wider in lateral aspect; plates (Figs. 33C,F) comparatively long 10

10(9). Apices of paired processes curving ventrad in lateral aspect; processes and shaft of aedeagus comparatively robust . . . *modica* Beamer & Tuthill

—   Apices of paired processes curving dorsad in lateral aspect; processes and shaft comparatively slender . . . . *arenicola* Lowry & Blocker

Key to Females of the *flexulosa* Group

1.   Ovipositor with base of each first valvula curved

dorsad and laterad, forming angle of more than 45 degrees with long axis of valvula and extending laterad beyond lateral margin of valvula when viewed from above (Figs. 63Q,R,AA) 2

—   Ovipositor with recurved portion of each first valvula not extending laterad beyond lateral margin of valvula (or only very slightly so); if longer than broad, then with long axis forming angle of less than 45 degrees with axis of valvula in dorsal aspect 4

2(1).   Recurved base of each first valvula very slender in dorsal aspect, posterior margin concave (Fig. 63AA) . . . . *stylata* (Ball)

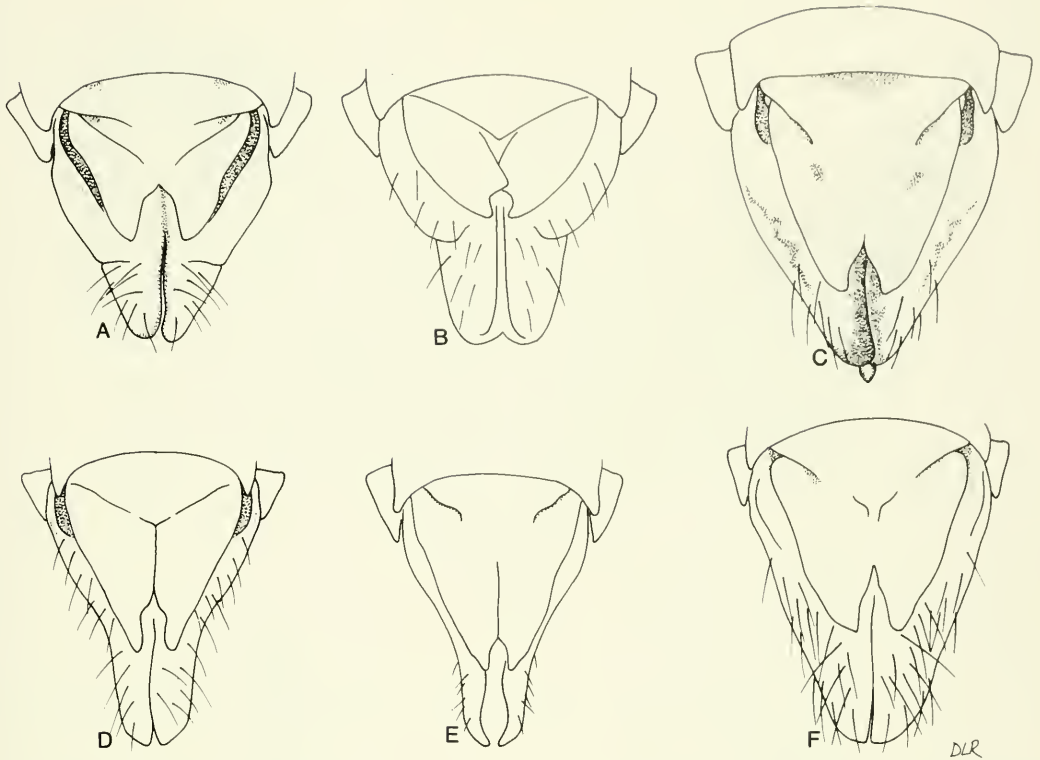—   Recurved base of each first valvula broader in

Fig. 33. Male plates and pygofers of the *Flexamia flexulosa* group: A, *flexulosa*; B, *arizonensis*; C, *arenicola*; D, *decora*; E, *youngi*; F, *modica*.

dorsal aspect, anterior margin straight or convex   3

3(2). Recurved base of each first valvula more distant from broadest part of valvula and with dorsal portion often lightly sclerotized and with small, anterior point (Fig. 63Q) . . . .*decora* Beamer & Tuthill

— Recurved base of each first valvula without small, anterior point and closer to broadest part of valvula (Fig. 63R)   . . . *modica* Beamer & Tuthill

4(1). Recurved portion of each first valvula short, with acute, dorsal projection directed anterolaterad (Fig. 63T) . . . .   *inflata* (Osborn & Ball)

— Recurved portion of first valvula without such projection   5

5(4). Recurved portion of first valvula concave posteriorly in dorsal aspect (Fig. 63Y) . . . . *arizonensis* Young & Beirne

— Recurved portion of each first valvula not so   . . .   6

6(5). Recurved portion of each first valvula directed almost caudally (Fig. 63BB) . . . . . . *flexulosa* (Ball)

— First valvula not so   7

7(6). Upper New York State . . . . *beameri*, n. sp.

— South central Texas . . . . . . *texana* Young & Beirne

22. *Flexamia arizonensis* Young & Beirne

Flexamia arizonensis Young & Beirne 1958: 30.

IMPORTANT CHARACTERS.—Length of ♂ 3.3 (3.0–3.8) mm, of ♀ 3.6 (3.2–4.0) mm. Head variably produced (1.40 x interocular width; 0.70 x head width) (♂ n = 20; ♀ n = 20). Face pale white with black interocular band. [♂] Pygofer with posterior lobe (Fig. 62MM) apically truncate, ventral portion extending ventrad as short, heavily sclerotized process. Plates short, less than 1/2 length of pygofer, apically divergent. Aedeagus symmetrical, paired apical processes arising on each side of subapical gonopore, unpaired ventral process about one-third length of shaft. [♀] Sternum VII with broad, median projection. Ovipositor with each first valvula (Fig. 63Y) curved at base more than 90 degrees, recurved portion concave caudally in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—This species is more widely distributed than had been previously supposed, occurring (Fig. 29) from
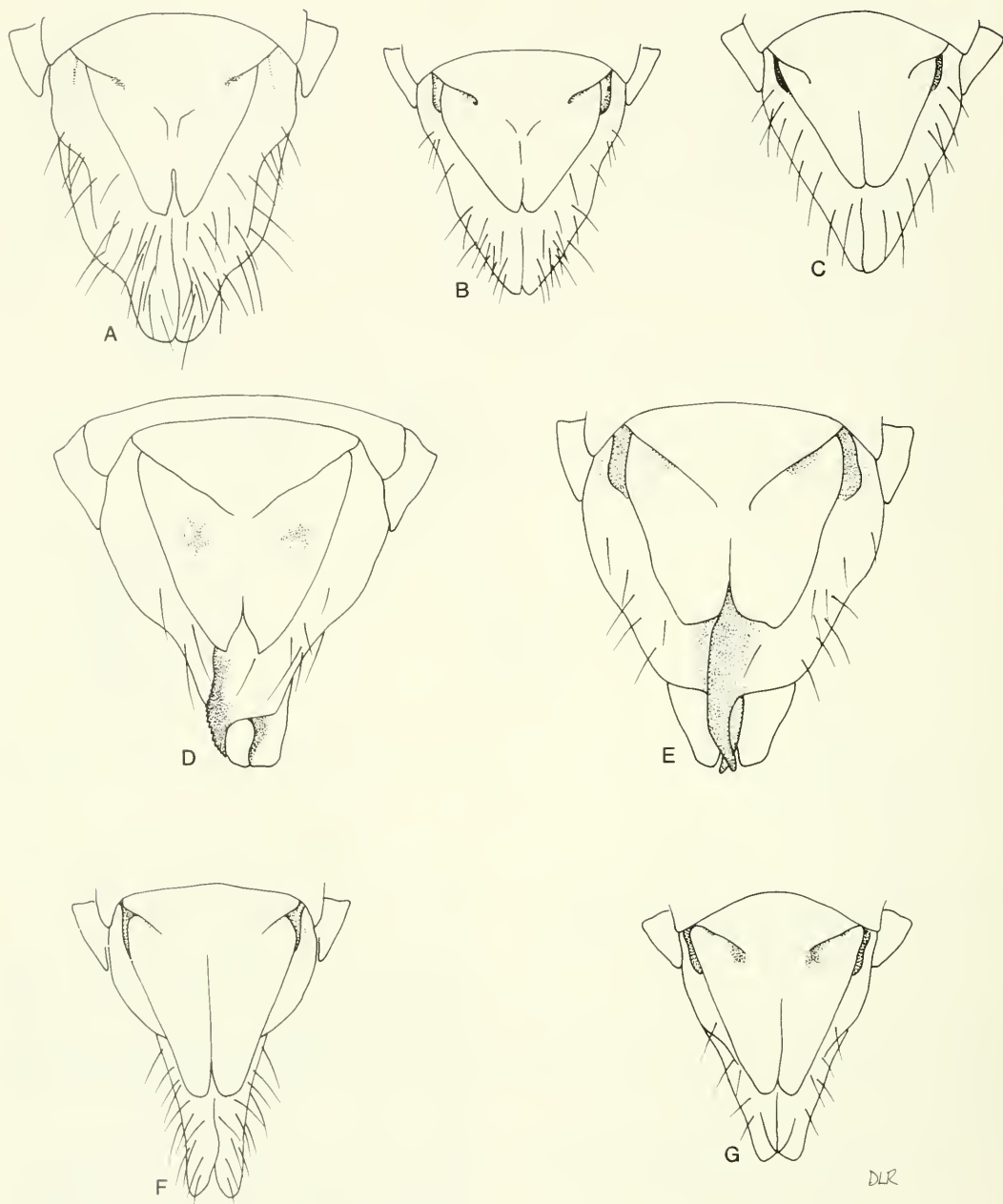
Fig. 34. Male plates and pygofers of the *Flexamia flexulosa, imputans,* and *areolata* groups, ventral aspect: A, *inflata*; B, *texana*; C, *beameri*; D, *celata*; E, *stylata*; F, *imputans*; G, *areolata*.

western Nebraska, Colorado, Utah, central Texas, and Arizona to northern Mexico (Sonora and Chihuahua). Two females from southern California (Pine Flats Camp, Indio, L. H. Banker, 12 July 1941 [KU]) may represent this species.

BIOLOGY.—This species is a specialist on perennial *Aristida* spp., especially *A. purpurea*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Aristida* spp. 0.932.

Fig. 35. Geographic distribution of *Flexamia flexulosa* and its host, *Bouteloua gracilis*.

REMARKS AND DIAGNOSIS.—Prior to the study of Young and Beirne, *arizonensis* had been confused with *flexulosa*. Males of these species can be distinguished by the lateral aspect of their undissected pygofers (Fig. 32E,F; see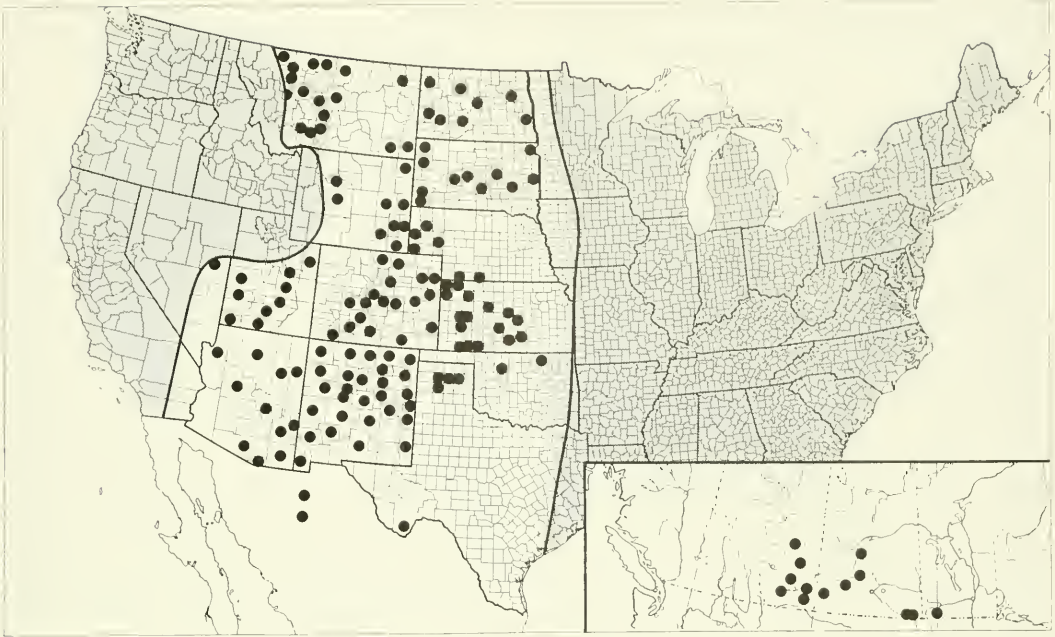 discussion under *flexulosa*). Although the dorsum of *arizonensis* is usually pale, several specimens from southern Arizona show dorsal stripes that are reminiscent of those of *ritana*. Since the external genitalic characteristics of *arizonensis* are very distinct from those of *ritana*, such specimens pose no problem for identification. However, they are important in suggesting an evolutionary link between the *ritana* and *flexulosa* groups.

23. *Flexamia flexulosa* (Ball)

Deltocephalus flexulosus Ball 1899: 189.
Deltocephalus (Flexamia) flexulosus, DeLong 1926: 31.
Flexamius flexulosus, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 3.2 (2.9–3.7) mm, of ♀ 3.5 (3.0–4.1). Head variably produced (1.26 x interocular width; 0.60 x head width) (♂ n = 40; ♀ n = 44). Face pale with black interocular stripe. [♂] Pygofer (Fig. 62NN) with posterior lobe rounded apically. Plates very short, less than 1/2 length of pygofer, apically divergent. Aedeagus symmetrical, gonopore anteapical on caudoventral surface; paired apical processes short, minutely serrulate along one edge; unpaired ventral process short, grooved, less than one-fourth length of the shaft, acute at apex. [♀] Sternum VII with hind margin produced to form convex lobe; ovipositor with each first valvula curved through more than 90 degrees at base, recurved portion slender, almost parallel to long axis of valvula, with narrow projection extending caudad at basal extremity.

GEOGRAPHIC DISTRIBUTION.—This species occurs (Fig. 35) from eastern Nevada, Utah, Wyoming, Montana, and the southern tier of Canadian provinces from Alberta to Manitoba, south through the Great Plains to western Texas, Arizona, and northern Mexico (Chihuahua).

BIOLOGY.—Although *flexulosa* and *abbreviata* are both specialists of blue grama (*Bouteloua gracilis*), their ranges do not completely overlap. Whereas *flexulosa* appears to be adapted solely to blue grama in cool, dry climates, *abbreviata* is adapted to warmer grasslands, especially the mixed *Bouteloua*

grasslands of Texas, New Mexico, and Arizona. Such differences may be important clues to the evolutionary origins of these *Flexamia* species.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000, Chloridoideae 0.973; *Bouteloua gracilis* 0.889 (n = 380).

REMARKS AND DIAGNOSIS. — Young and Beirne (1958) consider *flexulosa* to be "greatly variable." Actually, we have found substantial variability in all *Flexamia* species for which large sample sizes were available; *flexulosa* seems to us to be no more or less variable than other species. The face pattern of *flexulosa* (black interocular band contrasting with a pale face) is, in fact, remarkably stable. Unfortunately, this contrasting pattern is shared by other members of the *flexulosa* group (*arizonensis*, *modica*, *arenicola*, *decora*, and *youngi*). Although the definitive identity of these species should be ascertained by examination of genitalic characteristics, *flexulosa* is an abundant species, so it is important to define external characters that permit it to be sorted from less common species. The lateral aspect of the male pygofer (Figs. 32A–F) is a useful character in sorting white-faced members of the *flexulosa* group. In *flexulosa* the posterior margin of uncleared male pygofers appears rounded. The pygofer (Fig. 32E) of the widely distributed *arizonensis* is truncate apically, but it is necessary to clear the specimen to see the distinctive, heavily sclerotized ventral process. In regions where both *decora* and *flexulosa* occur, *decora* can often be recognized by its characteristic habitus (see discussion under that species), and by its pygofer (Fig. 32D), which appears narrower than that of other white-faced species. The pygofer of *modica* (Fig. 32B), an uncommon but locally abundant (New Mexico mountains) specialist of *Muhlenbergia repens*, is also diagnostic. The pygofer of *arenicola* (Fig. 32C) is also more or less diagnostic; this insect is an inhabitant of *Muhlenbergia pungens* in the Nebraska Sand Hills and the Four Corners region of the Colorado Plateau (Fig. 36). Thus, the combination of male pygofer, geographic range, and host data (if available) provides an excellent character set that permits tentative recognition of pale-faced males of the *flexulosa* group. Nevertheless, the identity of these species, including *flexulosa*, should be confirmed by examination of characters of the genitalia.

24. *Flexamia arenicola* Lowry & Blocker

Flexamia arenicola Lowry & Blocker 1987: 59.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.5–3.9) mm (Sand Hills form), 3.4 (3.2–3.8) mm (Anasazi form); of ♀ 4.0 (3.8–4.3) mm (Sand Hills form), 3.7 (3.3–4.1) mm (Anasazi form). Crown moderately produced (median crown length 1.19 x [Sand Hills form] or 1.35 x [Anasazi form] interocular width; 0.63 x head width [both forms]) (♂ n = 20, ♀ n = 7 [Sand Hills form]; ♂ n = 20, ♀ n = 18 [Anasazi form]). Crown moderately produced (median crown length 1.25 x interocular width; 0.67 x head width). Face pale, with conspicuous, black interocular band. [♂] Pygofer (Fig. 62LL) broadly ovate; plates (Fig. 33C) broadly triangulate, diverging apically. Aedeagus (Fig. 31J) symmetrical with gonopore anteapical on the caudoventral surface, lateral, apical processes approximately one-fourth shaft length and curved laterodorsad; unpaired process approximately the same length and directed anteriorly. [♀] Sternum VII with posterior margin produced medially with small, median notch. Ovipositor with recurved process at base of first valvula (Fig. 63S) not exceeding lateral margin, process extending caudad, sinuate and digitate apically.

GEOGRAPHIC DISTRIBUTION.—There are two disjunct populations of *arenicola* (Fig. 36). One population occurs in the sandhills of western Nebraska and northeastern Colorado. The other population occurs in the Colorado Plateau and adjacent regions of New Mexico. The disjunct distribution of *arenicola* can be readily explained by the essentially disjunct distribution of its host (Fig. 36).

BIOLOGY.—*Flexamia arenicola* has been found almost exclusively on sandhill muhly, *Muhlenbergia pungens*.

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 1.000; *Muhlenbergia pungens* 0.989 (n = 91).

REMARKS AND DIAGNOSIS.—The unpaired processes of the aedeagus in males of the Four Corners population (which we term the "Anasazi form" in honor of the pre-Columbian residents of the area) is uniformly absent, but on close inspection it can be seen to be broken; this presumably occurs during copulation. The occurrence of the Anasazi form is
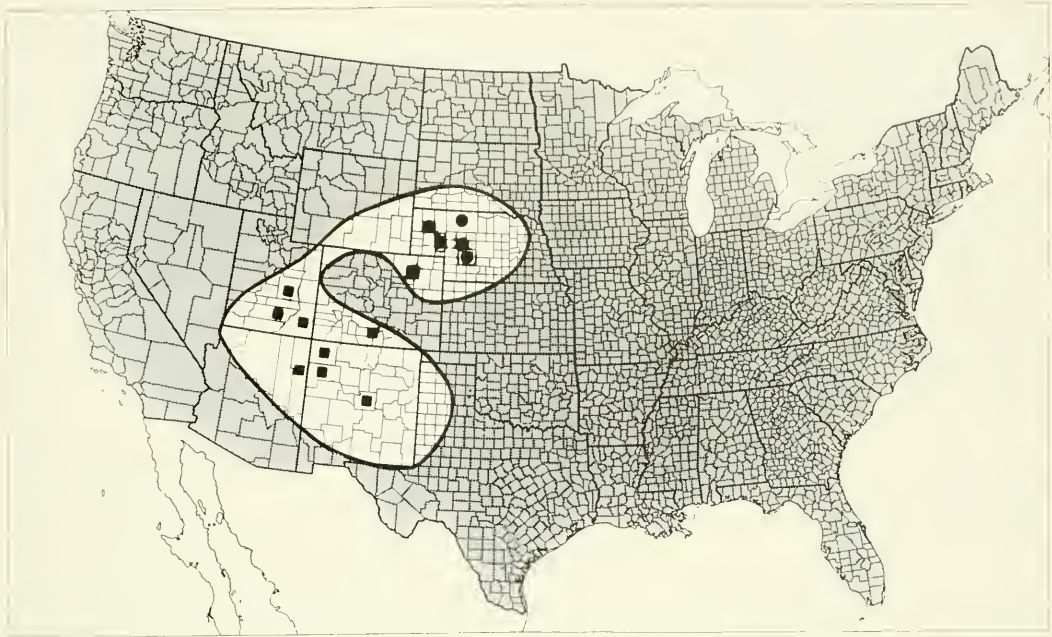
Fig. 36. Geographic distribution of *Flexamia arenicola* (Sand Hills [●] and "Anasazi" [■] forms) and the host, *Muhlenbergia pungens*.

patchy, and populations usually are low. Because the region occupied is now undergoing desertification and salinization as a result of climatic changes during the interglacial era, this form may be a relict population that, like the host population, is currently stressed by climatic change. Presumably, the outcome of these selective pressures could lead to extirpation or to evolution of a new species that would be better adapted to semiarid environments. The characteristics of the male pygofer (Fig. 32C) in lateral aspect, in combination with the face characteristics, are diagnostic for *arenicola*. Lowry and Blocker (1986) distinguished *arenicola* from *flexulosa* by the expanded dorsal keels of the *arenicola* connective, the more robust aedeagal shaft, and the longer aedeagal processes. They distinguished *arenicola* from *modica* by its larger size and nearly symmetrical aedeagus with lateral, dorsally curved, apical processes. In addition, the pygofer of *modica* (Fig. 32B) is very different from that of *arenicola*. Some characters in *arenicola* are similar to those of *celata* and *stylata*, but the general facies of the latter two species separate them from *arenicola*.

25. *Flexamia celata* Lowry & Blocker

Flexamia celata Lowry & Blocker 1987: 57.

IMPORTANT CHARACTERS.—Length of ♂ 4.1 (3.9–4.4) mm, of ♀ 4.5 (4.4–4.7) mm. Crown not produced (1.13 x interocular width; 0.58 x head width) (♂ n = 19; ♀ n = 6). Face, as in *stylata*, pale with broad interocular band consisting of parallel, discrete lines. [♂] Pygofer (Fig. 62PP) with central margin strongly produced to form spinelike process, as in *stylata*. Plates (Fig. 34D) extending to approximately 2/3 length of pygofer, fused mesally for 1/2 length, narrowed apically to rounded, lateral lobe, apices meeting in V-shaped notch. Aedeagus (Fig. 31I) symmetrical, shaft slender, neither conspicuously curved nor expanded apically, ventral and paired apical processes approximately equal in length and less than 1/4 length of shaft; gonopore apical on caudoventral surface. [♀] Sternum VII with posterior margin medially produced, with slight median notch; ovipositor with basal processes of first valvulae recurved and extending laterad beyond lateral margin.

GEOGRAPHICAL DISTRIBUTION.—Nebraska Sand Hills and southwestern Kansas (Fig. 37).
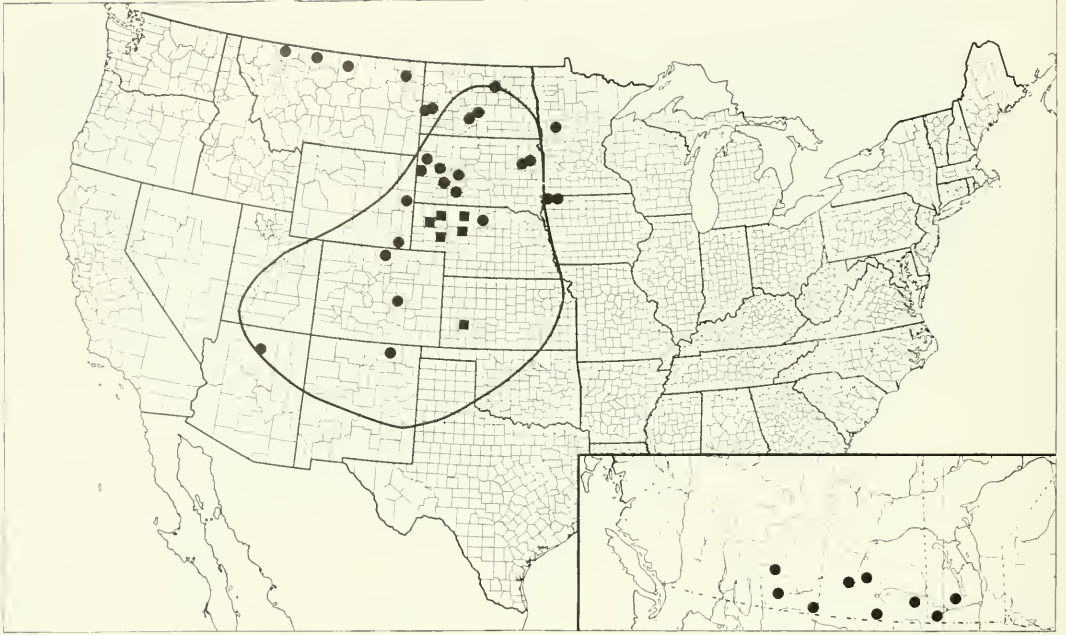
Fig. 37. Geographic distribution of *Flexamia stylata* (●) and *celata* (■) and a host of *celata*, *Redfieldia flexuosa*.

BIOLOGY.—This species occurs on sand blowout grass, *Redfieldia flexuosa*, the primary colonist of bare sand in the Sand Hills. It may also occur on other sandhill grasses. It has been recorded from *Calamovilfa longifolia* in southwestern Kansas (1 ♂, 3 ♀, Garden City, Finney County, 12 June 1948, R. H. Beamer).

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; *Redfieldia flexuosa* 0.612; *Muhlenbergia pungens* 0.265 (n = 49).

DIAGNOSIS AND REMARKS.—This is a close sister species with *stylata*, under which diagnostic characters have been discussed. The present-day area of endemism was apparently created by the southern interface of the ice sheet during the last glacial maximum (Wright 1970), suggesting that *celata* could represent a recent speciation. On the other hand, its morphological characters are much closer to the ground plan for the *flexulosa* group than are those of *stylata*. The aedeagal symmetry and wide pygofer of *celata* suggest a relationship with *arenicola*, which occurs with it in the Nebraska Sand Hills.

26. *Flexamia stylata* (Ball)

Deltocephalus stylatus Ball 1899: 190.

Deltocephalus (Flexamia) stylatus, DeLong 1926: 34.
Flexamius stylatus, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 4.1 (3.7–4.6) mm, of ♀ 4.2 (3.8–4.6) mm. Crown not strongly produced (1.17 x interocular width; 0.54 x head width) (♂ n = 33; ♀ n = 33). Face pale, except for broad interocular band consisting of discrete, parallel lines. [♂] Plates (Fig. 34E) with conspicuous, subrectangular apices; pygofer (Fig. 62OO) with posterior margin strongly produced, gradually narrowed, forming curved, spinelike process. Aedeagus asymmetrical; shaft subcylindrical; gonopore subapical, at base of three processes on caudoventral surface; pair of apical processes directed laterobasad, unpaired ventral process extending basad to midlength of shaft, but not parallel to axis of shaft, the three processes appearing subequal in length in caudoventral aspect; paired processes appearing shorter in lateral aspect, each slightly serrate on dorsal edge. [♂] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63AA) curved dorsad through slightly more than 90 degrees, recurved portion extending laterad beyond lateral margin

of valvula in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Southern tier of Canadian provinces south through the western Great Plains, eastern Rocky Mountains, northern New Mexico, and Arizona (Fig. 37).

BIOLOGY.—This species has been collected from *Muhlenbergia* on upland slopes in Montana and Wyoming. In northern New Mexico the host is *Muhlenbergia wrightii*. This host may also account for records from northern Arizona.

DIAGNOSIS AND REMARKS.—The male plates of this species are unique. The face pattern (interocular bands with discrete lines) that *stylata* shares with *celata* is very distinctive; superficially similar species almost always have bands with coalesced lines. Finally, *stylata* specimens are larger than those of most other species. Females of *stylata* and *celata* are similar but can be distinguished by characteristics of the bases of the first valvula of the ovipositor. Also, *stylata* is a widely distributed *Muhlenbergia* specialist, whereas *celata* is restricted largely to the Nebraska Sand Hills, where it is a rare inhabitant of *Redfieldia flexuosa* and other chloridoid grasses.

27. *Flexamia decora* Beamer & Tuthill

Flexamia decora Beamer & Tuthill 1934: 2.

IMPORTANT CHARACTERS.—Length of ♂ 3.6 (3.0–4.2) mm, of ♀ 3.9 (3.4–4.2) mm. Head not strongly produced (median crown length 1.07 x interocular width, 0.62 x head width) (♂ n = 20; ♀ n = 20). Face pale with broad black interocular stripe. [♂] Pygofer (Fig. 62FF) with slightly truncate rear margin. Plates (Fig. 33D) broadly divergent, with narrow apices. Aedeagus (Fig. 31G) symmetrical. Gonopore anteapical on caudoventral surface; pair of retrorse processes arising on each side of gonopore, each serrate on dorsal edges. Unpaired ventral processes, with entire edges, extending basad more than half length of shaft. [♀] Sternum VII with hind margin concave at each side of median convex projection, notched apically, with teeth on each side of notch. Ovipositor with each first valvula (Fig. 63Q) with base expanded dorsally and laterally.

GEOGRAPHIC DISTRIBUTION.—*Flexamia decora*, as defined herein, is a specialist of *Muh-*

lenbergia richardsonis in the New Mexico and Colorado Rockies north to the Peace River region of northwestern Alberta, and east to Manitoba and North Dakota (Fig. 39). Its host occurs in eastern North America but does not occur south of Maine. We have examined specimens reported by Young and Beirne (1958) from Kentucky and Virginia. The Kentucky specimen is a female referable to *inflata*. The Virginia specimen labeled only "Oct. 12, Va., ED. Ball" appears to have been recently relabeled (and therefore possibly mislabeled), perhaps at the time of acquisition of the Ball collection. There are therefore no reliable records for *decora* east of the mixed-grass prairie.

BIOLOGY.—*Flexamia decora* appears to be largely a specialist of *Muhlenbergia richardsonis*. Large populations are not uncommon, and *decora* is the most abundant *Flexamia* species in the CNC (Appendix I).

OLIGOPHAGY COEFFICIENTS.—Gramineae 1.000; Chloridoideae 0.874; *Muhlenbergia richardsonis* 0.874. [Note: *M. richardsonis* has been present in all communities where *decora* occurs.]

REMARKS AND DIAGNOSIS.—Many individuals of *decora* have a rather distinctive habitus, with very dark forewing markings, especially on the apical portions, and along the veins of the forewing that contrast sharply with the lighter pronotum and crown. Unfortunately, paler specimens are not rare; the identity of these specimens is often indicated by the extremely short crown length. *Flexamia decora* and its close sister species, *youngi*, are apparently restricted to *Muhlenbergia richardsonis*.

28. *Flexamia youngi*, n. sp.

Length of ♂ 3.7 (3.4–3.9) mm, ♀ 3.8 (3.7–4.2) mm; head width of ♂ 1.12 mm, ♀ 1.18 mm. Crown not produced; median length of crown approximately 1.11 x head width and 0.58 x interocular width (♂ n = 16; ♀ n = 20).

Color stramineous. Crown with at most a trace of basal or midlength markings. Pronotum with or without traces of wide, brown stripes. Face with black interocular line contrasting with white lower face. Venter stramineous.

MALE.—Pygofer (Fig. 38D) as in *decora* but with posterior lobe less angulate, more
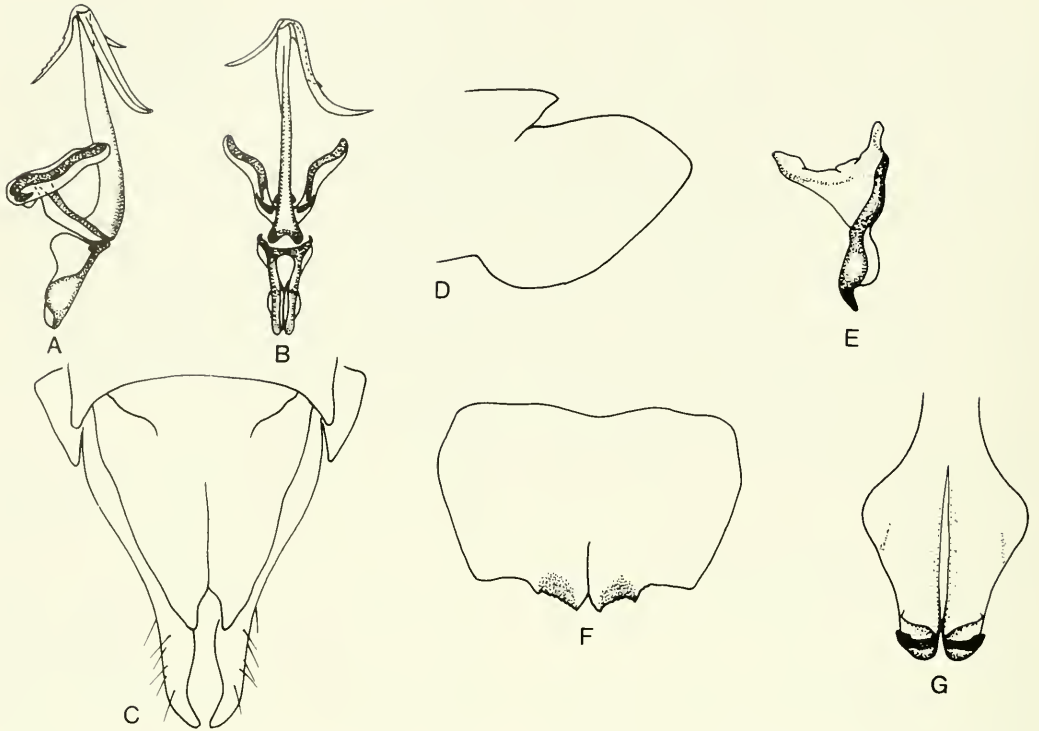
Fig. 38. *Flexamia youngi*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, male plates and pygofers, ventral aspect; D, male pygofer, lateral aspect; E, right style, dorsal aspect; F, female sternum VII; G, bases of first valvulae of female, dorsal aspect.

broadly rounded ventrally; plates (Fig. 38C) extending approximately 2/3 length of pygofer, fused basally for 2/3 length, connective in lateral aspect (Fig. 38A) with dorsal keels broad, approximately 1/3 height of dorsal apodeme; apodemal processes sinuate in ventral view, bell-shaped in caudal aspect; styles as in other members of *decora* subgroup; aedeagus (Fig. 38B) asymmetrical, shaft elongate, apparently twisted 1/8 turn counterclockwise in caudal aspect, tapering gradually in lateral aspect, slightly enlarged apically in ventral aspect; three apical processes extending basad; unpaired process recurved, entire, with median ventral groove almost 1/2 length of shaft. Paired processes recurved, serrate on dorsal edges, approximately 1/3 length of unpaired process. Gonopore small, circular, and apical.

FEMALE.—Sternum VII (Fig. 38F) with posterior margin produced medially, pro-nounced median notch with infuscated spots on either side. Ovipositor with base of first valvula (Fig. 38G) recurved, appearing tear-shaped and only slightly exceeding lateral margins when viewed dorsally.

TYPES.—Holotype ♂: White Pine County, Nevada, Baker, 10 August 1986, R. F. Whitcomb (IPL 002590, *Muhlenbergia richardsonis*). Deposited USNM. Paratypes: 10 ♂, 11 ♀, same collection data; 1 ♀, Mt. Wheeler, White Pine County, Nevada, 10 August 1986, 8,500 ft, IPL 002569; 4 ♂, 4 ♀, Spring Valley, White Pine County, Nevada, 11 August 1986 (5,800 ft, R. F. Whitcomb, IPL 002596). Deposited in BARC, CNC, KSU, and USNM. Paratypes (KU) were also collected by R. H. Beamer (1 ♀, Deeth, Elko Co., Nevada, 21 July 1947); and D. H. Lindsay (1 ♂, 3 ♀ Soldier Summit, Utah, 13 August 1936).

REMARKS.—This species, apparently a Great Basin endemic (Fig. 39), is closely
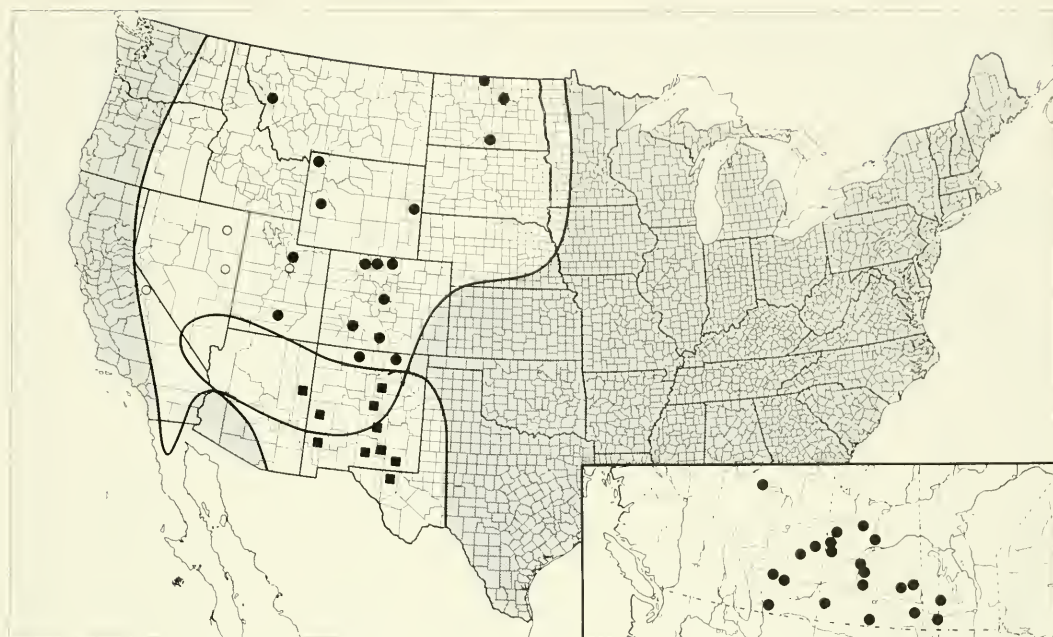
Fig. 39. Geographic distribution of *Flexamia decora* (●), *youngi* (○), and *modica* (■), and their hosts, *Muhlenbergia richardsonis* (*decora* and *youngi*) and *M. repens* (*modica*).

related to *decora* but can be distinguished from it by the shape of the aedeagus, which is straight and twisted rather than curved and symmetrical, and by the recurved, apical processes. The host so far as known is (like *decora*) *Muhlenbergia richardsonis*. This species is named in honor of D. A. Young, whose classic monograph, with B. P. Beirne, established the modern generic concept of *Flexamia*.

29. *Flexamia modica* Beamer & Tuthill

Flexamia modica Beamer & Tuthill 1934: 3.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.1–3.7) mm, of ♀ 3.8 (3.4–4.0) mm. Crown moderately produced (1.26 x interocular width, 0.62 x head width) (♂ n = 20; ♀ n = 20). Face ivory, with broad interocular band. [♂] Pygofer (Fig. 62JJ) as in *decora*. Plates (Fig. 33F) short, about 2/3 length of pygofer, broadly triangulate, widely divergent at apices. Aedeagus (Fig. 31M) asymmetrical, gonopore triangular; unpaired ventral process less than half length of shaft, base appearing fused to shaft in lateral aspect. [♀] Sternum

VII with broad median projection; ovipositor with base of each first valvula turned dorsad through 90 degrees and bilobed, recurved portion extending strongly laterad and exceeding lateral margin of valvula in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—High desert plains of southern New Mexico and adjacent counties of Trans-Pecos Texas and Arizona (Fig. 39). It is abundant in the Sacramento Mountains of southeastern New Mexico on its host *Muhlenbergia repens*. It is much less common in the Gila Mountains, where its host is more patchy, and occurs rarely in the central Guadalupe Mountains (Guadalupe Mountains National Park, Culberson Co., Texas) and northeastern Arizona (St. Johns, Apache Co.).

BIOLOGY.—Apparently a specialist of *Muhlenbergia repens*. Our records show seven series from this host 16–18 June 1985 (R. F. Whitcomb and K. A. Allred, approximately 440 ♂, ♀, and immatures). *M. repens* is closely related to *M. richardsonis* (Morden 1985, Morden and Hatch 1987). It is likely that *modica* arose from the *decora* lineage via

a host transfer from *M. richardsonis.*

Oligophagy coefficients.—Gramineae 1.000; Chloridoideae 1.000; *Muhlenbergia repens* 1.000 (n = 377).

30. *Flexamia inflata* (Osborn & Ball)

Deltocephalus inflatus Osborn & Ball 1897: 202.
Deltocephalus (Flexamia) inflatus, DeLong 1926: 35.
Flexamius inflatus, DeLong and Sleesman 1929: 84.

Important characters.—Length of ♂ 3.8 (3.1–4.4) mm, of ♀ 4.0 (3.6–4.6) mm. Crown short (1.11 x interocular width; 0.58 x head width) (♂ n = 26; ♀ n = 26). Face stramineous, with or (more frequently) without a basal, pale brown interocular band. [♂] Pygofer (Fig. 62GG) with upper portion of posterior lobe strongly produced posteriorly. Plates (Fig. 34A) short, about 1/2 length of pygofer, apically divergent. Aedeagus (Fig. 31E) asymmetrical; shaft elongate, slender, gradually broadened apically; gonopore apical on caudoventral surface; pair of short, recurved processes arising on each side of gonopore, slender, unpaired ventral process almost half length of shaft, slightly expanded anteapically, acute at apex, which extends to right of shaft, all processes with edges entire. [♀] Female sternum VII broadly, medially produced, medially notched with traces of teeth between notch and lateral margin; ovipositor with base of each first valvula (Fig. 63T) curved dorsad, small projection on dorsal edge extending dorsolaterad, entire curved portion more heavily sclerotized and appearing almost as separate sclerite in ventrolateral aspect.

Geographic distribution.—This species is distributed (Fig. 41) from Utah, Texas, and New Mexico north to British Columbia and Manitoba east to Pennsylvania.

Biology.—This species may be adapted to northern mixed grasslands where pooid grasses, *Juncus* spp., and *Muhlenbergia* grow in intermixed stands. In the Southwest, at least, *inflata* is a specialist on *Muhlenbergia asperifolia*; occasional collections have also been made on *Distichlis spicata.* We do not have host records from the Northwest, but the northern limit of the distribution of *inflata* coincides roughly with that of *Muhlenbergia asperifolia.* In Illinois it occurs on *Juncus tenuis.* In Maryland it occurs on *Juncus tenuis* and on the introduced grasses *Cynodon dacty-*

lon, Zoysia japonica, and *Eragrostis curvula.* This species has been reared on *J. tenuis* (Whitcomb 1957). Populations occasionally turn up for a time on *Festuca* or *Poa* but never seem to persist. We have observed no morphological indications of host races, although it is possible that the *Juncus* populations may be reproductively isolated from other populations. Rearing studies may be required to resolve the status of the biology of *inflata.*

Oligophagy coefficients.—Prairie and savanna: Gramineae 0.725, Juncaceae 0.275; Chloridoideae 0.725, *Muhlenbergia asperifolia* 0.562; *Eragrostis curvula* 0.066 (n = 379). Other records: Manitoba (Woodside, 24 August 1981, 16 ♂, 16 ♀, *Poa pratensis,* K. G. A. Hamilton, CNC).

Remarks and diagnosis.—Although definitive identification of *inflata* requires examination of the genitalia, it is important to learn to sort the majority of specimens of this often abundant species on the basis of habitus alone. The vast majority of specimens of *inflata* are very lightly pigmented; these can be recognized by their light stramineous color in combination with a black spot on the apical forewing cell (Fig. 4A), by the lack of a spot in the corium, and by their crown, which is one of the shortest in the genus.

31. *Flexamia beameri,* n. sp.

Length of ♂ 3.2 (3.1–3.3) mm, ♀ 3.4 (3.3–3.4) mm; head width of ♂ 0.93 mm, ♀ 1.06 mm. Crown moderately produced; median length of crown 0.67 x head width and 1.39 x interocular width (♂ n = 6; ♀ n = 2).

Color stramineous with dark markings on corium and apical cell of forewings; face as in *inflata* and *texana*; head with light markings, pronotum with wide, faint stripes; venter and legs with irregular, fuscous markings.

Male.—Pygofer (Fig. 40D) as in *texana*; plates extending to approximately 2/3 length of pygofer, fused basally for 3/4 length; connective in lateral aspect (Fig. 40A) with dorsal keels broad, approximately 2/3 height of dorsal apodeme; apodemal processes narrowly campanulate in caudal aspect; style (Fig. 40E) as in *inflata* and *texana*; aedeagus (Figs. 40A,B) slightly asymmetrical, shaft sigmoidal in lateral view, ventral unpaired process not quite in median plane of shaft and appearing slightly longer than strongly recurved, paired, lateral processes; all processes with edges entire; gonopore circular and apical.
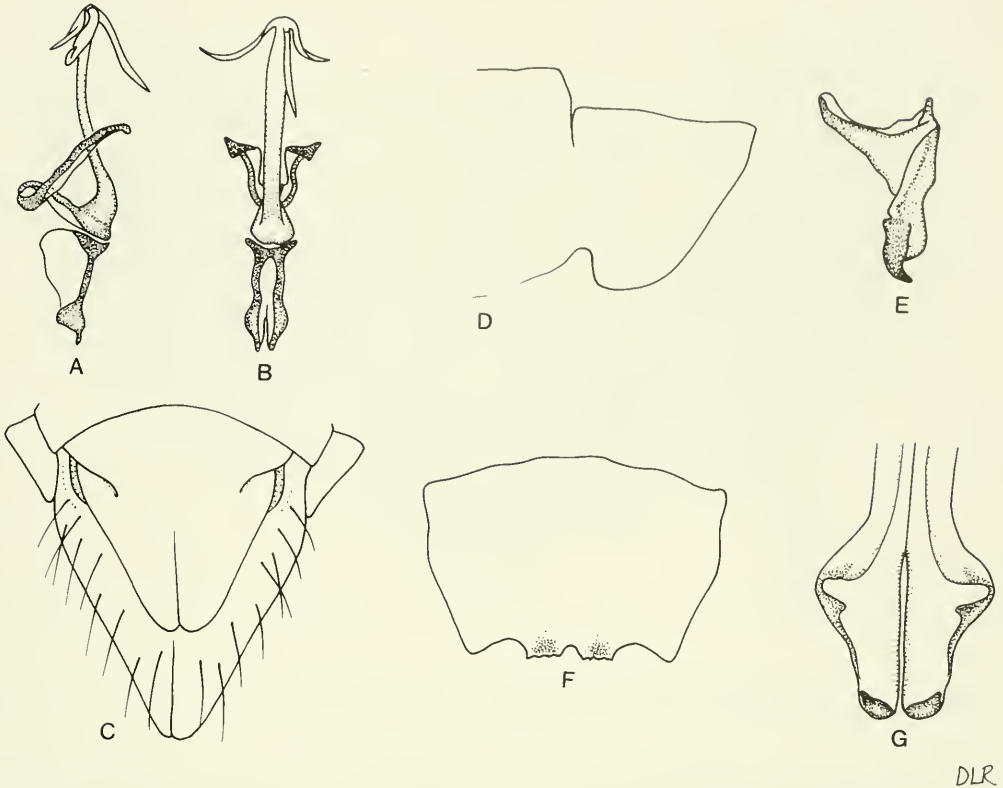
Fig. 40. *Flexamia beameri*, n. sp.: A, aedeagus and connective, lateral aspect; B, aedeagus and connective, dorsal aspect; C, male plates and pygofers, ventral aspect; D, male pygofer, lateral aspect; E, right style, dorsal aspect; F, female sternum VII; G, bases of first valvulae of female, dorsal aspect.

FEMALE.—Sternum VII (Fig. 40F) similar or identical to *texana*, with median notched projection adjoined on each side by serrulate, infuscated projections; ovipositor with recurved portion of the bases of each first valvula (Fig. 40G) narrowing to diverging apices in dorsal aspect.

TYPES.—Holotype ♂: Otter Lake, Oneida County, New York, 25 June 1946, R. H. Beamer. Deposited KU. Paratypes: 5 ♂ and 2 ♀, same locality, deposited KU and USNM.

REMARKS.—This species, known from a single collection at its type locality (Fig. 41), is a sister to *texana*, a species also known from a single collection made long ago. *Flexamia beameri* can be readily separated from *inflata* and *texana* by the shape and length of the aedeagal processes. The aedeagal characters of *beameri* resemble those of *texana*, but the processes of *beameri* are not twisted. Presumably, the ranges of *beameri* and *texana* are

very different. In contrast to the hot climate of south central Texas, the type locality of *beameri* is located in one of the coolest regions of New York (see Notes, Appendix III). Since we have not yet encountered these species in the field, their biology is a mystery. This species has been named in honor of R. H. Beamer, who described several interesting species of the genus and who collected the holotype and paratypes at a geographic site far from his home base.

32. *Flexamia texana* Young & Beirne

Flexamia texana Young & Beirne 1958: 29.

IMPORTANT CHARACTERS.—Length of ♂ 3.1 (2.9–3.2) mm, of ♀ 3.2 (3.0–3.5) mm. Crown not strongly produced (1.30 x interocular width, 0.63 x head width) (♂ n = 8; ♀ n = 2). [♂] Pygofer (Fig. 62HH) with upper margin flat in lateral aspect, posterior margin gradually rounded. Aedeagus
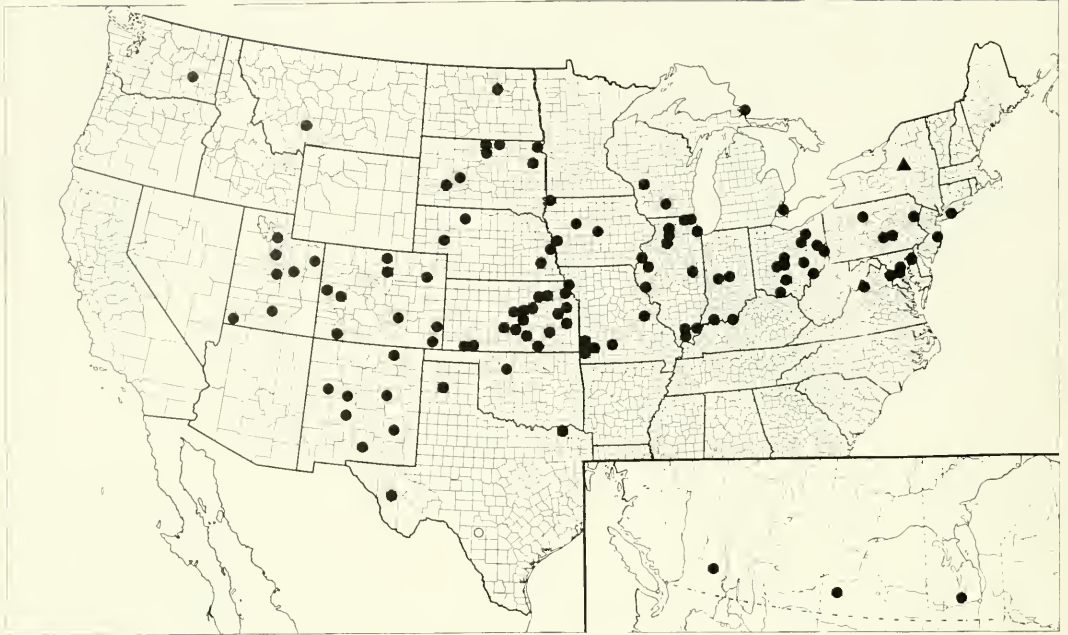
Fig. 41. Geographic distribution of *Flexamia inflata* (●), *beameri* (▲), and *texana* (○).

(Fig. 31A) asymmetrical; unpaired ventral and pair of lateral processes, all about equal in length, arising near gonopore; ventral process not in sagittal plane, lateral processes not in symmetrical planes. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63CC) curved dorsad through about 90 degrees in lateroventral aspect, base acute in lateral aspect, regularly convex in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Known only from the type locality (Uvalde, Texas).

BIOLOGY.—The host of *texana* is unknown. Uvalde is situated just south of the southern edge of the Edwards Plateau. We have surveyed the main, dominant, warm-season grasses of the Edwards Plateau searching for this species. Although these searches turned up a new species, *collorum*, they failed to locate *texana*. The grasslands of the mesquite-acacia savannah south of Uvalde have been largely plowed for agricultural crops. Perhaps E. D. Ball was afforded an opportunity to collect in these grasslands before they were sacrificed for agriculture. If this is the explanation for the rarity of this species, we may experience continuing difficulty in our search

for this elusive species. On the other hand, discovery of the sister species *beameri*, whose type locality suggests a marshy wetland, raises the possibility that *texana* may turn up in wetlands in south Texas, which were overlooked in our searches.

XI. The *imputans* Group

The *imputans* group consists of a single species, which is apparently a *Muhlenbergia* specialist in the northern prairie. This species retains the plesiomorphic articulation between connective and aedeagus; it could otherwise be regarded a close sister species to *areolata*, with which it shares a distinctive aedeagal morphology. These two species are both greenish dorsally and have black faces.

33. *Flexamia imputans* (Osborn & Ball)

Deltocephalus imputans Osborn & Ball 1898: 75.
Deltocephalus (Flexamia) imputans, DeLong 1926: 29.
Flexamius [sic] *imputans*, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.1–3.7) mm, of ♀ 3.7 (3.3–3.9) mm. Crown moderately produced (1.33 x interocular width; 0.62 x head width) (♂ n = 10; ♀ n =
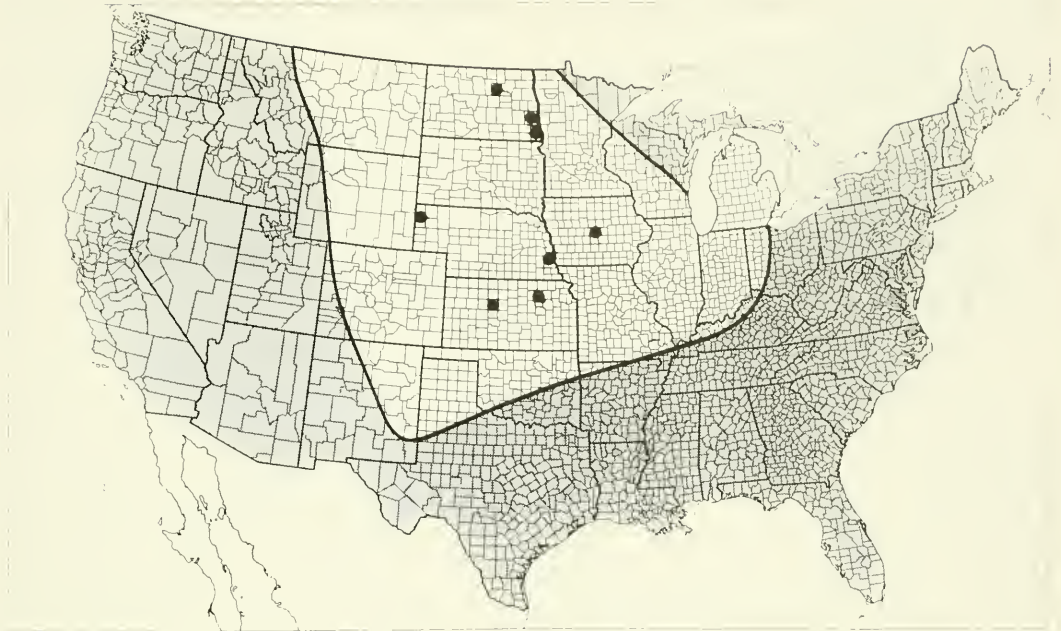
Fig. 42. Geographic distribution of *Flexamia imputans* and a probable host, *Muhlenbergia cuspidata*.

14). Face usually entirely black but occasionally with oblique, pale streak on each gena. [♂] Genitalia (Fig. 31B) similar to those of *areolata* but with hind margin of pygofer (Fig. 62V) convex and with distinct joint between connective and aedeagus. [♀] Sternum VII (Fig. 10P) with hind margin broadly, slightly convexly produced with slight median notch; ovipositor with bases of first valvulae (Fig. 63II) not recurved.

GEOGRAPHIC DISTRIBUTION.—Northern Great Plains from the Dakotas south to Kansas, east to Iowa and Wisconsin (Fig. 42).

BIOLOGY.—This species is apparently a *Muhlenbergia* specialist and may occur largely on *Muhlenbergia cuspidata*. It is one of the rarest of the *Flexamia* species and, given the extensive turnover of its original upland prairie habitat to croplands, may become increasingly rare.

REMARKS AND DIAGNOSIS.—This species is unique in its lack of markings on head and pronotum, in combination with its black face.

XII. The *areolata* Group

This group consists of a single species.

34. *Flexamia areolata* (Ball)

Deltocephalus areolatus Ball 1899: 188.
Deltocephalus (Flexamia) areolatus, DeLong 1926: 25.
Flexamia areolatus, DeLong and Sleesman 1929: 84.

IMPORTANT CHARACTERS.—Length of ♂ 2.8 (2.6–3.2) mm, of ♀ 3.6 (3.2–4.0) mm. Crown strongly produced (1.77 x interocular width; 0.75 x head width) (♂ n = 20; ♀ n = 22). Face entirely black. [♂] Pygofer (Fig. 62Z) with dorsal portion of posterior lobe produced caudodorsad, posterior margin oblique and slightly concave. Plates (Fig. 34G) elongate, gradually narrowed from base to apex, fused basally for about 1/3 length. Aedeagus and connective fused. Aedeagus (Fig. 31C) asymmetrical; three tapering apical processes, two short, with serrate edges, extending basad along right side of shaft; third process extending basad for about half the length of right side of shaft, minute projections in middle, broader than other two processes, bearing gonopore as elongate slit through almost entire length. [♂] Sternum VII (Fig. 10Q) with posterior margin concave on each side of apically notched, median, convex projection; ovipositor with first valvulae not curved dorsad at bases.
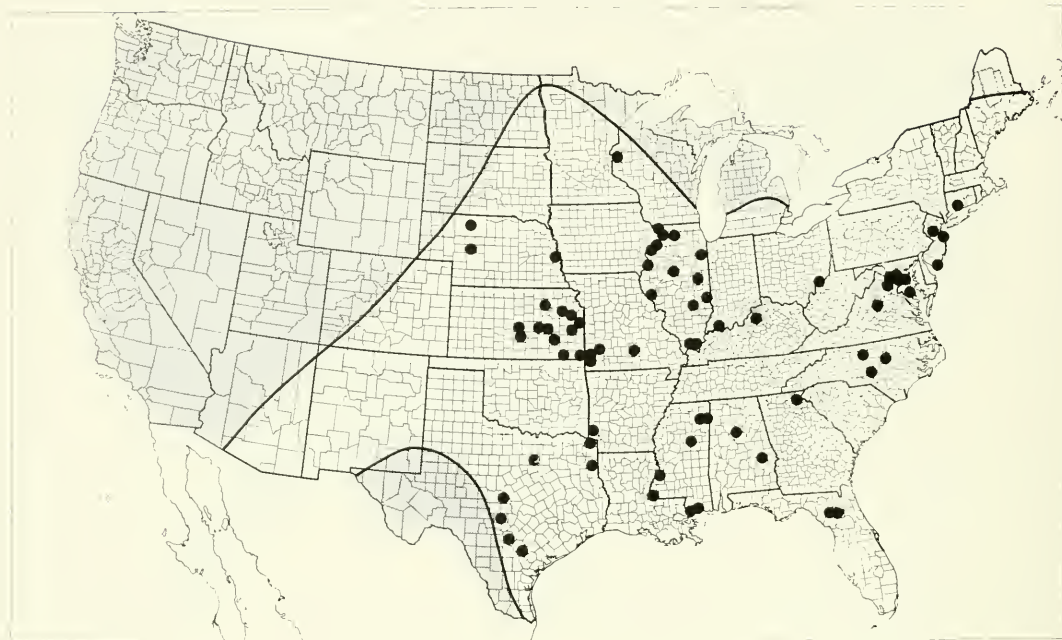
Fig. 43. Geographic distribution of *Flexamia areolata* and its host, *Eragrostis spectabilis*.

GEOGRAPHIC DISTRIBUTION.—This species occurs from Connecticut to Wisconsin, south to Florida and Texas, covering much of the geographic range of its host (Fig. 43). One of the three specimens from the original cotype series is labeled "Phoenix, Arizona, May, 1897." One specimen in the CNC is labeled "San Diego, Calif., 19-6-71, GL1251, H. H. Ross." Nevertheless, occurrence of *areolata* in the Southwest requires confirmation.

BIOLOGY.—We consider *areolata* to be a specialist of *Eragostis spectabilis*. DeLong (1949) believed that the host was "*Panicum* or a closely related genus." *Panicum capillare*, an annual that commonly occurs with *E. spectabilis* in sandy habitats, has a superficially similar inflorescence characterized by wide panicles that redden when mature. As if this were not confusing enough, *Leptoloma cognatum*, a representative of a genus that is indeed closely related to *Panicum*, not only occurs with the above two plant species in the same sandy habitats, but also has low, wide panicles that redden when mature. Unsure whether we may have overlooked components of this confusing plant association, we have returned to several communities where

areolata occurs and have found *E. spectabilis* growing in the absence of the other two grasses. Furthermore, we have collected this species in the Nebraska Sand Hills⁻ on *E. spectabilis*, northwest of the range of *Leptoloma cognatum*. Osborn (1928) recorded *areolata* from *Eragrostis pectinacea* in North Carolina. Because *E. pectinacea* is an annual, this report requires confirmation.

REMARKS AND DIAGNOSIS.—The habitus of *areolata* is unique.

XIV. The *prairiana* Group

The *prairiana* group is named for its most plesiomorphic member, *F. prairiana*, a widespread resident of tall-grass prairie and southwestern semiarid grasslands. The group consists of 10 species that share a similar general facies. All members of the group are medium-sized and brown but lack distinctive markings. Definitive identification requires examination of genitalia; the aedeagus and connective are fused, a condition we define as synapomorphic. In *prairiana* a trace of the plesiomorphic articulation remains and constitutes an autapomorphy defining that species. Species of this complex are largely

inhabitants of prairie, savanna, or forest glades. Members of the group specialize largely on andropogonoid grasses (*Andropogon*, *Schizachyrium*, and *Bothriochloa* spp.). Exceptions are (1) *atlantica*, which is often associated with switchgrass (*Panicum virgatum*) or, in the Southwest, chloridoid grasses such as *Sporobolus* spp.; and (2) *producta*, a southern coastal species that appears to be associated with chloridoid grasses. Both *atlantica* and *producta* regularly colonize an introduced chloridoid grass, *Cynodon dactylon*.

There are two sets of closely related sister species. One is *sandersi-delongi*. Ross and Cooley (1969) separated *delongi* from *sandersi* on the basis of the greater divergence of its apical, paired processes and lesser appression of the unpaired process to the aedeagal shaft (Figs. 44B,C). Hamilton and Ross separated *satilla* from *clayi* on the basis of a narrower aedeagal shaft (Figs. 44H,J). The distinctions between the species of these two sets are fine; some workers would consider the differences to represent infraspecific geographic variation. However, we have retained *satilla* and *delongi* because, in each case, they can be unambiguously identified, and a geographic and historical basis can be presented to explain both their divergence and maintenance of reproductive isolation. In the case of *delongi*, which probably specializes on *Schizachyrium scoparium*, the geographic range (Fig. 50) was almost entirely glaciated during the most recent glacial maximum. In contrast, *sandersi* occupies a region that was never glaciated, where it apparently specializes largely on *Andropogon virginicus*. These circumstances provide a hypothetical scenario for speciation and an explanation of ecological factors that may now enforce isolation between the two species. Similarly, *satilla*, described by Hamilton and Ross (1975) from south Georgia, is probably a Gulf Coast species (Fig. 51) that is at least partially sympatric with *producta*. Discovery of its sister species, *clayi*, as far north as Maine suggests that differentiation of these species, like that of *sandersi* and *delongi*, may be a postglaciation event that is phenologically enforced by contemporary climate. As closely related as *clayi* and *satilla* are, the sister set that they comprise is also very closely related to *graminea*. A more distant pair of sister species is that of

prairiana and *reflexa*. The most significant apomorphy shared by these sister species is the dorsal position of the gonopore (Figs. 44D,G). These species also share a common general facies and cannot be distinguished on the basis of external characters. Each of these sister species has a variable aedeagal morphology, and we found that careful study was required to separate them. Both species are residents of tall-grass prairie, where they occur on *Andropogon* and *Schizachyrium* species. Other species of the *prairiana* group are more distantly related.

Description of *prairiana* Group

Medium-sized. Length of ♂ 3.0–4.2 mm, of ♀ 3.0–4.6 mm. All species with similar general facies. Brown, or in darkest specimens, black on face or venter. Vertex moderately produced. Crown often stramineous with conspicuous transverse line at midlength. Male plates elongate, in some species notched apically. Aedeagus and connective fused, or with at most (in *prairiana*) a faint trace of the plesiomorphic articulation. Aedeagus with paired, apical, serrate processes and an unpaired, lateral or dorsal process partially fused to shaft in some species, or in others entirely fused or absent. Aedeagus asymmetrical in all but one species (*dakota*). Gonopore in primitive species oval and anteapical, in more advanced species located on the unpaired process or, in the most highly specialized species, replacing the unpaired process as a spiral groove originating dorsally on the shaft. Female sternum VII produced posteriorly at middle in a convex, apically notched protuberance.

Key to Males of the *prairiana* Group

1. Aedeagus with 3 processes on shaft 2
— Aedeagus with 2 processes on shaft 6

2(1). Pygofer with posterior lobe strongly expanded on ventral margin (Fig. 5D) . . . *producta* (Walker)
— Pygofer with ventral margin of posterior lobe not strongly expanded 3

3(2). Gonopore dorsal, anteapical, located on a process or at the base of one (Figs. 44D,G) 4
— Gonopore on dorsolateral surface of shaft at base of retrorse process 5

4(3). Gonopore near apex of aedeagal shaft, at base of a process (Fig. 44G) . . . . *prairiana* DeLong
— Gonopore located on a process (Fig. 44D) . . . . *reflexa* (Osborn & Ball)
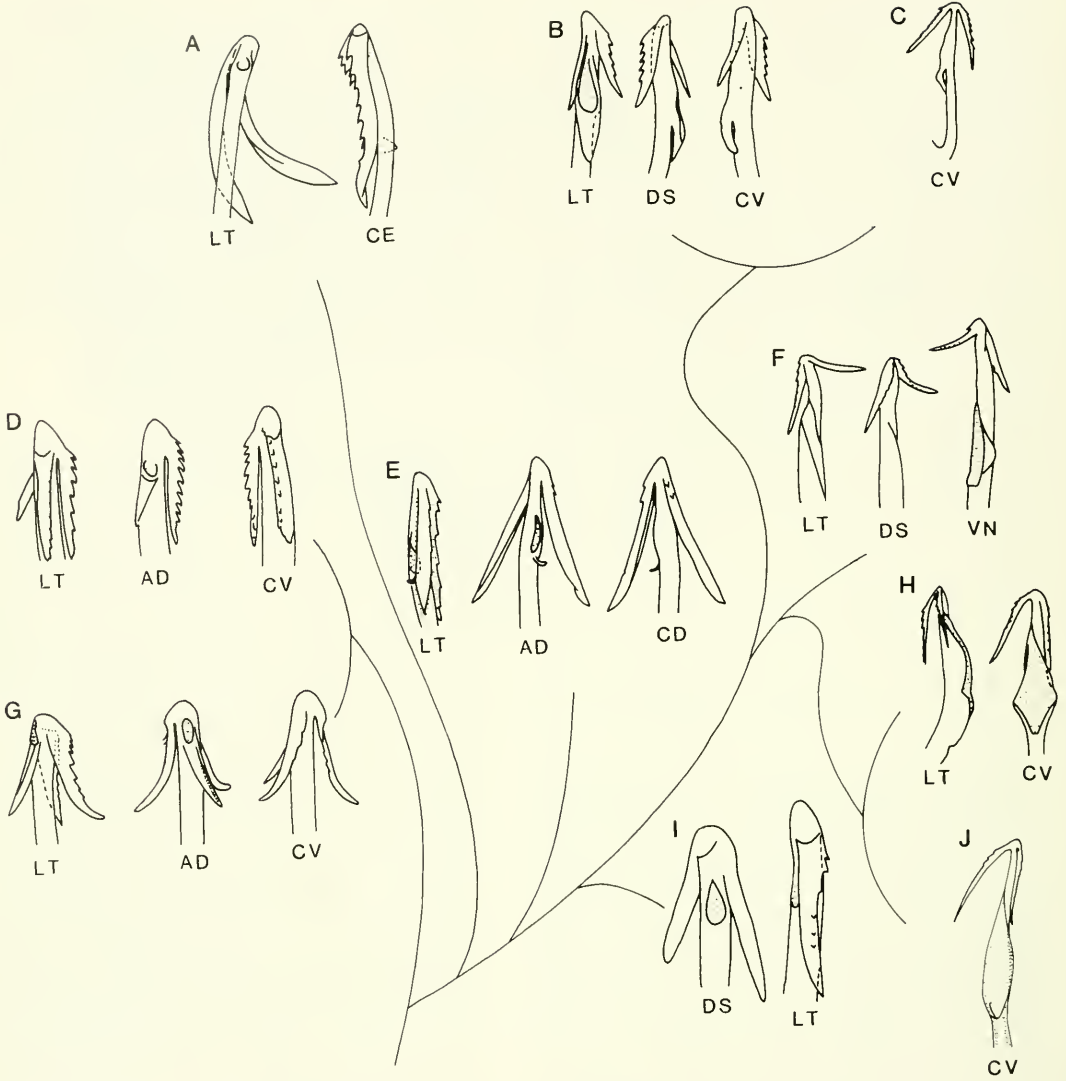
Fig. 44. Aedeagal apices of the *Flexamia prairiana* group: A, *atlantica*; B, *sandersi*; C, *delongi*; D, *reflexa*; E, *producta*; F, *graminea*; G, *prairiana*; H, *clayi*; I, *dakota*; J, *satilla*. Aspects: AD, anterodorsal; CD, caudodorsal; CE, cephalic; CV, caudoventral; DS, dorsal; LT, lateral; VN, ventral. Redrawn from Young and Beirne (1958) and Hamilton and Ross (1975).

5(3). Apical processes of aedeagus more divergent, each with 6–9 teeth; when viewed in a position with apical processes horizontal, a space is visible between the base of the gonopore extension and the shaft (Fig. 44C) . . . *delongi* Ross & Cooley

— Apical process of aedeagus less divergent, each with 3–5 teeth; when viewed as above, no space is visible between the base of the gonopore extension and the shaft (Fig. 44B) . . . . *sandersi* (Osborn)

6(1). Gonopore spiral 7

— Gonopore not spiral 8

7(6). Aedeagal appendages of aedeagus without prominent, anteapical processes; aedeagal shaft usually not strongly expanded at base of gonopore (Fig. 44F) . . . . *graminea* (DeLong)

— Apodemal appendages of aedeagus each with prominent, anteapical protuberance directed mesad; aedeagal shaft strongly expanded at base of gonopore (Fig. 44H) 9

8(6). Aedeagal shaft with apical process on each side; gonopore anteapical on anterodorsal surface (Fig. 44I) . . . . *dakota* Young & Beirne

— Aedeagal shaft with apical processes arising on

one side; gonopore anteapical on lateral surface of shaft (Fig. 44A) .... *atlantica* DeLong

9(7). Shaft of aedeagus comparatively robust (Fig. 44H); north Georgia to Maine ....
.... *clayi* Young & Beirne

— Shaft of aedeagus slender (Fig. 44J); Gulf Coast (Florida, south Georgia, Mississippi) ....
.... *satilla* Hamilton & Ross

Key to Females of the *prairiana* Group

1. Ovipositor with base of each first valvula re-curved dorsally in dorsal aspect 2

— Ovipositor with base of each first valvula not recurved dorsally 5

2(1). Recurved portion of each first valvula parallel to anteriormost border of each valvula in dorsal aspect, appearing as rim above the valvula (Fig. 63LL) 3

— Recurved portion appearing wider in dorsal as-pect .... *prairiana* DeLong

3(2). Anteriormost border of each first valvula ap-pearing somewhat angular in dorsal aspect, re-curved portion very narrow and not produced dorsad (Fig. 63LL) .... *graminea* DeLong

— Anteriormost border of each first valvula rounded, recurved portion much broader and produced dorsad (Fig. 63GG) 4

4(3). Range north Georgia to Maine ....
.... *clayi* Young & Beirne

— Range Gulf Coast .... *satilla* Hamilton & Ross

5(1). Bases of first valvulae obliquely truncate, valvu-lae apparently membranous basally (Fig. 63HH) .... *reflexa* (Osborn & Ball)

— Bases of first valvulae convex basally 6

6(5). First valvulae broadest near bases in dorsal as-pect (Fig. 63EE,KK) 7

— First valvulae broadest more posteriorly in dor-sal aspect 8

7(6). Face often with brown interocular line contrast-ing with pale color of remainder; if without line, then irregularly darkened; Southeast (Fig. 49) .... *producta* (Walker)

— Face tan to dark brown with alternating sinuate, dark and light lines; dry prairie (Fig. 49) ......
.... *dakota* Young & Beirne

8(6). Face with black interocular line, or at least with this area black in addition to other black marks on face .... *atlantica* DeLong

— Face brown or tan; interocular area never black 9

9(8). Range southern Illinois southeastward ....
.... *sandersi* (Osborn)

— Range northern Illinois northward to Ontario, northwest to North Dakota ....
.... *delongi* Ross & Cooley

35. *Flexamia prairiana* DeLong

Flexamia prairiana DeLong 1937: 32.

IMPORTANT CHARACTERS.—Length of ♂ 3.6

(3.2–3.9) mm, of ♀ 3.9 (3.4–4.6). Crown moderately produced (0.60 x head width, 1.40 x interocular width) (♂ n = 73; ♀ n = 32). Face (Fig. 3D) usually pale in lower half, with broad, black interocular band; in darkly marked specimens almost completely black (Fig. 3C). Habitus characteristic of group. Male plates (Fig. 45A) elongate, unnotched. [♂] Pygofer (Fig. 62W) with upper part of hind margin produced posteriorly. Aedeagus (Figs. 6F, 44G) asymmetrical, shaft slender, elongate, gradually broadened apically; gono-pore oval, anteapical on anterodorsal surface. Three retrorse apical processes diverging slightly from shaft, about one-third length of shaft. Unpaired process arising basad of gonopore, margins entire with dorsal, longi-tudinal groove on apical half; pair of distad, ventral, lateral processes, serrate on ventral margin. [♀] Sternum VII as for group; ovipos-itor with each first valvula (Fig. 63JJ) recurved slightly dorsad at base.

GEOGRAPHIC DISTRIBUTION.—Widely dis-tributed (Fig. 46) from Manitoba to Colorado, Arizona, and Mexico, east to Missouri and Illinois. Two females from Michoacán, Mex-ico (21 October 1981, M. W. Nielson), have been tentatively referred to *prairiana*. A sin-gle male (Baker 2361, USNM) is recorded from Auburn, Alabama, 10 September 1897.

BIOLOGY.—Southwestern populations usu-ally occur on *Bothriochloa* species. In the tall-grass prairie the usual hosts are *Schiz-achyrium scoparium* and *Andropogon ger-ardii*. Most reported hosts are andropogonoid grasses, but in tall-grass prairie *prairiana* may move short distances to more suitable hosts in drought periods or in late summer. Thus, oligophagy coefficients calculated for *prairi-ana* tend to be among the lowest for all *Flex-amia* species (Whitcomb et al. 1988). The green coloration of live specimens of *prairi-ana* fades to orange upon drying. In midsum-mer the intensity of coloration varies greatly. In the fall, coloration may be very dark; un-cleared, late-season specimens have often been misidentified.

OLIGOPHAGY COEFFICIENTS.—Tall-grass and mixed-grass prairies north of Texas: Grami-neae 0.922; Panicoideae 0.730; *Schiza-chyrium scoparium* 0.438; *Andropogon ger-ardii* 0.241 (n = 527).

REMARKS AND DIAGNOSIS.—Because this species is one of the most abundant of *Flex-amia* species, it is important to recognize it
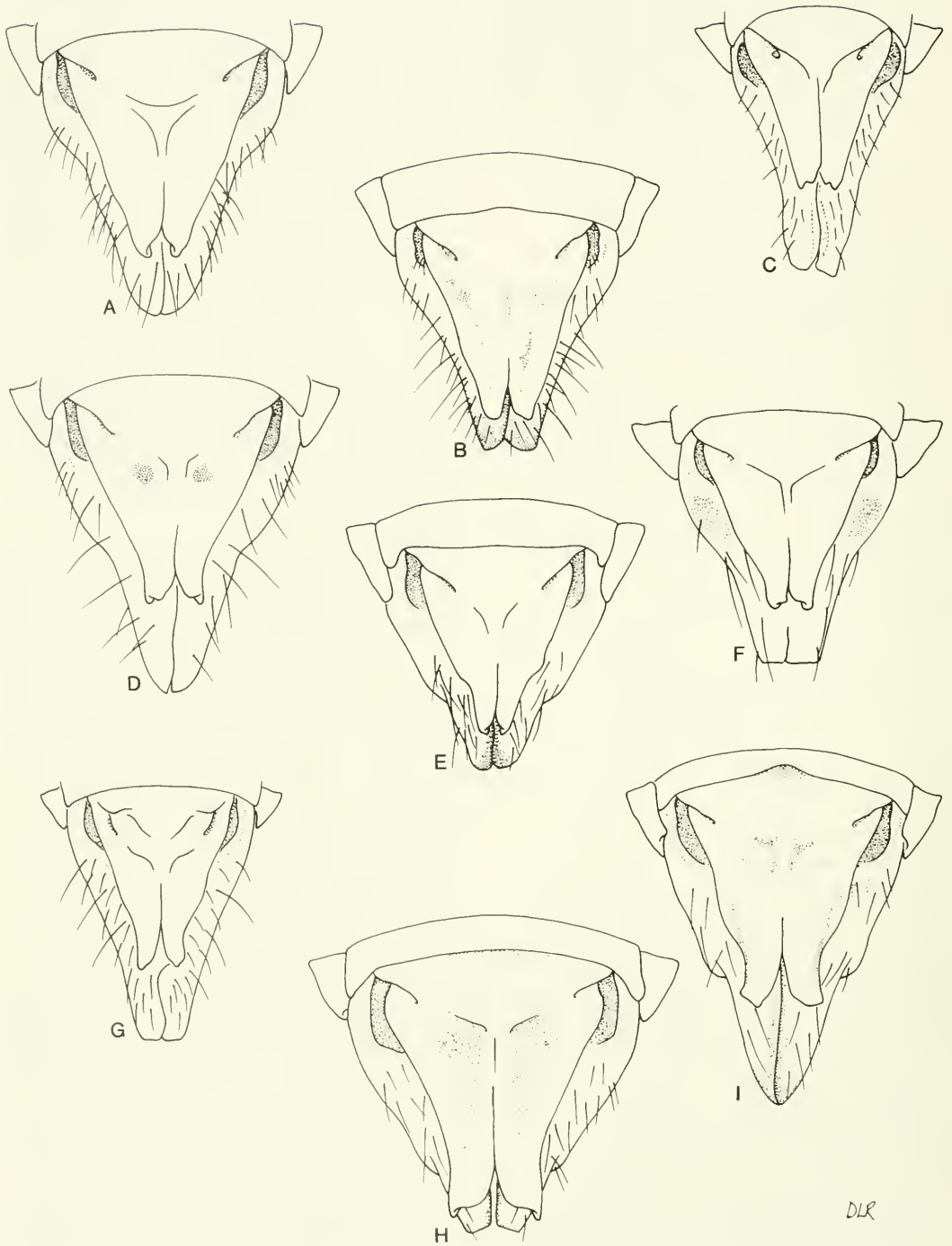
Fig. 45. Male plates and pygofers of the *Flexamia prairiana* group, ventral aspect: A, *prairiana*; B, *reflexa*; C, *atlantica*; D, *producta*; E, *dakota*; F, *sandersi*; G, *delongi*; H, *graminea*; I, *clayi*.
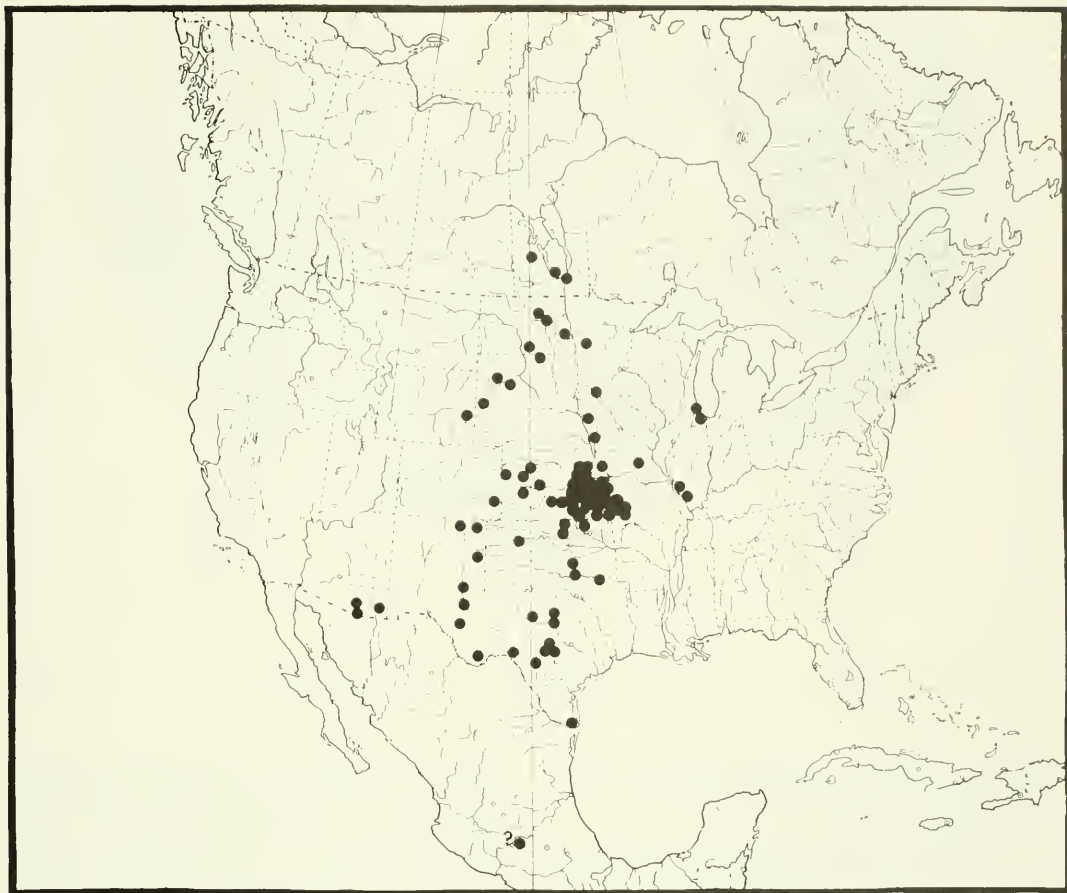
Fig. 46. Geographic distribution of *Flexamia prairiana*.

(tentatively) without dissection. The *prairi-ana* face type is almost always distinguishable from the faces of *graminea*, *sandersi*, *delongi*, or *dakota*, which may occur with it in *Andro-pogon* prairies. Dissected male specimens reveal an aedeagus that might be confused only with that of *reflexa*. Female specimens may prove difficult to identify because the bases of the first valvulae vary geographically. In southwestern populations this structure is rarely sclerotized, as illustrated by Young and Beirne (1958).

36. *Flexamia reflexa* (Osborn & Ball)

Deltocephalus reflexus Osborn & Ball 1897: 203.
Deltocephalus (Flexamia) reflexus, DeLong 1926: 28.
Flexamius reflexus, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.5 (3.1–4.0) mm, of ♀ 3.7 (3.2–4.2) mm. Crown moderately produced (1.49 x interocular width; 0.68 x head width) (♂ n = 20; ♀ n = 15). Face variable, often pale on lower half with broad interocular band; band may be obscured in dark specimens. [♂] Pygofer (Fig. 62X) with posterior lobe strongly produced, truncate apically. Plates (Fig. 45B) elongate, without notches or lateral projections. Connective in lateral aspect with dorsal keels extending almost as far dorsad as aedeagal apodeme. Aedeagus (Fig. 44D) asymmetrical, shaft elongate, gradually tapered; gonopore anteapical on anterodorsal surface, associated with short, apically grooved, unpaired process. Paired apical processes serrate along ventral edge, extending basad less than half length of shaft in lateral aspect. [♀] Ovipositor
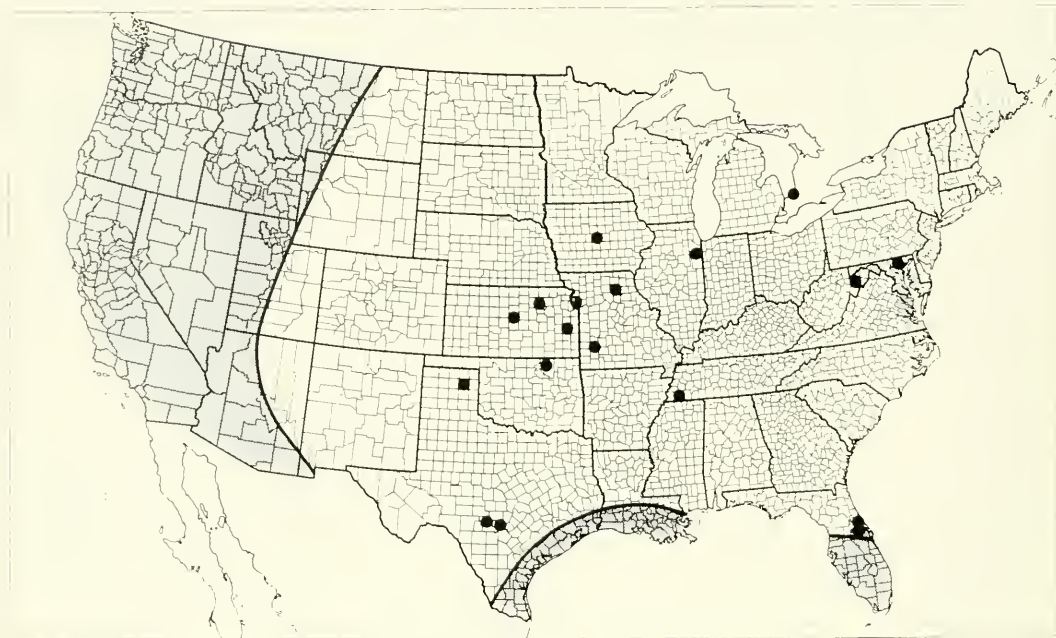
Fig. 47. Geographic distribution of *Flexamia reflexa* and a host, *Andropogon gerardii*.

with first valvulae membranous basally, not curved dorsad; sclerotized portion obliquely truncate in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Tall-grass prairie (Cwikla and Blocker 1981), savanna, and glades and prairie mosaic of deciduous forest, Kansas and Iowa to Texas, Ontario, Maryland, and Florida (Fig. 47).

BIOLOGY.—This species is associated with *Andropogon gerardii* in the East (Maryland and West Virginia) and may be associated with that host in the tall-grass prairie. However, in Texas it occurs in mixed-prairie associations in which big bluestem is a minor component.

DIAGNOSIS AND REMARKS.—Given the paucity of specimens of *reflexa* in collections, it is remarkable that it was the second member of the *prairiana* group to be described and that it is the type species of the genus. Almost all uncleared specimens "identified" as this species in museum drawers turn out to be other *prairiana* group species. The abundant *prairiana*, which occurs through much of its range on little bluestem (*Schizachyrium scoparium*), is much more apt to be encountered in the prairie. Since we have found no reliable external characters for sorting *reflexa* from

prairiana, a search for this species involves sifting through numerous *prairiana* specimens. The position of the gonopore (some distance from the aedeagal apex, situated basally on a short, appressed, unpaired process) contrasts sharply with the simpler, oval, anteapical gonopore of *prairiana*. Some specimens of *atlantica* and *producta* may also resemble *reflexa* in general facies, but their genitalia bear little resemblance to those of *reflexa*.

37. *Flexamia atlantica* (DeLong)

Deltocephalus (Flexamia) atlanticus DeLong 1926: 29.
Deltocephalus atlanticus, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.2–4.2) mm, of ♀ 4.1 (3.6–4.5) mm. Crown moderately produced (1.31 x interocular width; 0.59 x head width) (♂ n = 20; ♀ n = 20). Face black in upper half, often forming interocular band contrasting with pale lower half. [♂] Pygofer (Fig. 62Y) with posterior lobe narrow, without ventral lobe. Plates (Fig. 45C) elongate, notched apically. Aedeagus (Fig. 44A) asymmetrical, shaft nearly uniform in width, gonopore simple, anteapical on
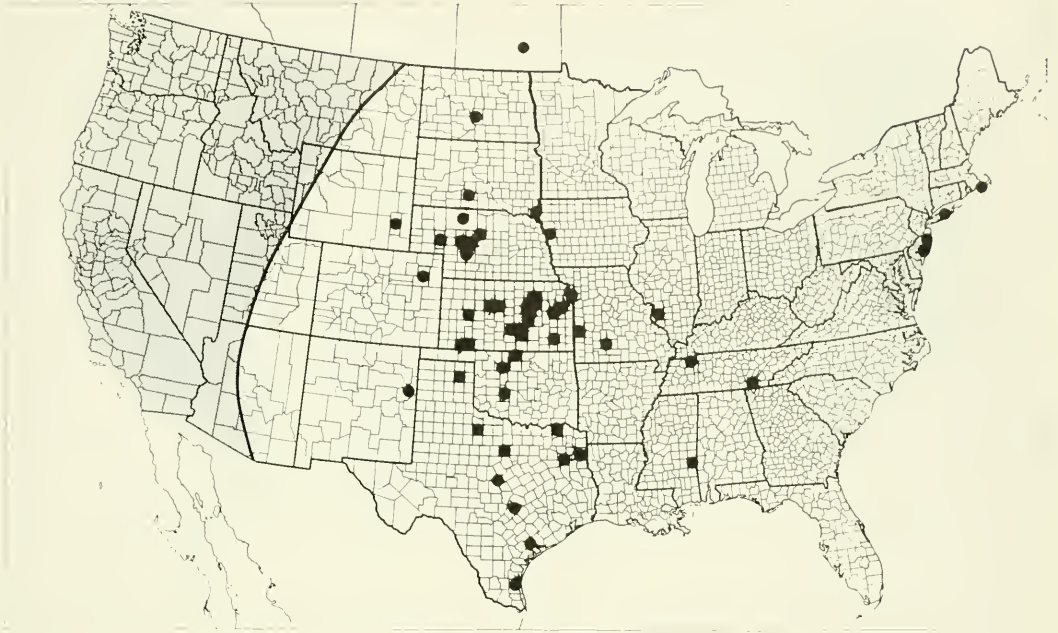
Fig. 48. Geographic distribution of *Flexamia atlantica* and a host, *Panicum virgatum*.

the right side. Pair of elongate, retrorse, ser-rate, apical processes extending basad approx-imately half length of shaft. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63DD) not curved dorsad.

GEOGRAPHIC DISTRIBUTION.—Prairie from Manitoba, North Dakota, Wyoming, and New Mexico east to Illinois (Fig. 48). Also along the Atlantic coastal prairie of the Northeast, and very patchily in the Southeast.

BIOLOGY.—In tall-grass prairie *atlantica* is usually associated with switchgrass (*Panicum virgatum*). This grass, a dominant in the northeastern coastal prairie, probably ac-counts for the occurrence of *atlantica* there. In mixed-prairie and southwestern grass-lands, *atlantica* occurs on native *Sporobolus* spp. and is the major *Flexamia* colonist in the extensive stands of two exotic chloridoid grasses (weeping love grass [*Eragrostis cur-vula*] and bermudagrass [*Cynodon dactylon*]) in Texas and Oklahoma.

OLIGOPHAGY COEFFICIENTS.—Texas and Oklahoma: Gramineae 0.994; Chloridoideae 1.000; *Eragrostis curvula* 0.243; *Cynodon dactylon* 0.633 (n = 161). Kansas, Missouri, and Nebraska: Gramineae 1.000; Panicoideae

0.876; *Panicum virgatum* 0.783; *Sporobolus* spp. 0.124 (n = 177).

DIAGNOSIS AND REMARKS.—*Flexamia at-lantica* is the only pale-faced *Flexamia* prairie species with apically notched plates. Also, individuals of *atlantica* tend to be larger than those of *reflexa* or *prairiana*. In the South-east, *atlantica* may occur with *producta*, which tends to be smaller, and which usually has a much more produced crown. Although these characters permit tentative recognition, definitive recognition is readily accomplished by examining the aedeagal morphology, which is unique.

38. *Flexamia producta* (Walker)

Iassus productus Walker 1851: 891.
Deltocephalus visendus Crumb 1915: 189.
Deltocephalus (Flexamia) productus, DeLong 1926: 43.
Flexamia producta, DeLong and Knull 1945: 35.

IMPORTANT CHARACTERS.—Length of ♂ 3.2 (3.0–3.5) mm, of ♀ 3.5 (3.2–3.9) mm. Crown usually conspicuously produced (1.62 x inter-ocular width; 0.75 x head width) (♂ n = 20; ♀ n = 20). Face variable but usually with clearly delimited interocular band; band occasionally obscured in darker specimens. [♂] Plates

Fig. 49. Geographic distribution of *Flexamia dakota* (●) and *producta* (■) and the host of *dakota*, *Scizachyrium scoparium*, which does not occur on the Atlantic coastal plain.

(Fig. 45D) elongate, notched at apex. Pygofer (Fig. 62AA) with posterior lobe produced and rounded apically, ventral portion extending mesad as pronounced lobe, serrate along margin, the two lobes often overlapping in ventral aspect (but not necessarily in prepared specimens). Aedeagus (Fig. 44E) asymmetrical apically; shaft elongate, slender, slightly swollen anteapically; gonopore irregularly oval, on left side of dorsal surface of shaft; pair of processes arising asymmetrically at apex of shaft, extending basad almost half of shaft length, each process laterally compressed and conspicuously toothed along ventral edge; with short, small, curved process arising near proximal portion of gonopore, extending sinistrad. [♀] Female sternum VII as for group, ovipositor with bases of first valvulae (Fig. 63EE) not curved dorsad, broad basally in dorsal aspect.

GEOGRAPHIC DISTRIBUTION.—Gulf Coast and Atlantic seaboard from Mississippi to Maryland (Fig. 49).

BIOLOGY.—This species has been collected commonly in coastal prairies, but there are few host records. We have recorded it from several exotic chloridoid grasses (e.g., *Zoysia*

japonica and *Cynodon dactylon*) in Maryland but have little field experience in the coastal prairies where it is most abundant. We note that *Sporobolus virginicus* is a common dominant in southeastern coastal prairies; this chloridoid grass should be examined as a possible natural host. On the other hand, there are indications that cicadellid host specialization decreases in mesic and wet prairies (Whitcomb et al. 1987, 1988). Given its occurrence in wet southeastern grasslands, *producta* may turn out to be a habitat specialist.

DIAGNOSIS AND REMARKS.—The produced crown of this species affords a tentative indication of its identity. Unfortunately, *satilla* and *sandersi*, which occur with *producta*, also have produced crowns that approach the length/width ratios of *producta*. Although the latter species are similar to *producta* in most aspects, their faces are without conspicuous interocular bands. It is therefore possible to sort, from an assemblage of southeastern *Flexamia*, a large subset of *producta* specimens that have either an extremely produced crown or a distinct interocular band (or both). Unfortunately, this will leave a mixture of atypical

producta specimens and specimens of *sandersi* and *satilla*, or perhaps even *clayi*. The aedeagal characters of *producta* readily diagnose the species.

39. *Flexamia dakota* Young & Beirne

Flexamia dakota Young & Beirne 1958: 44.

IMPORTANT CHARACTERS.—Length of ♂ 3.0 (2.8–3.6) mm, of ♀ 3.3 (3.0–3.6) mm. Crown moderately produced (1.40 x interocular width; 0.64 x head width) (♂ n = 21; ♀ n = 18). Face brown to tan, with parallel lines. [♂] Pygofer (Fig. 62BB) with upper portion of posterior lobe produced posteriorly. Plates (Fig. 45E) with apical third narrowed. Aedeagus (Fig. 44I) symmetrical; shaft elongate, slender, narrower near midlength than at base or apex. Gonopore anteapical on anterodorsal surface; pair of recurved processes extending basad amost half length of shaft; each process serrate on ventral margin. [♀] Sternum VII as for group. Ovipositor with bases of first valvulae broadest near base (Fig. 63KK).

GEOGRAPHIC DISTRIBUTION.—Semiarid Great Plains of western North and South Dakota, eastern Wyoming, Nebraska Sand Hills to Oklahoma, and the Edwards Plateau of Texas (Fig. 49). A presumably disjunct population occurs in the Loess Hills of western Iowa. This species has recently been recorded from Mexico (2 ♂, 42 km S Piedras Negras, Coahuila, 13 October 1987, A. L. Hicks and J. E. Lowry).

BIOLOGY.—This species is apparently a specialist on little bluestem (*Schizachyrium scoparium*) in dry prairie.

OLIGOPHAGY COEFFICIENT.—Gramineae 1.000; Panicoideae 0.990; *Schizachyrium scoparium* 0.990 (n = 209).

DIAGNOSIS AND REMARKS.—This species often occurs in the absence of other specialists of andropogonoid grasses. However, in the Edwards Plateau of Texas, *dakota* occurs with *graminea* (which it closely resembles in general facies), *prairiana*, and, rarely, *reflexa*. Although it can be tentatively sorted from the latter two species on the basis of face pattern, we have found no reliable external character to sort it from *graminea*. The symmetrical aedeagus of *dakota*, which has only paired apical processes, is unique. Young and Beirne (1958) described only males; Lowry and Blocker (1987) described the female.

40. *Flexamia sandersi* (Osborn)

Deltocephalus sandersi Osborn 1907: 164.
Deltocephalus (Flexamia) sandersi, DeLong 1926: 27.
Flexamia sandersi, DeLong and Sleesman 1929: 83.
Flexamius bidentata DeLong 1935: 155.

IMPORTANT CHARACTERS.—Length of ♂ 3.2 (2.9–3.5) mm, of ♀ 3.4 (3.2–3.9) mm. Crown produced (1.48 x interocular width; 0.69 x head width) (♂ n = 11; ♀ n = 10). Face (Fig. 3H) varying from dark above and shading to paler apically to brown or black throughout, in former case with dark area shading gradually along lower margin; no interocular band. [♂] Pygofer (Fig. 62CC) truncate on dorsal portion of posterior margin. Plates (Fig. 45F) elongate, apically notched, in some specimens bidentate. Aedeagus (Fig. 44B) asymmetrical; shaft elongate, gradually tapered; gonopore on dorsolateral surface of shaft at base of retrorse, unpaired process, which is closely appressed to the shaft, has one minutely serrate margin, and extends basad to midlength of shaft; pair of apical, retrorse processes, dorsal slightly longer than ventral, each acute apically and with distinctly serrate margin. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63FF) not curved dorsad.

GEOGRAPHIC DISTRIBUTION.—Eastern Kansas to Louisiana, east to southern Illinois, Massachusetts, and South Carolina (Fig. 50).

BIOLOGY.—The principal host appears to be broomsedge (*Andropogon virginicus*), but this conclusion requires further study.

DIAGNOSIS AND REMARKS.—Throughout much of its range, *sandersi* occurs with *clayi*. These species usually have been collected in the summer before their host grasses have flowered. Many host records are listed simply as "*Andropogon* sp." In the Maryland Piedmont *sandersi* occurs abundantly on broomsedge in the absence of *clayi*; in Maryland we have found the latter species only in the Appalachians. We have found no reliable external character that separates *sandersi* from *clayi*, *satilla*, *graminea*, or *delongi*. However, the characters of the aedeagus described above and in the key readily separate *sandersi* from all other *prairiana* group species, with the exception of *delongi*. We have discussed the relationship of these very closely related sister species in the corresponding section under *delongi*.
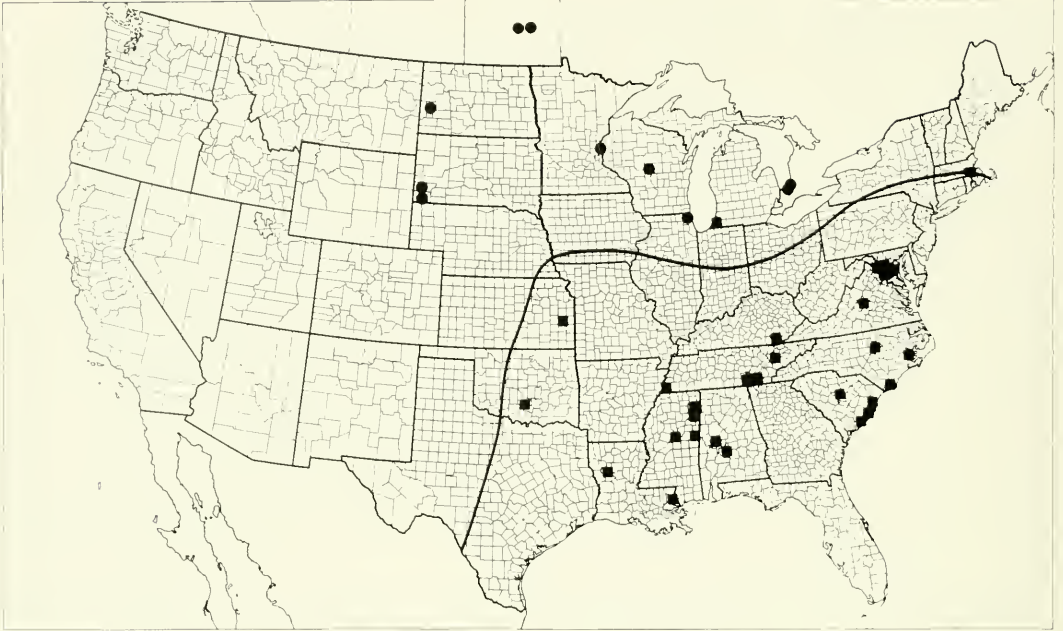
Fig. 50. Geographic distribution of *Flexamia sandersi* (■) and *delongi* (●) and the presumed major host of *sandersi*, *Andropogon virginicus*.

41. *Flexamia delongi* Ross & Cooley

Flexamia delongi Ross & Cooley 1969: 246.
Flexamia sandersi, Young and Beirne 1958: 164. (In part.)

IMPORTANT CHARACTERS.—Length of ♂ 3.7 (3.4–4.1) mm, of ♀ 3.8 (3.4–4.4) mm. Crown variably produced (1.34 x interocular width; 0.65 x head width) (♂ n = 17; ♀ n = 21). Face varying from dark above, shading to paler apically to black or brown throughout, dark area often fading gradually along lower margin, interocular band absent. [♂] Pygofer and plates as in *sandersi*. Aedeagus (Fig. 44C) asymmetrical; shaft elongate, not cylindrical, gradually tapered; gonopore on dorsolateral surface at base of retrorse process, which extends basad to midlength of shaft; pair of lateral, apical, retrorse processes extending more than one-third but less than one-half length of shaft, each with a distinct, coarsely serrate margin and with very acute apex. [♀] Sternum VII as for group; ovipositor with base of each first valvula as for *sandersi*.

GEOGRAPHIC DISTRIBUTION.—Northern Indiana and Illinois, Wisconsin, and Ontario, west to South Dakota, Saskatchewan, and Manitoba (Fig. 50).

BIOLOGY.—This species is presumably a specialist of little bluestem, *Schizachyrium scoparium*.

DIAGNOSIS AND REMARKS.—The pair of sister species consisting of *delongi* and *sandersi* is (with the exception of *satilla* and *clayi*) the most closely related of all *Flexamia* sister pairs. Ross and Cooley (1969) acknowledged this closeness, pointing out that *delongi* previously had been considered a variant of *sandersi*. Ross and Cooley examined material from the East but did not examine specimens from Canada or from the Dakotas. Thus, their interpretation of *delongi* as a geographic replacement for *sandersi* made the identity of the northern prairie material a crucial test. We examined specimens from these regions from the USNM and CNC and found them to be referable to *delongi*. We retain herein the concept of *delongi*, because it can be defended on morphological, biological, and historical grounds. The species occurs in a region that was largely or completely glaciated during the Wisconsinan. The principal (or sole) host of *sandersi* (*Andropogon virginicus*) does not occur in this region. Thus, *sandersi* and *delongi* appear to utilize different

hosts, whose phenological asynchrony may reinforce reproductive isolation. Finally, although genitalic differences between *delongi* and *sandersi* are slight, they are consistent. The apical, aedeagal processes of *delongi* are more divergent than those of *sandersi;* each process has 6–9 teeth. Further, the gonopore extension is more divergent from the shaft than in *sandersi.*

In the northern prairies *delongi* may occur on little bluestem with *graminea, prairiana,* or *dakota,* but its aedeagal structure readily separates it from these species.

42. *Flexamia graminea* (DeLong)

Deltocephalus (Flexamia) gramineus DeLong 1926: 30.
Flexamius gramineus, DeLong and Caldwell 1937: 27.

IMPORTANT CHARACTERS.—Length of ♂ 3.6 (3.3–4.0) mm., of ♀ 3.7 (3.4–4.1) mm. Crown moderately produced (1.40 x interocular width; 0.68 x head width) (♂ n = 25; ♀ n = 20). Face variable, from entirely stramineous to stramineous with clypeus darkened, from tan to almost black with pale arcs; interocular band absent. [♂] Pygofer (Fig. 62EE) with posterior lobe not well differentiated ventrally, posterodorsal portion produced caudodorsad and truncate apically. Plates (Fig. 45H) divergent at apex, often appearing to be notched. Aedeagus (Fig. 44F) asymmetrical; shaft elongate, slender, twisted in apical half; gonopore consisting of a spiral groove originating at shaft midlength; pair of asymmetrical, retrorse, apical processes, with one minutely serrate edge. [♀] Sternum VII as for group. Ovipositor with base of each first valvula (Fig. 63LL) angular in dorsal aspect, narrowly curved dorsad anterolaterally, recurved portion extending only slightly dorsad.

GEOGRAPHICAL DISTRIBUTION.—Tall-grass prairie of North Dakota, Kansas to Blackland Prairie, and south Texas east to Missouri and Illinois (Fig. 51). A specimen from the Ball collection is labeled "DC." If this is an abbreviation for "District of Columbia," and if the hastily scrawled, penciled label is correct, then it would be necessary to explain a widely disjunct distribution for *graminea.* Recently, little bluestem and several unusual prairie forb species have been found in a band of savannalike habitat along the north bank of the Potomac River between Great Falls Park (Maryland) and the District of Columbia

(D. Boone, personal communication). The possibility that *graminea* (and perhaps other prairie insects) may have colonized such a habitat cannot be completely discounted.

BIOLOGY.—This species appears to be a specialist of little bluestem (*Schizachyrium scoparium*), but in late summer it may take refuge on other hosts.

OLIGOPHAGY COEFFICIENT.—*Schizachyrium scoparium* 0.91.

REMARKS AND DIAGNOSIS.—Throughout most of the tall-grass prairie, *graminea* occurs regularly with *prairiana* on little bluestem. It can be distinguished from *prairiana* by its consistent lack of an interocular band and by its notched plates. However, through portions of its range it may also occur with *sandersi, dakota,* or *delongi,* or in mixed-prairie habitats with *atlantica* or *reflexa.* The structure of its aedeagus separates it readily from these species, but it is most closely related to *clayi* and *satila.* For differential diagnosis of these three species, see the corresponding section under *clayi.*

43. *Flexamia clayi* Young & Beirne

Flexamia clayi, Young and Beirne 1958: 64.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.3–4.0) mm, of ♀ 3.7 (3.1–3.8) mm. Crown variably produced (1.44 x interocular width; 0.71 x head width) (♂ n = 20; ♀ n = 20). Face brown to black above, usually shading gradually to paler below. [♂] Pygofer (Fig. 62DD) with posterior lobe more distinct than in *graminea.* Plates (Fig. 45I) divergent apically, outer margins widened at midlength. Aedeagus (Fig. 44H) much as in *graminea* but with shaft usually much more expanded at base of gonopore. [♀] Sternum VII as for group; ovipositor with base of each first valvula (Fig. 63GG) rounded, with recurved portion broader than in *graminea.*

GEOGRAPHIC DISTRIBUTION.—Appalachian region from Maine to north Georgia, west to Illinois (Fig. 51).

BIOLOGY.—Some records for *clayi* are for broomsedge (*Andropogon virginicus*); others are for little bluestem (*Schizachyrium scoparium*). Many are for "*Andropogon.*" Since broomsedge does not occur in Maine, at least some of the records for little bluestem must be correct. Many records, including our own, are
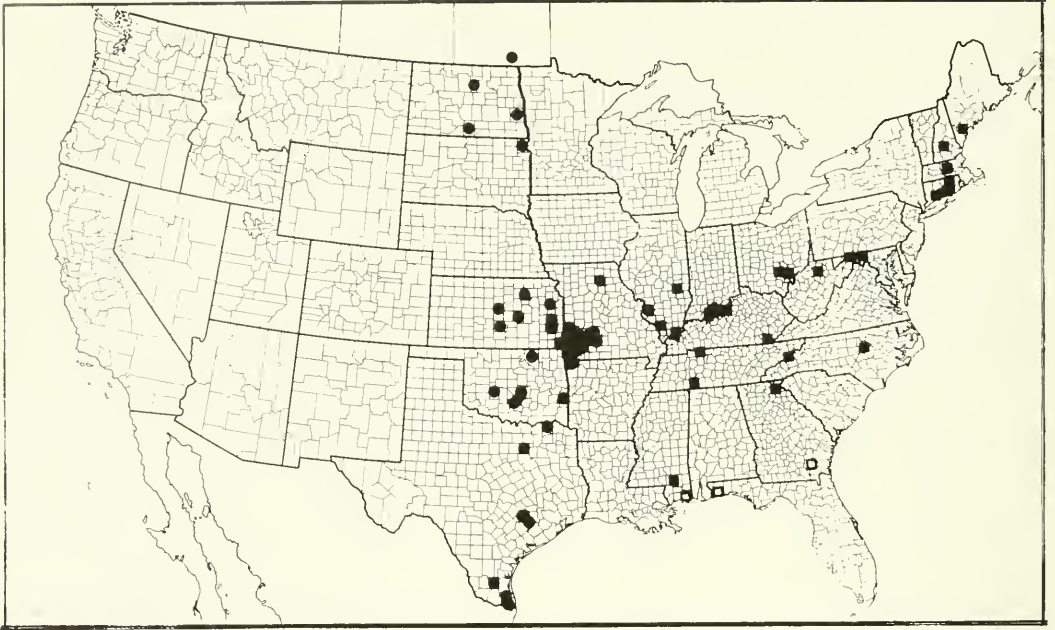
Fig. 51. Geographic distribution of *Flexamia graminea* (●), *clayi* (■), and *satilla* (□).

inadequate to discriminate between these two andropogonoid grasses.

REMARKS AND DIAGNOSIS.—We are unaware of any region in which *graminea*, *clayi*, or *satilla* occur together. As in the case of *sandersi* and *delongi*, they may represent vicariant populations that have become reproductively isolated and diverged morphologically. The initial description of *clayi* from Kentucky, and subsequent collections of the species from Georgia and Tennessee, obscured the extent of the range of *clayi*. Our collections of the species from Ohio and the Maryland and West Virginia Alleghenies, and identification of material from Maine and New Hampshire as *clayi* present a different picture, portraying the species as a cool-temperate species of the eastern mountains. This contrasts with that of *graminea*, whose range is essentially the tall-grass prairie, and *satilla*, whose known range is the Gulf Coast (Florida and south Georgia to Mississippi).

Members of this complex can be readily separated from other *prairiana* group species by aedeagal characters. The aedeagal shaft of *clayi* is much more expanded basad of the gonopore than the usual condition in *grami-*

nea. However, some specimens of *graminea* from south Texas have a basally expanded gonopore that could be confused with that of *clayi*. The most consistent character that separates *clayi* and *graminea* is the condition of the anteapical lobes of the apodemal processes. In *clayi* the processes each have a prominent anteapical lobe, which is directed mesad. The shaft in *satilla* is much narrower than that of *clayi*.

44. *Flexamia satilla* Hamilton & Ross

Flexamia satilla Hamilton & Ross 1975: 606.

IMPORTANT CHARACTERS.—Length of ♂ 3.4 (3.3–3.4) mm, of ♀ 3.6 mm. Crown produced (1.49 x interocular width; 0.74 x head width). Face variable, but without distinct interocular band; usually dark brown or nearly entirely black. [♂] Genitalia much as in *clayi*, but with aedeagal shaft (Fig. 44J) not as expanded at base of gonopore. [♀] Sternum VII as for group; ovipositor with base of first valvula rounded, with recurved portion broad and extending dorsad.

GEOGRAPHICAL DISTRIBUTION.—The type locality in south Georgia is just north of

Okefenokee Swamp. We have found other specimens, collected by Beamer, from the Gulf Coast in Florida and Mississippi.

BIOLOGY.—This species was collected on an andropogonoid grass, probably *Andropogon virginicus* (K. G. A. Hamilton, personal communication).

REMARKS AND DIAGNOSIS.—This species is sympatric with *producta* in the Gulf Coast region, and two specimens had been filed in the KU collection in the *producta* drawer. These specimens were tentatively separated from *producta* by the face, which was black, without a conspicuous interocular band. Unfortunately, some specimens with equally dark faces turned out, when they were cleared, to be *producta*. It is therefore easy to understand how this species escaped recognition for many years.

The degree of genitalic difference between *clayi* and *satilla* falls well within that considered by some workers to represent geographic variation. However, we feel that *satilla* is subject to the same phenological constraints as *producta*. The hypothesis that the *graminea* complex in the East is divided into Appalachian and Gulf Coast species seems reasonable, and, given our ability to distinguish the species on (admittedly minor) morphological grounds, justifies retention of *satilla*.

This species is safely separated from its sympatric cohort, *producta*, only by genitalic examination, although the latter species (unlike *satilla*) often has a distinct interocular band. For distinctions within the *clayi* complex, see the comparable section under *clayi*.

BIOLOGY OF *FLEXAMIA*

Flexamia species are residents of North American grasslands, where they specialize predominantly on dominant, warm-season grasses (Panicoideae and, especially, Chloridoideae). Several species, however, appear to breed on sedges (Cyperaceae) or rushes (Juncaceae). The genus is divided into 13 species groups; host choice is related to membership in these groups.

No *Flexamia* species are known to be univoltine; as a result, they are inhabitants of mesic grasslands and are poorly adapted for semiarid grasslands. The habitats of the genus include true prairie, short-grass plains, semitropical grasslands, high desert plains or montane grasslands, riparian grasslands, and saline or nonsaline lakeshores.

In semiarid grasslands, grass hosts that support *Flexamia* species tend to be capable of growth with minimal precipitation, but are unlikely to undergo repeated episodes of dormancy through the summer. Perhaps this is why, despite their proclivity for chloridoid grasses, not a single *Flexamia* species specializes on *Hilaria* or *Sporobolus* species. This is true despite the fact that some members of these grass genera are among the major dominants in southwestern grasslands and comprise a significant fraction of the regional grassland biomass. [Note: As a control to this "natural experiment," *Hilaria* and *Sporobolus* species have acquired specific non-*Flexamia* cicadellid guilds of their own (Whitcomb et al. 1987).]

The relation of *Flexamia* species to their hosts ranges from habitat specialization (in primitive species), to various degrees of inter- and intrageneric oligophagy, to absolute monophagy. Narrow oligophagy is the most common strategy. Body size of *Flexamia* species appears to be correlated with size of the host plant. Intraspecific variation in body size may reflect host plant quality; individuals from populations at the range periphery are often small.

Flexamia species respond to several aspects of grassland structure. Disturbances such as mowing or burning tend to reduce populations or to extirpate them altogether; for this reason *Flexamia* is an excellent genus for assessing habitat quality of grassland reserves (Whitcomb 1987). On a local level, populations of *Flexamia* species are almost always much higher in more mesic segregates of grasslands defined by minor topographic variation than in adjacent xeric sites (Whitcomb et al. 1987). On a regional level the degree of fidelity to single hosts appears to be least in mesic prairie or, perhaps, in southeastern grasslands (Whitcomb et al. 1987). The structure of grassland dominance hierarchies may determine host choice.

Habitat patchiness has had a profound effect on *Flexamia* species on both historical and contemporary time scales. For monophagous species, their hosts are evolutionary islands. Contemporary host patchiness may affect

presence or absence of *Flexamia* species within their ranges. However, no *Flexamia* species is able to track its host throughout the entire range of the host. This not only is the result of patchy host occurrence at the range periphery, but is often reinforced by climate. In many instances host colonization appears to be blocked by climatic factors. For example, the *Flexamia* complex that colonizes side-oats grama (*Bouteloua curtipendula*) is divided into six species, none of which is known to overlap in range. The isolating mechanisms are those associated with the different climatic regimes of prairie, Chihuahuan and Sonoran desert, interdesert grasslands of the Gila Mountains of southeastern New Mexico, and the eastern and western Mexican grasslands. *Buchloë dactyloides, Schizachyrium scoparium*, and *Muhlenbergia porteri* are similarly partioned, as is *Bouteloua gracilis* (although less spectacularly so). The possible role of host biotype (in its inherent genetic composition), apart from the purely phenologically determined availability of growing host, has not been determined.

We have seen no evidence that *Flexamia* species are highly fecund; they are rarely captured at lights or in aerial traps. There is no evidence of seasonal movement under conditions that permit observation of immigration of *Athysanella* macropters or *Laevicephalus* adults into suitable grassland. We therefore predict that the life history strategy of *Flexamia* species will be found to resemble K- rather than r-selection (MacArthur and Wilson 1967).

Eggs of most species are presumably oviposited in host tissue. In temperate regions it is reasonable to assume that eggs laid in the field in autumn are in diapause. In central latitudes first-generation adults appear in early June. In subtropical latitudes, such as south Florida and south Texas, collection records from December, January, and February indicate that reproduction may occur throughout the year.

SPECIES CONCEPT IN *FLEXAMIA*

The species concept that emerges from our treatment of *Flexamia* is a composite of individual decisions concerning species. We faced difficult decisions in several *Flexamia* species groups.

In the *prairiana* group there are three sets of close sisters. In one of these sets (*prairiana-reflexa*), the types differ so substantially that no immediate problem is evident. When specimens from different geographic regions were examined, however, problems emerged. The holotype of *prairiana*, from Illinois, represents the northeastern periphery of the range of this species (Fig. 46). Females from the southwestern part of the range, especially those from the montane grasslands of the Chihuahuan Desert region or the Trans-Pecos shrub savanna, differ from northern individuals in certain features of the first valvulae; these populations colonize *Bothriochloa* spp. rather than little bluestem (*Schizachyrium scoparium*). However, we found no characters of the male genitalia that distinguish the *Bothriochloa* populations. Further, as discussed by Young and Beirne (1958), the male aedeagal characteristics of *reflexa* and *prairiana* vary intraspecifically. It appears that both species, although widespread, are distributed patchily in some parts of their ranges. Under these circumstances it is reasonable to suspect the existence of reproductively isolated populations. For example, we would not be surprised if the Chihuahuan populations of *prairiana* proved to be reproductively isolated from the tall-grass prairie populations.

Our decision to retain species concepts proposed by Ross and Cooley (1969) and Hamilton and Ross (1975) defining the *sandersi-delongi* and *satilla-clayi* sister pairs has been discussed under the species descriptions of *delongi* and *satilla*. In each case we elected to retain the newly described species on the criterion of probable phenological isolation and consistency of (admittedly) minor morphological differences.

The Anasazi form of *arenicola* presents a more difficult problem. This population, centered in the Four Corners area of the Southwest, is reproductively isolated from populations of *arenicola* in the Nebraska Sand Hills. Further, it has a distinctive morphological characteristic—the unpaired, aedeagal process is invariably broken, presumably in copulation. Although this character tends to define the Anasazi form, we have found one specimen of *arenicola* from Nebraska with a broken aedeagus. Thus, despite our strong suspicion

that a certain amount of morphological divergence has occurred between the two populations, we have found no consistent character to separate the two populations. Because we feel that a taxonomic designation is inappropriate, we refer to the Four Corners population simply as the Anasazi form of *arenicola*.

The *celata-stylata* and *beameri-texana* sister pairs also merit brief mention. The distinctive process of the male pygofer that occurs in both members of the *celata-stylata* set suggests that the divergence is relatively recent. Because the area of present-day occurrence of *celata* was largely created by the most recent glacial maximum (Wright 1970), we at first thought that this speciation event was Holocene in origin, as the minor degree of morphologic divergence would suggest. The geographic proximity of the ranges of the two species seemed to suggest that speciation occurred by dispersal of *stylata* or a similar ancestor into sandhill grasslands that emerged postglaciation. However, the morphological evidence contradicts this tidy explanation. The aedeagal symmetry of *celata* and the presence of presumably plesiomorphic, tapered, notched plates similar to those of *arenicola* or *decora* demand that *celata* be considered the most closely related to the ancestral lineage. Perhaps during various glacial episodes sandy grasslands were much more common than they are today. The existence of three other uncommon sand-inhabiting *Flexamia* species (*grammica, arenicola,* and *areolata*), in combination with other studies (Whitcomb et al. 1986, 1987, 1988) indicating that only dominant grasses accumulate specialists, supports this hypothesis.

The divergence of *texana* and *beameri* is also unclear. This murkiness is perhaps an artifact of the rarity of the species; each is known from single collections of E. D. Ball and R. H. Beamer, respectively. We therefore know little of the ecology of these species. Each of these species occurs just outside the periphery of the known range of *inflata*, in one case in a cold region in New York, in the other a hot region of south central Texas. The propensity of *inflata* to form ephemeral, isolated colonies on a variety of hosts (Whitcomb et al. 1986) ought, theoretically, to spawn peripheral new species. Although *beameri* and *texana* appear to be closely related, the biogeographic data suggest that an independent

origin for the two species from the *inflata* lineage should not be completely discounted.

Species problems in the *prairiana* and *flexulosa* groups, though interesting and challenging, pale when compared to the *pectinata* group. This group, prior to this study, consisted of only two species. We now report expansion of the group to nine species. Three of the new species (*mescalero, jacala,* and *collorum*) differ profoundly from previously recognized species. The remaining four species (*gila, bandarita, minima,* and *zamora*) are closely related members of a complex that includes the previously recognized *pectinata* and *doeringae*. It is likely that all of the species are specialists of side-oats grama (*Bouteloua curtipendula*). This grass host is important (in many regions dominant) throughout most of the prairie, from North Dakota to Ohio to Kansas to north Texas to eastern New Mexico; throughout this region of importance the characters of the styles, aedeagal tips, and female sternum VII of *pectinata* are relatively constant. Similarly, populations of *doeringae* in southeastern Arizona (where the climate has a strong Sonoran influence) show an intraspecifically constant profile in the morphology of the aedeagus, style, and female sternum VII. We now report discovery of a species (*bandarita*) from the Chisos Mountains and Marathon Basin of Texas which, in some respects, is intermediate between *pectinata* and *doeringae. Flexamia bandarita* occurs in an area that is rich in endemism, as attested by our description herein of *zacate*, a new Chihuahuan sister of the Sonoran *canyonensis*.

We were delighted to find this endemic until we examined *Flexamia* specimens taken from side-oats grama in the intervening region between the Chisos Mountains and southeastern Arizona that could be referred to neither *bandarita* nor *doeringae*. Rather, they possessed a mosaic of characteristics representative not only of *bandarita* and *doeringae*, but of *pectinata* as well. With collections from three widely separated localities in New Mexico and Chihuahua, Mexico, totaling eleven individuals, we were compelled to recognize another new species (*gila*).

Although we are uncomfortable separating a large complex occurring on a single host into a number of species, we would be even more uncomfortable illustrating the variation

within a single hypothetical polymorphic "species" and attempting to explain why we included such divergent characters under a single name. In our view such a treatment would require redefinition of the species concept in deltocephaline leafhoppers.

Once we recognized the existence of a species complex of side-oats grama specialists, it was easier for us to accept the results of our reexamination of *minima* DeLong & Hershberger and *zamora* DeLong & Hershberger from Mexico. In these examinations we were assisted by the availability of eight previously unidentified specimens referable to *minima* from Monterrey, Mexico, a location considerably north of the type locality. These specimens and the type of *minima* reveal a morphologic profile similar in some respects to *zamora* and *pectinata,* but with substantial differences in the male plates and styles and the female sternum VII. Similarly, on the basis of the female sternum VII and, to a lesser extent, the male plates and styles, *zamora* can be separated from all other members of the complex.

Construction of a map (Fig. 15) of the geographical distribution of members of the complex clarifies the taxonomic status of the species. The distribution of the complex, like that of the host (side-oats grama), encompasses a large percentage of North American grassland area. However, the six species of the complex occur in very different vegetational regions, some of which are recognizable at the biome level. Furthermore, side-oats grama is rare in the Texas mesquite-acacia savanna, so there is an essential discontinuity in host distribution that probably inhibits gene flow between the United States and Mexican populations of side-oats grama specialists. Part of the barrier between *pectinata* and *minima* and *zamora* is, in fact, the area occupied by *doeringae, bandarita,* and *gila.* Therefore, the existence of reproductively isolated populations of *Flexamia* specialists on side-oats grama in grasslands of the United States and Mexico is probable, and the reinstatement of *minima* and *zamora* is justified.

The concept of climatically limited specialists that geographically partition a single grass host is supported to some extent by studies in Mexico (Triplehorn and Nault 1985) of *Dalbulus* species, most of which appear to be *Tripsacum* specialists. Further support is

given by the recent demonstration (Hicks et al. 1988) that in New Mexico blue grama (*Bouteloua gracilis*) is colonized by seven *Athysanella* species, but that the distribution of each species is confined to regions that are readily interpretable in terms of recognized biogeographic regions (e.g., Colorado Plateau, high plains, short-grass prairie, Chihuahuan grasslands). We believe that *Bouteloua curtipendula* is also partitioned by its *Flexamia* specialists.

In an ideal world we would have postponed all decisions concerning this complex and instead organized an expedition to the Southwest and Mexico to collect *Flexamia* from side-oats grama. However, publication of the conclusions herein need not discourage such exploration; perhaps it will encourage it.

In summary, we have defined *Flexamia* species as populations with consistent and readily demonstrable morphological differences whose reproductive isolation from possibly conspecific populations can be inferred on biogeographic grounds.

PHYLOGENY OF *FLEXAMIA*

Young and Beirne (1958) established the groundwork for a *Flexamia* phylogeny by their careful descriptions of genitalic and other characters of the genus. Also, although they did not propose a formal phylogeny, they discussed species relationships at some length. With a minimum of assumptions, these proposals and relationships can be presented as a cladogram (Fig. 52).

H. H. Ross was intrigued by *Flexamia* and in 1970 published a preliminary phylogeny of the genus in which the species were identified only by number and no apomorphies were described. Although Ross did not present an explicit proposal, his unpublished notes, which specify apomorphies and synapomorphies, make it possible to diagram his phylogeny also (Fig. 53).

OUTGROUPS.—Ross considered *Spartopyge* Young & Beirne and *Aflexia* Oman to represent *Flexamia* outgroups. Young and Beirne (1958) felt that *Aflexia* was not especially closely related to *Flexamia.* Although the habitus of *Alapus* DeLong and Sleesman is very different (Beamer and Tuthill 1934) from that of *Spartopyge* (Fig. 54), its genitalic characters (Figs. 55F,G) suggest relationship with this genus.
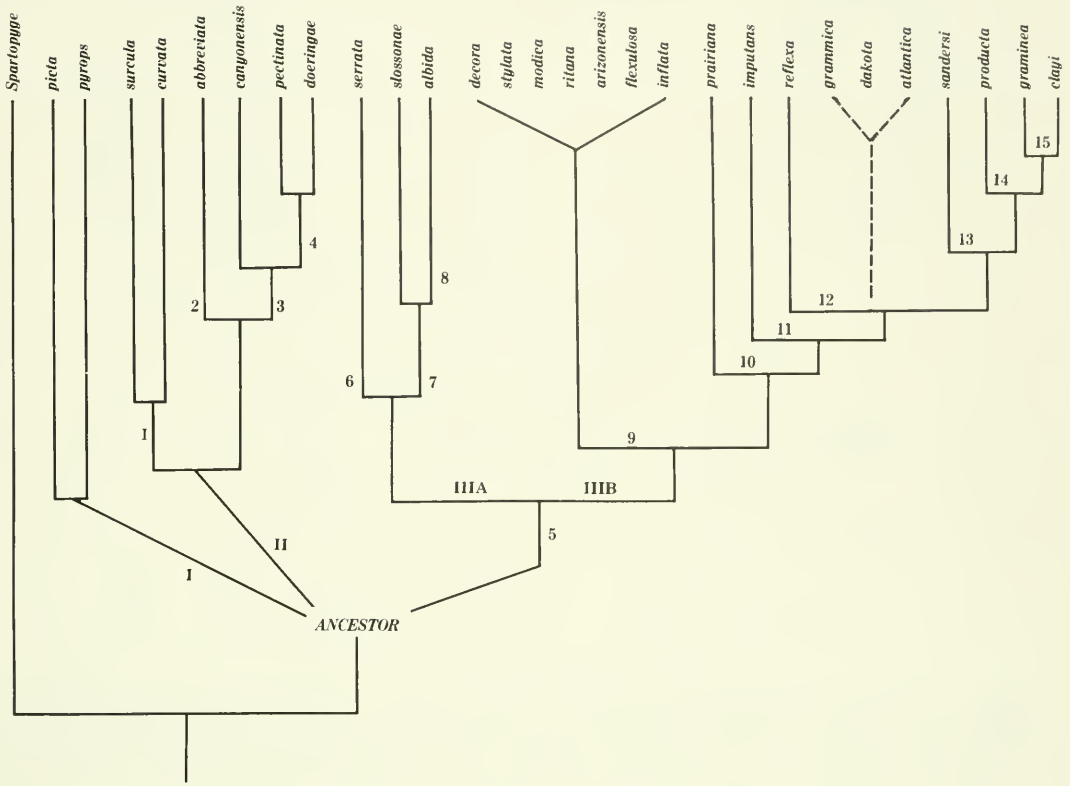
Fig. 52. Species relationships in *Flexamia*: proposal of Young and Beirne (1958). These authors proposed an ancestral condition in which the *Flexamia* aedeagus possessed two pairs of recurved, bilaterally symmetrical appendages at or near the apex of the aedeagal shaft. From this ancestral condition, the authors proposed three or four independent lines of development, without specifying a phylogenetic sequence in which the lines diverged. In one line of development (I), the apical pair of processes tended to fuse and the anteapical to remain separate (*picta* and *pyrops*). In a second line of development (II), the pairs of processes are (1) either preserved, as in *surcula* and *curvata*, or (2) the apical processes are reduced and the basal processes absent (*abbreviata*), or both processes are absent (3) but the location of the gonopore (in *canyonensis*) suggests a derivation from the condition in *abbreviata*. Young and Beirne suggested that *pectinata* and *doeringae*, lacking any trace of aedeagal processes, represent the culmination of one of the developmental lines. We take the liberty of placing these two species (4) at the culmination of line II. In the final lineage the important event was (5) the development of an unpaired ventral aedeagal process. In IIIA this occurred either (6) with additional processes, as in *serrata*, or (7) with branching of more apical processes, as in *slossonae* and *albida*. In *albida* (8) the unpaired ventral process is adherent to the shaft. The final sublineage (IIIB) encompasses most species of the genus. In the more generalized species, the gonopore is small, not elongated, and located on the caudoventral surface of the aedeagus near the apex (9). Young and Beirne placed seven species (*decora*, *stylata*, *modica*, *ritana*, *arizonensis*, *flexulosa*, and *inflata*) in this cluster. In *prairiana* a phyletic torsion of the shaft has occurred (10) so that the gonopore is anteapical on the anterodorsal surface of the shaft. This species has a pronounced groove on the unpaired process, which in *imputans* constitutes the gonopore (11). In *reflexa* the unpaired process is fused basally to the aedeagal shaft (12) but is free at its extremity; the gonopore is circular, but at some distance from the base of the process. In *sandersi* the gonopore has become elongate (13). In *producta* the movement of the gonopore, to the left side of the dorsal surface of the shaft, far removed from the apex, approaches a maximum (14). In *graminea* and *clayi* the unpaired process has almost completely disappeared and the gonopore is spiral (15). In *grammica*, *dakota*, and *atlantica* the anteapical processes have been lost; these species were tentatively placed in line IIIB.
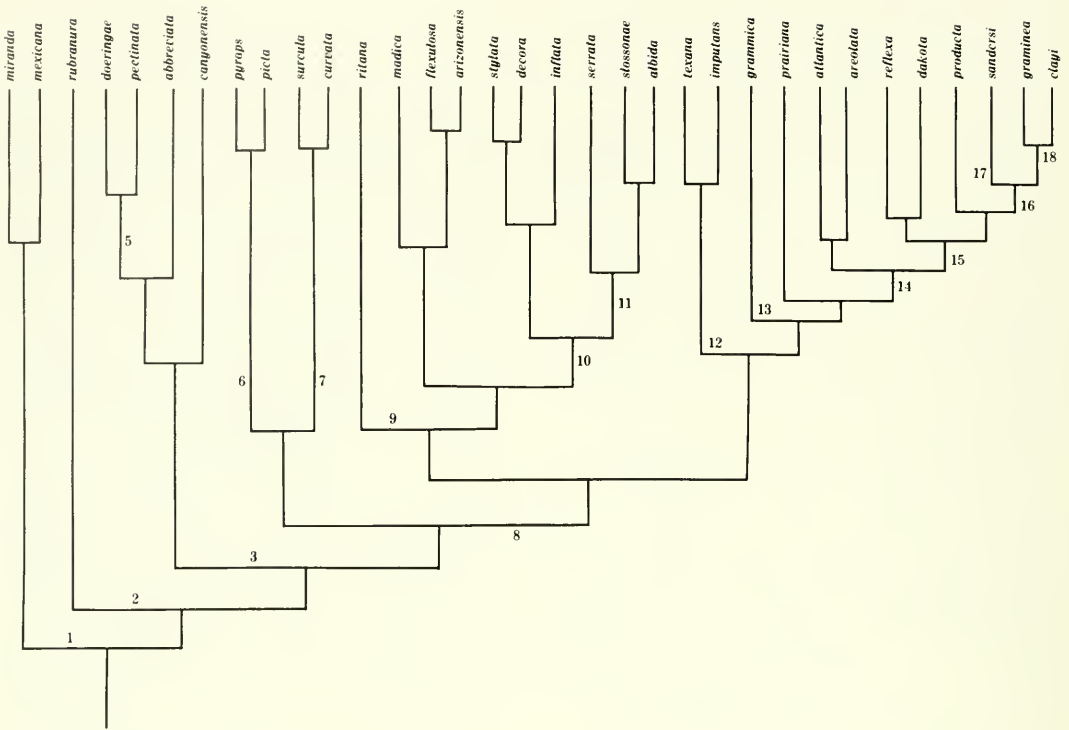
Fig. 53. *Flexamia* phylogeny proposed by Ross (1970, and unpublished notes). The tree diagram was transposed to a cladogram. Identification of species and apomorphies used by Ross to construct the cladogram are taken from unpublished notes. The apomorphies and conserved plesiomorphies designated were (1) mesal brush on pygofer; (2) thin aedeagal shaft with basal processes; (3) lack of aedeagal processes; (4) width of aedeagus, thick (4) or thin (4′); (5) length of male style; (6) angulate pygofer; (7) four aedeagal processes; (8) aedeagus with mesal process; (9) acute aedeagal apex; (10) long, mesal aedeagal process; (11) unpaired aedeagal process bifurcate; (12) aedeagal processes twisted; (13) dorsal location of gonopore; (14) fusion of connective and aedeagus; basal location of median process and gonopore (somewhat = 15, more so = 16); widening (17) of median process to bean-shaped structure appressed to shaft; (18) loss of medial process.

Future phylogenetic hypotheses concerning *Flexamia* should be broadened to include a much wider range of outgroups than those discussed above. Candidates for study should perhaps include *Enantiocephalus* Haupt, a Eurasian genus (Figs. 55A,B). K. G. A. Hamilton (personal communication) has suggested that *Mocuellus* Ribaut and related genera should not be overlooked as outgroups. Finally, we will soon add a new genus (in preparation), presumably also related to *Flexamia*. This genus consists, so far as known, of a single species that specializes on *Muhlenbergia arenacea* in saline flats in semiarid regions of New Mexico and Arizona. The former genus *Acurhinus* (= *Dorydium*) may be more distant from *Flexamia* than once thought (Linnavuori 1959). *Acurhinus maculatus* (Osborn),

known only from three females in the Ohio State University collection, is currently regarded as a species of *Hododoecus* Jacoli, an essentially African genus of the Stirellini (Linnavuori and DeLong 1978). It is evident that a phylogeny of deltocephaline genera, especially those with linear connectives articulated with the aedeagus, would greatly enhance all phylogenies of deltocephaline species.

In this study we have chosen two *Spartopyge* species [*miranda* (Knull) and *mexicana* (DeLong & Hershberger)] and *Alapus elongatus* Beamer & Tuthill for outgroup comparison.

PHYLOGENY OF *FLEXAMIA* GROUPS. — We have developed an intuitive phylogeny utilizing many of the characters and concepts
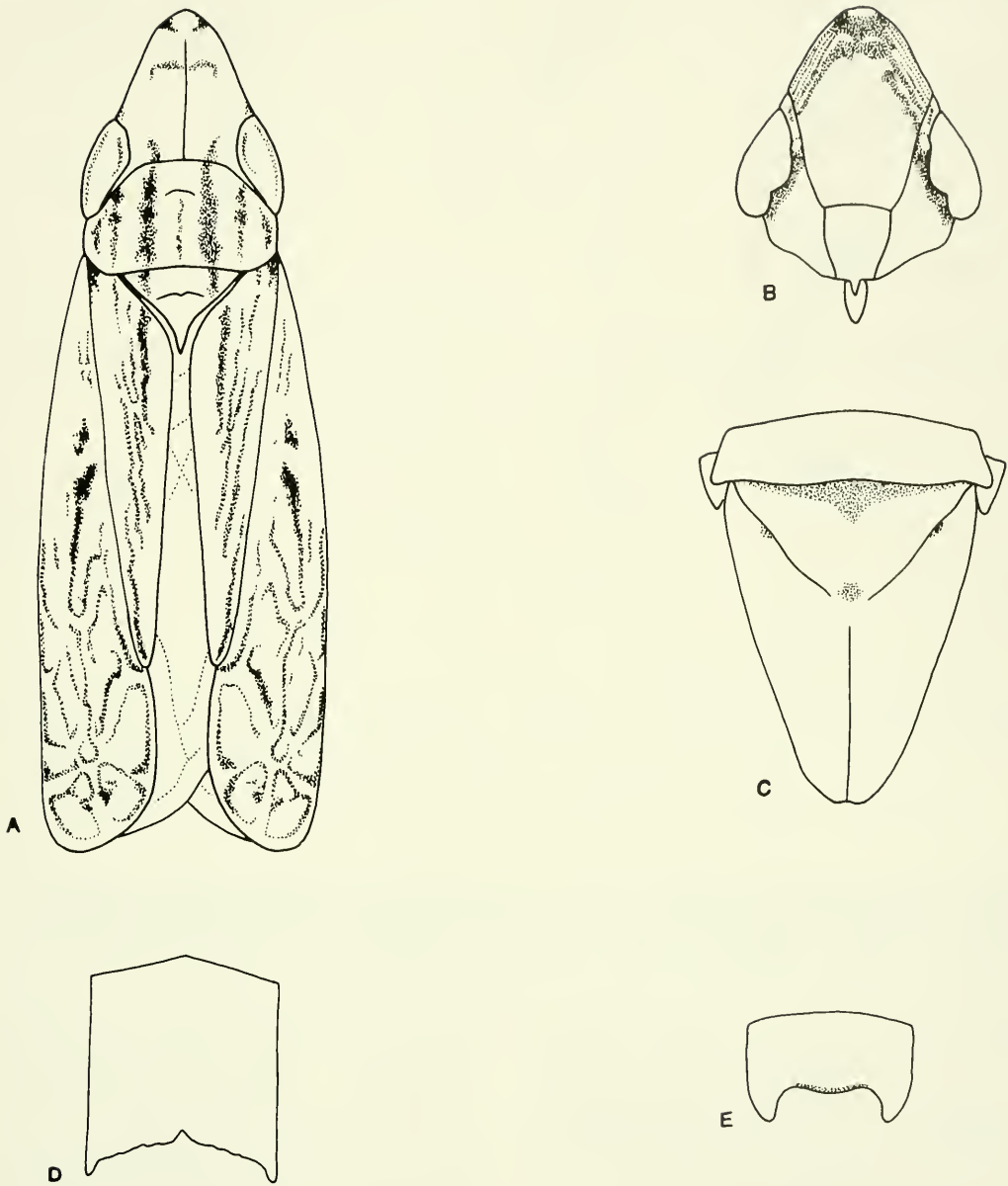
Fig. 54. *Spartopyge* Young & Beirne, the principal *Flexamia* outgroup. *Spartopyge mexicana* (DeLong & Hershberger): A, habitus; B, face; C, male plates, ventral aspect; D, female sternum VII; E, *S. miranda* (Knull), female sternum VII.

developed by Young and Beirne (1958) and Ross (1970, unpublished notes). Details of our reconstruction follow:

A. *Designation of sister species.* We first identified synapomorphies that define close sister species sets. We also assigned polarities within these sets by defining significant autapomorphies of one of the set members.

The sets and defining synapomorphies [s] and autapomorphies [au] were:
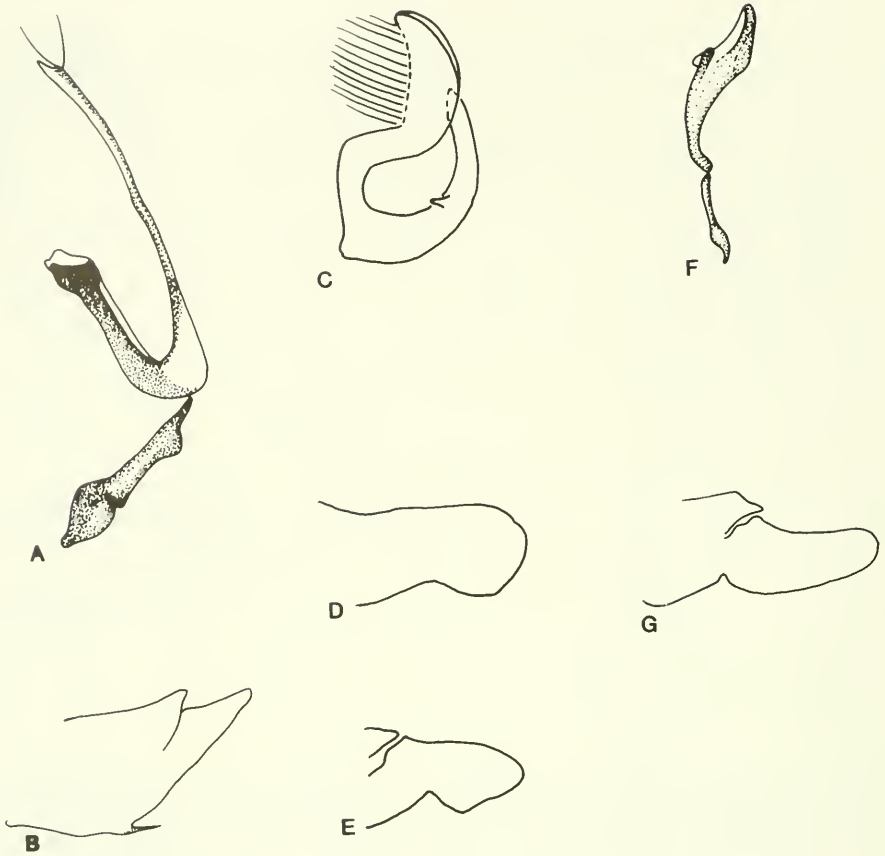
Fig. 55. Male genitalia of genera related to *Flexamia*. *Enantiocephalus cornutus* (Herrich-Schäffer): A, aedeagus and connective, lateral aspect; B, male pygofer, lateral aspect. *Spartopyge mexicana* (DeLong & Hershberger): C, aedeagus, lateral aspect; D, male pygofer, lateral aspect. *Spartopyge miranda* (Knull): E, male pygofer, lateral aspect. *Alapus elongatus* Beamer & Tuthill: F, aedeagus and connective, lateral aspect; G, male pygofer, lateral aspect.

surcula → curvata [s] Aedeagus with two pairs of processes, one apical, one anteapical (Figs. 7F,G).

host — *Buchloë dactyloides* [au] Apical processes long and not in bilaterally symmetrical plane (Fig. 7F). Gonopore an elongate channel.

zacate → canyonensis [s] Aedeagus curved, acute apically, without aedeagal processes (Figs. 7I,J).

host *Muhlenbergia porteri* [au] Gonopore at midlength of aedeagal shaft.

minima → zamora [s] Style apices in lateral aspect bluntly produced (Figs. 13A,B).

host unknown [au] Outer teeth of female sternum VII incurved, longer than inner teeth (Fig. 14B).

bandarita → gila [s] Female sternum VII with two produced, median teeth (Figs.

host = *Bouteloua curtipendula* 14D,E). Male plates broad, bluntly rounded (Figs. 11D,E). [au] Male plates nearly as long as pygofer (Fig. 11E).

albida → slossonae [s] Posterior lobe of male pygofer undifferentiated (Figs. 62Q,T).

habitat specialists [au] Male plates exceed pygofers (Fig. 8B); female sternum VII trilobed (Fig. 10B). Aedeagus and connective partially fused.

picta → pyrops [s] Aedeagal tip capitate, toothed, with pair of subapical processes (Figs. 7K,L); pygofers (Figs. 5A, B) angulate with ventral process.

host = *Aristida* spp. [au] Vertex extensively produced, anteapical aedeagal processes (Fig. 7L) more remote from apex, male plates (Fig. 9B) very short, rounded.

arizonensis →
    flexulosa
hosts = *Aristida*/
Bouteloua gracilis

[s] Male plates [Figs. 33A,B] short, divergent apically.
[au] Apical aedeagal processes short (Fig. 31K).

youngi → *decora*

host =
Muhlenbergia
richardsonis

[s] Unpaired ventral aedeagal processes (Figs. 31F,G) symmetrical and much longer than paired processes.
[au] Unpaired process (Fig. 31G) without median groove, aedeagal shaft curved.

celata → *stylata*

hosts =
Redfieldia/
Muhlenbergia spp.

[s] Face (Fig. 3B) with discrete lines forming interocular band; three aedeagal processes angularly divergent from shaft (Figs. 31H,1). Pygofer with distinct posterior process (Figs. 62OO,PP).
[au] Apices of male plates subrectangular; aedeagus (Fig. 31H) asymmetrical.

beameri → *texana*

hosts
unknown

[s] Aedeagal processes about equal in length, but ventral processes not in sagittal plane (Figs. 31 A,D).
[au] Aedeagal processes twisted apically (Fig. 31A).

imputans → *areolata*
hosts =
Muhlenbergia
cuspidata/
Eragrostis
spectabilis

[s] Unpaired process lateral, with ventral groove (Figs. 31B,C).
[au] Aedeagus and connective fused, unique habitus (Fig. 2F).

prairiana → *reflexa*
hosts
andropogonoid
grasses

[s] Gonopore dorsal (Figs. 44D,G).
[au] Groove absent on unpaired process (Fig. 44D).

sandersi → *delongi*

hosts
andropogonoid
grasses

[s] Lateral process appressed to aedeagal shaft (Figs. 44B,C).
[au] unpaired process (Fig. 44C) at less acute angle with aedeagal shaft.

satilla → *clayi*
hosts =
andropogonoid
grasses

[s] Flared, elongate gonopore (Figs. 44H,J).
[au] Gonopore broad basally (Fig. 44H).

B. Designation of clades. The next step consisted of appending other species to the sister sets to define clades:

minima →
zamora → *pectinata*
host probably =
Bouteloua
curtipendula

[s] Style with apical lobe not constricted (Figs. 11A–C);
[au] Male plates (Fig. 11C) subrectangular; style tip (Fig. 13C) not produced in lateral aspect.

bandarita → *gila* →
doeringae
host =
Bouteloua
curtipendula

[s] Middle teeth (Figs. 14D–F) of female sternum VII longer than outer teeth.
[au] Middle teeth long, associated to form process (Fig. 14F).

graminea → *satilla* →
clayi
hosts =
andropogonoid
grasses

[s] Spiral gonopore (Figs. 44F,H,J)
[au] Flared gonopore (Fig. 44H)

C. Establishment of species groups. Clades were next assembled into species groups. These are the groups (I–XIII) described herein. Synapomorphies defining clades and species groups are given in the descriptions to the groups and in the legends to Figures 56–59.

D. Establishment of polarity between Spartopyge and Flexamia. The dorsal and facial habitus of *grammica* (Fig. 2C), *albida* (Fig. 2A), and *Spartopyge* (Fig. 54) are clearly homologous. On the other hand, few characters of *grammica* are clearly homologous to those of other *Flexamia* species. The morphology of the male aedeagus and connective places this species in the genus, but the reduced number of aedeagal apices and their apparent phyletic twisting make it difficult to assign homology. The male pygofer and female sternum VII suggest retention of plesiomorphic characters of an ancestor allied to *Spartopyge*. We therefore hypothesize the polarity *Spartopyge* →

grammica. Derivation of the similarly striped *albida* group, of course, could have occurred only after development of paired aedeagal processes and fusion of the anteapical pair into a single, unpaired process (Fig. 56). Reversing the polarity between *grammica* (or *albida*) and *Spartopyge* would require generation of a wide array of apomorphies present in *Spartopyge*, including a brush of setae on the interior of the pygofer and the complex structures of the male genitalia (Fig. 55C), accompanied by complete loss of all apical processes. Also, the unique sternum VII (Figs. 54D,E) of *S. mexicana* and *S. miranda* would have to arise suddenly. Finally, if *Spartopyge* were derived from the *Flexamia* lineage, it would be necessary to postulate a significant apomorphic increase in size. This would constitute a reversal of the overall trend for size reduction and simplification in the Deltocephalinae in general (Whitcomb et al. 1986) and *Flexamia* in particular. We therefore
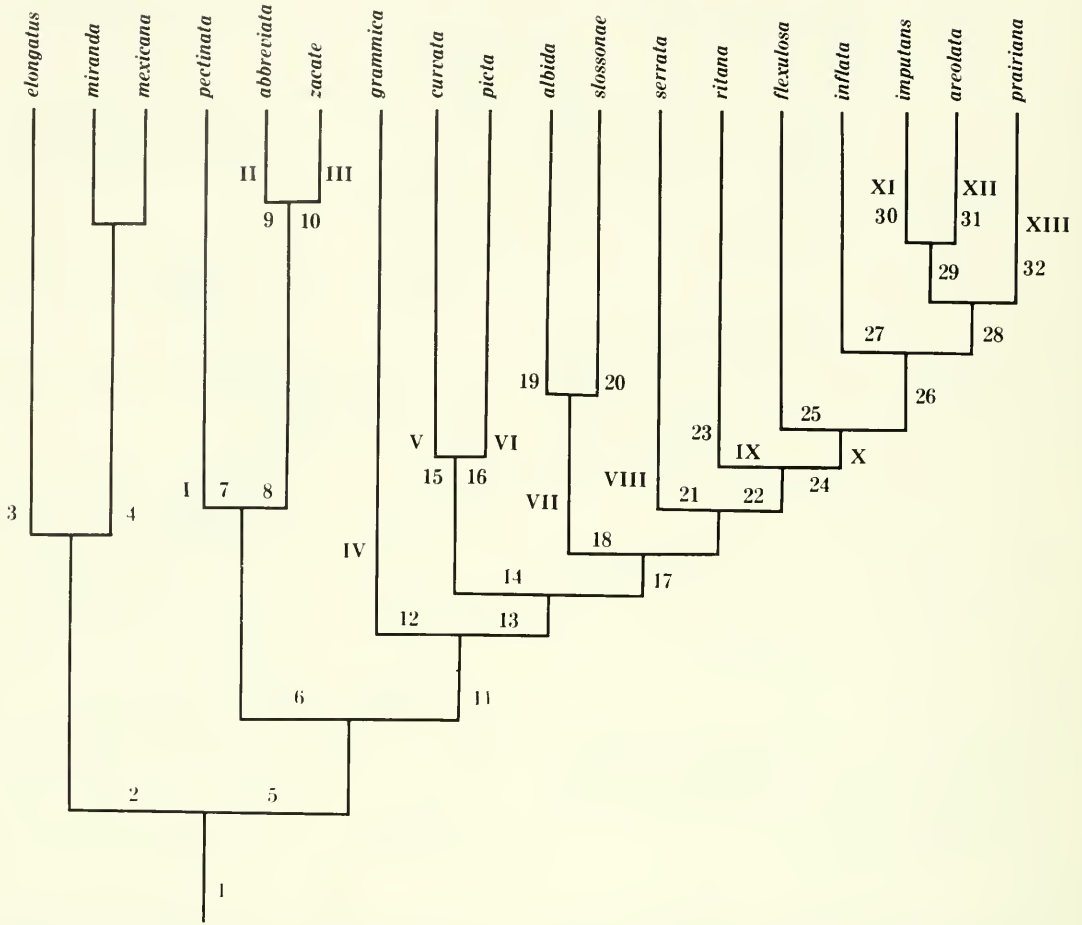
Fig. 56. See facing page.

hypothesize (with Young and Beirne, and Ross) that *Spartopyge* is an outgroup of the *Flexamia* lineage. We believe, with these workers, that a primitive *Flexamia* ancestor arose from the *Spartopyge* lineage and later gave rise to a lineage with paired, aedeagal processes. This lineage in some way gave rise to *grammica* but, ultimately, to all *Flexamia* groups IV–XIII. We assume that the dorsal location of the gonopore in *grammica* and *prairiana* is a result of independent evolutionary events, since these species share few other significant characters. Whether the minute, paired processes that occur midlength on the *Spartopyge* aedeagus are homologous with the *Flexamia* aedeagal processes is conjectural.

PHYLOGENY OF *FLEXAMIA* GROUPS AND SPECIES. The postulated relationships and polari-ties permit a cladogram to be drawn relating *Flexamia* groups and key species to the outgroups *Alapus* and *Spartopyge* (Fig. 56). Several significant possible variations of the proposed tree are given in Figure 57. Finally, the phylogeny of *Flexamia* species was inferred on the basis of the characters discussed above. We present cladograms for groups I–IX (Fig. 58), groups VII–XI (Fig. 59), and groups XI–XIII (Fig. 60). Synapomorphies used to define clades within each group are given in the legends to the figures.

CHARACTER TRANSFORMATIONS.—Our intuitive phylogeny provided general guidelines concerning character transformation in *Flexamia*. From these concepts we constructed branched transformations for the PHYSYS program of Mickevich and Farris (1984). These transformations, which are described

Fig. 56. Proposed phylogeny of *Flexamia* groups and key species. Synapomorphies [s] or, for monobasic groups, autapomorphies [au] are indicated. We hypothesize an ancestral form (1) that possessed dorsal stripes (Fig. 54A) and a pale face with a contrasting black interocular band (Fig. 54B) similar to those of Figs. 3A and 3B, relatively wide male plates (Fig. 54C); an aedeagus distinctly jointed with the connective, without apical processes, and with an anteapical gonopore on the caudoventral surface. Divergence of this lineage led (3) to *Alapus* (Figs. 55F,G), represented in this diagram by *elongatus*, and to *Spartopyge*, represented (4) in this diagram by *miranda* and *mexicana*, in which [s] the dorsal aedeagal apodeme is large and hoodlike (Fig. 55C). The transformations between *Flexamia* and its outgroups are tenuous (see text). In *Flexamia* [s] the dorsal aedeagal apodeme (Fig. 6) has a pair of conspicuous appendages directed caudoventrad or caudad (5). In the first lineage (6) to diverge, the plesiomorphic aedeagal apex, which lacked processes, was retained, as were the caudoventral position of the gonopore and broad, ancestral plates; the contrasting face was retained in a minority of species, but the striped habitus was completely lost. Synapomorphies defining this lineage include [s] the curved aedeagus lacking processes (Figs. 7I,J; 16A, 17A, 20A) and the male pygofers, which possess both dorsal and ventral constrictions (Figs. 62A–I). This lineage diverged into the *pectinata* (7) and the *abbreviata-zacate* lineages (8). In the *pectinata* group the plates (Fig. 11) are distinctively parallel-sided basally (except in *collorum*). In the *abbreviata-zacate* lineage the gonopore was at first elongate (Fig. 24) and [s] the posterior lobe of the male pygofer strongly produced (Figs. 62H,I). In the *abbreviata* group (II) the plates (Fig. 8E) are reduced (9), and [au] a distinctive pair of minute apical processes (Fig. 7H) developed. The small aedeagal processes of the *abbreviata* group are not clearly homologous with other aedeagal processes in *Flexamia*. In the *zacate* group (III) the gonopore (Fig. 24) was at first elongate (10) but in *canyonensis* moved to the aedeagal midpoint. At this point a significant apomorphy appeared. An ancestral form (11) is hypothesized in which two pairs of aedeagal processes were present. It is unclear whether this form had fully developed before divergence of *grammica* (IV), in which the plesiomorphic feature of dorsal stripes was retained (12), but in which [au] the aedeagal processes were distinctively modified (Fig. 7E) and the gonopore had moved to the dorsal surface (12). A possible apomorphy linking *grammica* with the *curvata* group is the foot-shaped style apex (see illustrations of Young and Beirne 1958). In the *curvata-picta* lineage [s] both pairs of aedeagal processes are present (14), but many habitus features, including stripes and contrasting face, have been lost. In the *curvata* group (V) two pairs of processes are present (15) and [s] unmodified (Figs. 7F,G). In the *picta* group (VI) the apical processes are [s] modified (Figs. 7K,L) as flangelike, toothed appendages (16). Remaining species are defined by an apomorphy that developed with the presumed fusion (17) of the anteapical processes into a single, unpaired process that was plesiomorphically located ventrally in the sagittal plane (Figs. 31, 61A). A second apomorphy characterizing this divergence is the bifurcation (Figs. 7A–C) of the apical aedeagal processes, a feature that was subsequently lost (22). The plesiomorphic state of dorsal stripes and contrasting face was preserved (18) during the fusion of subapical processes and is present (Figs. 2A,B) in the *albida* group (VII). This lineage, which can be defined [s] in terms of the absence of dorsal or ventral constrictions in the posterior lobe of the male pygofer (Figs. 62Q,T), is represented today by the distantly related sister species *albida* (19) and *slossonae* (20); for autapomorphies defining these species, see text. In *serrata* (VIII) [au] additional dorsal aedeagal processes (Fig. 7A) developed (21), and, while the contrasting face was retained, dorsal stripes were lost (Fig. 1). In *ritana* (IX) the dorsal stripes were retained (Fig. 2D) but greatly reduced. This monobasic group (23) is defined [au] by the unique, pointed aedeagal apex (Fig. 7D). In one lineage of the *flexulosa* group (25), the unpaired aedeagal process is, plesiomorphically, ventral in the sagittal plane, permitting retention of aedeagal symmetry (Figs. 31G,I,J,K,L). The plesiomorphic pale face with black interocular band (Figs. 3B,F,G) was also retained. This clade is defined [s] by the triangulate plates (Figs. 33A–F, 34D) with conspicuous, apical divergence. (But in *stylata* [Fig. 34E], the plates [au] are truncated.) In the remaining species (26) the unpaired process underwent phyletic twisting (Figs. 61B–H) and the contrasting pale face, which had persisted through many nodes, was finally lost. In the *inflata* subgroup of group X, [s] the displacement of the unpaired process (Fig. 61B) was relatively small (27), but [s] in the *imputans-areolata* (XI-XII) lineage the process had become lateral (Figs. 31B,C) and bore the gonopore as an elongate slit (29). Before divergence of groups XI-XIII, the connective and aedeagus had remained articulated (but see discussion of group VI in text). We hypothesize that after divergence of the *imputans-areolata* lineage, a fusion of aedeagus and connective occurred (31) in *areolata*. The *imputans-arcolata* lineage is very specialized in the location of the unpaired process, in the black face, and the greenish dorsal pigmentation. Of the two species, *areolata* is the more highly specialized (Figs. 2F, 10Q); in fact, it may be the most highly specialized of all *Flexamia* species. It is most unlikely that the widely distributed and variable *prairiana* (see text) and the entire *prairiana* group (XIII) were derived from the specialist *areolata* lineage. Instead, we propose that divergence of a second lineage in which aedeagus and connective fused (32) led to the *prairiana* group. This fusion, the traces of which are evident (Fig. 6F) in *prairiana*, is designated [s] as a synapomorphy defining group XIII, and the fusion in *areolata* is defined as an autapomorphy defining that species. Details of species phylogenies are presented in detail in Figures 58–60.

in Appendix II, Part III, involved the following characters: (1) relationship between aedeagus and connective; (2) morphology of the aedeagal apex; (3) morphology of anteapical aedeagal processes; (4) phyletic twisting of the unpaired ventral process (Fig. 61); (5) curvature (lateral aspect) of the aedeagus; (6) thickness (lateral aspect) of the aedeagus; (7) length of the aedeagus; (8) form of the aedeagal shaft; (9) form of margins of paired, aedeagal processes; (10) form and position of the gonopore; (11) morphology of apices of the apodemal arms; (12) position of apodemal arms; (13) width of dorsal keels of the connective; (14)
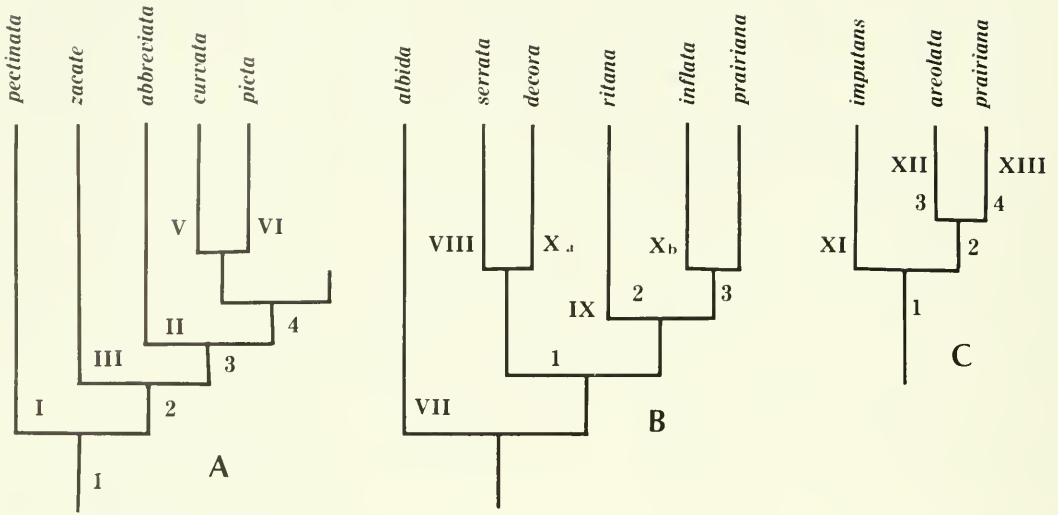
Fig. 57. Alternative resolutions for *Flexamia* group phylogenies. A. In this resolution (1) two groups (I and III) are defined by [s] curved aedeagus without processes (Figs. 7I,J, 16A, 21A). The alternative lineage (2) is defined by an apomorphic elongation of the gonopore. This was followed by derivation of a further lineage (3) in which aedeagal processes are present. At first these are [s] minute (II *abbreviata*, Fig. 7H) but later become (4) fully developed (see Figure 56). This resolution avoids hypothesizing independent origins for the aedeagal processes in *abbreviata* and *curvata* but hypothesizes additional nodes between *Spartopyge* and the *Flexamia* species with very similar habitus, implying repeated, independent losses of the complex pattern of striping in *Spartopyge*, *grammica*, and *albida*. B. In this resolution, it is hypothesized (1) that the *serrata* group and *decora* subgroup of group X belong to a common lineage, and that the *inflata* subgroup of group X is more closely related to *ritana*. This construction has considerable merit and takes into account the similarities between the *serrata* male plates (Fig. 8C) and those of the *decora* subgroup (Figs. 33, 34D,E), but deemphasizes many similarities between members of the *inflata* and *decora* lineages, and would augur for elevation of these lineages to groups. C. It is possible to hypothesize a single (2) fusion of aedeagus and connective, rather than the two fusions hypothesized in Figure 56. This construction, in our view, gives insufficient weight to several synapomorphies that link *areolata* and *imputans*, which would, in fact, have been designated as a close sister species set had they not differed in the crucial relationship of aedeagus to connective. See discussion in legend to Figure 56, and text.

morphology of the male pygofer (Fig. 62); (15) morphology of the male plates; (16) morphology of the female sternum VII; (17) presence or absence of dorsal stripes; (18) coloration of the face.

The above transformations, as presented in Appendix II, are suitable for entry into the PHYSYS program and should serve as a useful starting point for more refined analysis of *Flexamia* phylogeny.

SUMMARY OF PHYLOGENETIC MODEL.—In summary, after numerous iterations, we propose a formal phylogeny for *Flexamia*. The model is rooted in earlier informal work of Young and Beirne (1958) and Ross (1970, and unpublished notes). Our model, in addition to its formality, considers 14 species not available to earlier workers and proposes species groupings based in large part on synapomorphies. In particular, the addition of seven species to the *pectinata* group (I) and four species to the *flexulosa* group (X) adds new phylogenetic perspectives.

We have accepted the hypothesis of Young and Beirne of an ancestral form with two pairs of aedeagal processes. We also endorse the proposal of Young and Beirne (and Ross) that the anteapical pair of processes fused to form a single, unpaired process (Fig. 52). Further, we accept the proposal of Ross (Fig. 53) that the fusion of aedeagus and connective is an important synapomorphy that defines the *prairiana* group.

The informal proposal of Ross differed from that of Young and Beirne in one major way (in addition to its presentation as a tree). Ross believed that the lack of aedeagal processes in *pectinata* and *canyonensis* was plesiomorphic and related it to the similar lack of processes in his outgroups, *Spartopyge* and *Aflexia*. In our

proposal we have sided with Ross. Unless different outgroups were chosen, we feel such an assignment is inevitable. Also, transformations within *Flexamia* are best explained by the chosen polarity. For example, viewing the *pectinata* group as the terminus of a simplification of the aedeagus would require the transformation of male plates from narrow to broad, in direct contrast to the general tendency for streamlining of the plates that runs throughout the remainder of the *Flexamia* tree.

We have assumed, with Ross, that the minute processes in *abbreviata* are not homologous with other *Flexamia* aedeagal processes. This assumption, which permits many other reasonable character transformations to be postulated, appeared in our model only after numerous iterations failed to find a better resolution, considering all transformations. Such issues are best addressed by close examination of the structures themselves, preferably by scanning electron microscopy, for evidence that would bear on the question of homology. It is possible that a computerized search for a parsimonious tree would turn up a cladogram that avoids the pitfalls we encountered in our intuitive search. In any event, we present in Figure 57A an alternative cladogram that, whatever its other problems, assumes homology between the aedeagal processes of *abbreviata*, *grammica*, and *curvata*.

Young and Beirne (1958), although uncertain about the status of *dakota*, *atlantica*, and *grammica*, nevertheless placed them tentatively in their lineage IIIB (Fig. 52). We concur with Ross in his placement of *dakota* and *atlantica*. However, we disagree with both Young and Beirne and Ross in the placement of *grammica*. Whereas the dorsal location of the gonopore and the presence of two serrate, aedeagal processes of this species is clearly highly apomorphic, we see nothing else in *grammica* that links it to group XIII, in which the dorsal location of the gonopore is a significant apomorphy. For example, the male plates and pygofers, the female sternum VII, the clear articulation of aedeagus and connective, the striped habitus and pale face, and the overall large size of *grammica* are derivable as transformations from the outgroup *Spartopyge*, but they would produce chaos if inserted into transformations in group XIII (or

any other group or groups between VII and XII). In fact, the ties between *Spartopyge* and *grammica* are sufficiently reasonable that we have couched our argument for the polarity *Spartopyge* → *Flexamia* in terms of *grammica* (see earlier section).

The model we present solves many of the problems that we encountered. Resolution of many questions was made possible by proposing (1) that aedeagal processes arose in the course of *Flexamia* evolution and were not inherited from an unknown ancestor; (2) that aedeagal symmetry was plesiomorphic (but note the apomorphic symmetry in *dakota*). Further character transformations have been proposed (Appendix II, Figs. 61, 62) that lead to consistent hypotheses for transformation of other characters (e.g., bases of the first valvulae, which are presented in Fig. 63 in terms of our proposal but were not used to derive it). The proposed resolution avoids hypothesizing independent acquisitions of the unique striped habitus present in *Spartopyge*, and in *grammica*, *albida*, and *slossonae*. It further avoids hypothesizing independent derivations of the unique facial habitus of the outgroup, which was retained through a considerable segment of *Flexamia* evolution. We do hypothesize several independent losses of these distinctive sets of habitus characters. Finally, the proposed model follows the following general polarities: (1) tropical grasslands → subtropical grasslands → temperate grasslands → [semiarid grasslands, prairie]; (2) large → small size; (3) grass generalist → chloridoid specialist → mixed chloridoid-panicoid specialist → andropogonoid specialist; (4) striped habitus → [light habitus (semiarid), brown (prairie)]; and (5) aedeagal symmetry and caudoventral gonopore → highly specialized aedeagal configurations and gonopore locations.

But not all the problems have been solved. We regard the cladogram for groups I–III to be tentative. The position of *mescalero* as a member of group I is unclear; this unique species might have been more appropriately considered to be a separate group linking groups I and III. In fact, the general question of polarity of the *pectinata* group should be critically addressed. We are not certain how to interpret evidence of considerable recent speciation in this group (i.e., *bandarita/gila*, *minima/zamora/pectinata*). It is likely, given our
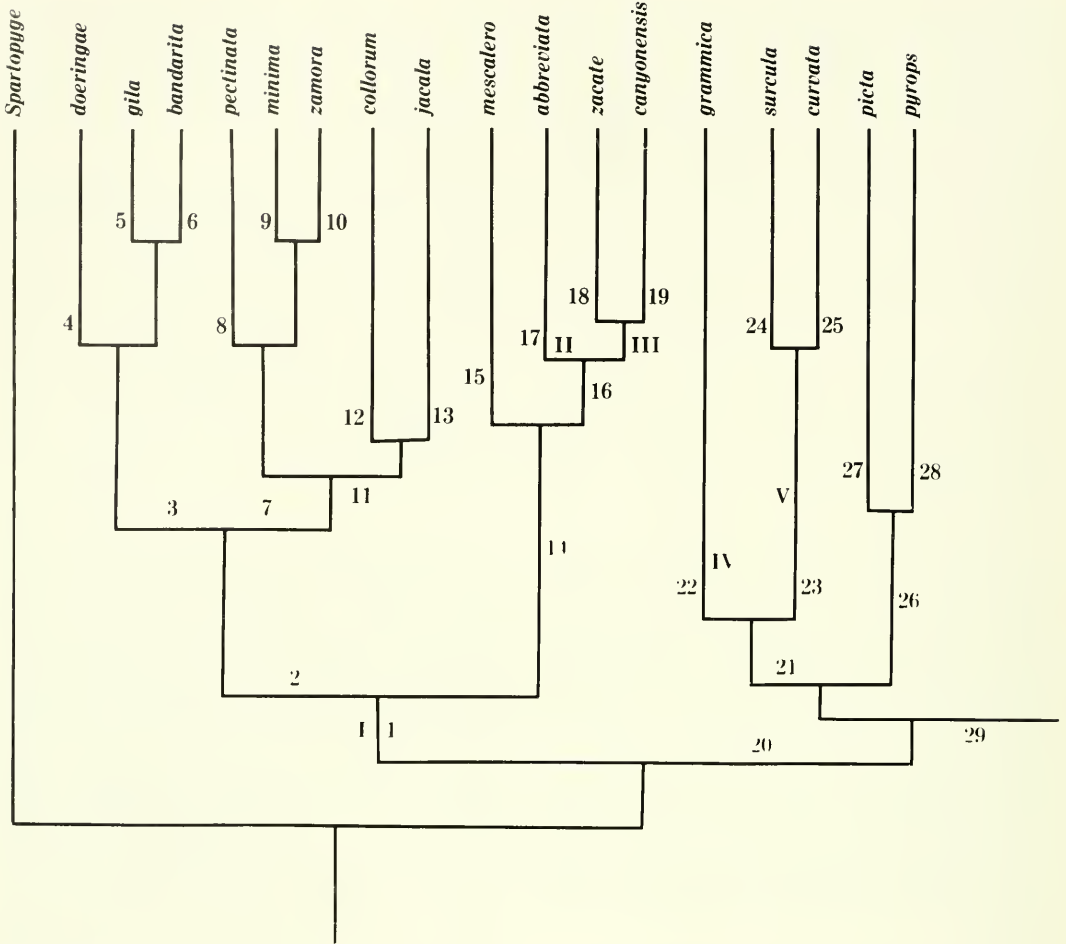
Fig. 58. See facing page.

discovery of many new species from the Southwest, that further acquisitions of *Flexamia* or related genera from Mexico may change our perceptions dramatically. Also, a wider selection of outgroups would clarify the status of the early *Flexamia* lineages.

Young and Beirne (1958) proposed that grooves on the unpaired aedeagal process were vestiges of a plesiomorphic condition in which the halves of the processes were separate. This condition occurs in several species (*youngi*, *imputans*, *prairiana*), but we have been unable to link these species in any transformation that is consistent with other transformations.

Finally, we propose, with some confidence, that the articulation between aedeagus and connective was subject to fusion or partial

fusion in four nodes of our model. These were in the lineages leading to *picta-pyrops*, to *areolata*, to *slossonae*, and to the *prairiana* group. Given the different products of each of these fusions, and the position on the tree in which they occurred, we have no problem in treating each as a synapomorphy.

The genus *Flexamia* is rich in characters and should provide an excellent model for the PHYSYS program. It is likely that careful study and numerous iterations using such a program will further improve phylogenetic hypotheses concerning *Flexamia*.

BIOGEOGRAPHIC IMPLICATIONS OF THE
PHYLOGENETIC MODEL

Ross (1965, 1970) felt that many speciation

Fig. 58. Phylogeny of species of groups I-IX. The following events, including synapomorphies [s] and autapomorphies [au] are postulated: (1) In the plesiomorphic state of the *pectinata-abbreviata* subtree, the male plates were broad (Fig. 11), the male pygofers constricted (Fig. 62F), the gonopore oval on the caudoventral surface, and the aedeagus (Figs. 12A–H) without apical processes; (2) In one subtree of the *pectinata* group (comprising eight of its nine species), the aedeagal tip remained unmodified but flared (Figs. 12A–H). In all three species of the *gila* division (3) of this group, the female sternum VII developed [s] long, median, paired teeth (Figs. 14D–F); in *doeringae* (4) these teeth [au] became associated into a medial process (Fig. 14F). In *gila* (5) [au] the male plates are elongate (Fig. 11E), in *bandarita* (6) [au] shortened (Fig. 11D). Evolution of this cluster, of *pectinata*, and, perhaps also of *minima* and *zamora*, occurred on *Bouteloua curtipendula*. The three species of the *minima* cluster are defined [au] by (8) subrectangular plates (*pectinata*: Fig. 11C), (9) short plates (*minima*: Fig. 11A), and (10) outer teeth of hind margin of female sternum VII longer than median teeth (*zamora*: Fig. 14B). Divergence from this cluster (11) involved [s] development of avicephaliform style tips. In *collorum* (12), which appears to be a specialist of *Bouteloua uniflora*, a close relative of *B. curtipendula*, [au] the plates (Fig. 11G) are extremely short. In *jacala* the plates (Fig. 11H) remained long and broad (13); this is the only *Flexamia* species with both long, broad plates and avicephaliform style tips. In another species cluster a tendency toward development of aedeagal processes developed. In *mescalero* (15) [au] the aedeagus (Fig. 22) is slightly capitate rather than flared. This specialist of *Muhlenbergia pauciflora* retained relatively broad plates (Fig. 11I) and constricted pygofers (Fig. 62B) typical of the *pectinata* group; we therefore regard it as a monobasic subgroup of group I. A monophyletic cluster of three species is presumed to have arisen (16) from this lineage. Each of these species has [s] a pygofer with a conspicuously produced posterior lobe (Figs. 62H,I). In *abbreviata* (group II) the aedeagal apex [au] bears (Fig. 7H) two minute, paired processes (17). In this species and in *zacate* (18) the gonopore (Fig. 24) is elongate. *F. zacate* is the only species of the genus that lacks aedeagal processes but has an elongate gonopore. In *canyonensis* the gonopore [au] is located (19) approximately at the midpoint of the aedeagal shaft, presumably as a consolidation of the elongate gonopore type of *zacate*. The shape [au] of the aedeagal shaft in *canyonensis* (Fig. 6C) is also unique. The sister species *zacate* and *canyonensis* are both specialists of *Muhlenbergia porteri*. In a very important divergence (20), development of two pairs of aedeagal processes is hypothesized. In *grammica* (22), a *Calamovilfa* specialist, the plesiomorphic habitus of the *Spartopyge* dorsum and face were retained. Two of the four hypothesized aedeagal processes may have been lost. The pygofers and male plates also suggest relationships with *Spartopyge*, but in contrast to this outgroup, aedeagal processes are present. The relationship of *grammica* to other *Flexamia* species with aedeagal processes is unclear, given the [au] specific asymmetry of these processes (Fig. 7E) and the location of the gonopore, which has moved to a dorsal position. It is possibly significant [s?] that the style apices of the *grammica* and *curvata* groups are foot-shaped (21). In the *curvata* set (23) of sister species (*Buchloë* specialists) [s] two pairs of processes are present. In *curvata* (25) [au] the gonopore is elongate. In the *picta* lineage (*Aristida* specialists) two pairs of processes are present but [s] the apical pair has been modified into flangelike, toothed structures (26). Several autapomorphies [au] characterize (28) *pyrops* (see text). From this subtree the remaining species of *Flexamia* were derived; this derivation was featured (29) by an apomorphic fusion of the anteapical pair of processes into a single, unpaired process located on the ventral surface of the aedeagus in the sagittal plane.

events involving phytophagous insects could be explained by host transfer; the genus *Flexamia* was one of the genera that he chose for the study of host choice and speciation in the Cicadellidae. Ironically, Ross happened to work largely in central, northern, and southeastern grasslands. In these regions the study of cicadellid host relationships is more difficult than in the Southwest, and, as it turned out, almost all of the undescribed species in the genus occurred outside the geographic regions in which he conducted his extensive fieldwork.

Today, in retrospect, we report that the choice of *Flexamia* was a wise one; however, fewer speciations appear to be due to host transfer than Ross might have predicted. Sister species have in many cases proved to be specialists of the same host or closely related hosts. Indeed, entire groups of species have proved to have similar (often congeneric) patterns of host selection.

The progression of evolutionary divergence in *Flexamia* can best be described in terms of the phylogeny we propose. In Figures 64–67 we illustrate the postulated biogeographic and host transfer events.

We believe that the most closely related outgroup is *Spartopyge*. We have no information on the host relationships of *mexicana*, but *miranda* occurs on *Bouteloua curtipendula* in Arizona. The general facies of *Spartopyge* appears to be homologous with that of some *Flexamia* groups (*albida*, *grammica*, and *ritana* groups). We propose that diversification of the *Spartopyge* lineage in Mexican grasslands led to *Alapus* and to *Flexamia*.

We propose that the initial divergence (Fig. 65) of the *Flexamia* lineage resulted from specialization of a generalist ancestor on side-oats grama, *Bouteloua curtipendula*. This lineage, influenced by host patchiness and/or regional climatic differences, diverged by dispersal or vicariance into at least six species. These are
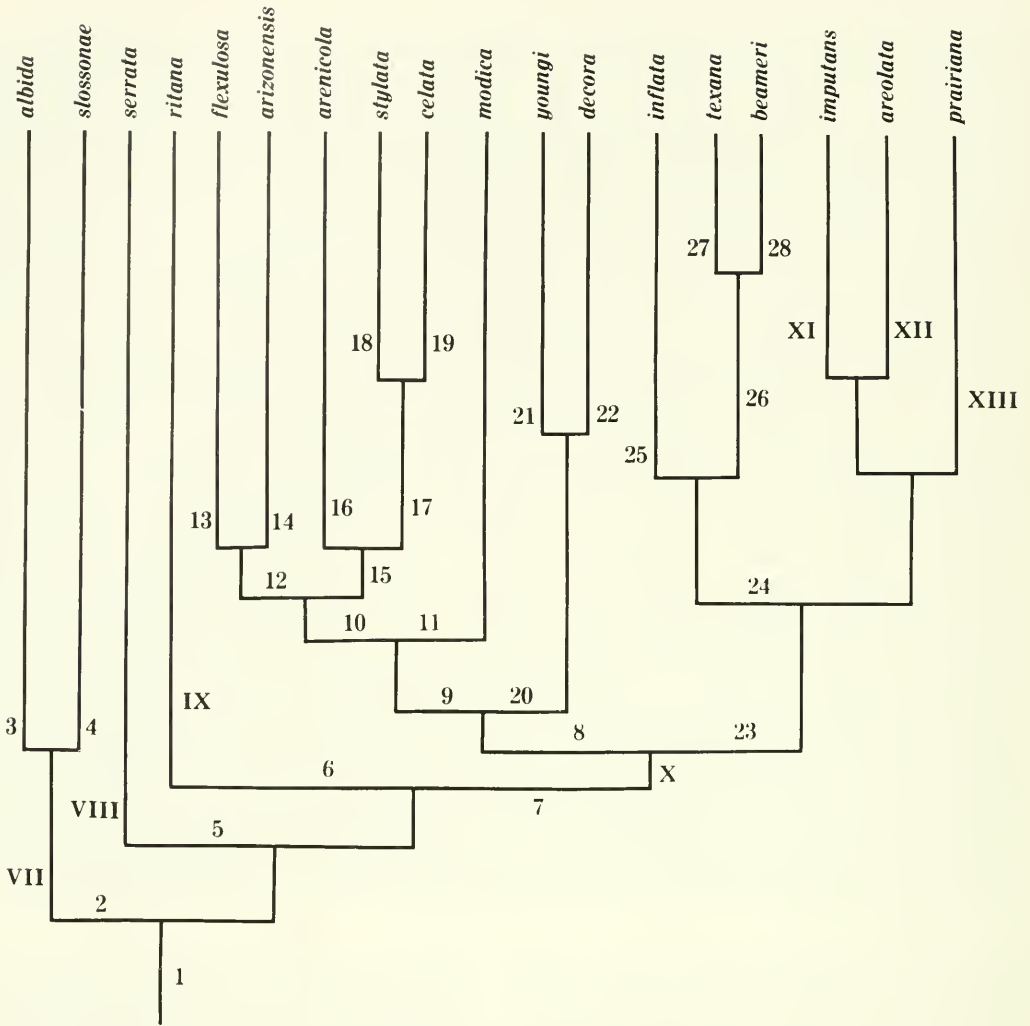
Fig. 59. Phylogeny of species of groups VII-XI. The following events, including synapomorphies [s] and autapomorphies [au] are hypothesized. Plesiomorphically, this cluster retained (1) certain features of the *Spartopyge* habitus (i.e., dorsal stripes and a pale face with black interocular band). However, prior to divergence, two pairs of aedeagal processes had developed, and, subsequently, the anteapical pair had fused to form a single, unpaired ventral process (Figs. 7A–C, 31). The lineage diverged into the (2) *albida* (VII), (5) *serrata* (VIII), and (6) *ritana* (IX) groups. The relationships of these groups is discussed in the legend to Figure 56. A large clade that then diverged (8) was associated mainly with *Muhlenbergia*. In all species of this subgroup the plesiomorphic character of a pale face with black interocular band was retained, but the dorsal stripes were lost. The subgroup is defined [s] by the triangulate male plates (Figs. 33A–F, 34D,E), which are strongly divergent apically (but see *serrata* [Fig. 8C]; the plates of this species suggest a link to the *decora* subgroup). In the *youngi* sister species set (host: *Muhlenbergia richardsonis*), the unpaired ventral process (Figs. 31F,G) retained its plesiomorphic position and length (20), but in the remaining species [s] the process was shortened (9). In *modica* the aedeagus is subsymmetrical (11) with [au] the short, unpaired process (Fig. 31M) slightly displaced from the sagittal plane and associated with the shaft basally; the pygofer is relatively undifferentiated. In the lineage that diverged subsequently, the pygofer (Fig. 62) became substantially modified (10). We hypothesize that it first became ovate, a condition that still persists [au] in *arenicola* (16). In *stylata* and *celata* [s] it developed [s] a distinctive posterior process (17: see text for further synapomorphies), and in *arizonensis* (au) it developed a conspicuous ventral process (14). The male plates of *flexulosa* and *arizonensis* (Figs. 33A,B) are in each case (13, 14) distinctive [au]. In the *inflata* subgroup of group X (24), the beginning of phyletic torsion of the aedeagus is evident (Fig. 61B). In this subgroup the face is modified; traces of the interocular band are present in some individuals, but, when present, it is brown and contrasts much less sharply with the remainder of the face. The plates are short, and [s] the dorsal margin of the pygofer is essentially flat, giving the pygofers a boatlike outline in lateral aspect (Figs. 62GG,HH,II). Two apparent (but see text) sisters, *texana* and *beameri*, are identified by [au] unique aedeagal configurations (Figs. 31A,D). From the moderately displaced aedeagus of the *inflata* group, further torsion (29) led to groups XI-XIII.
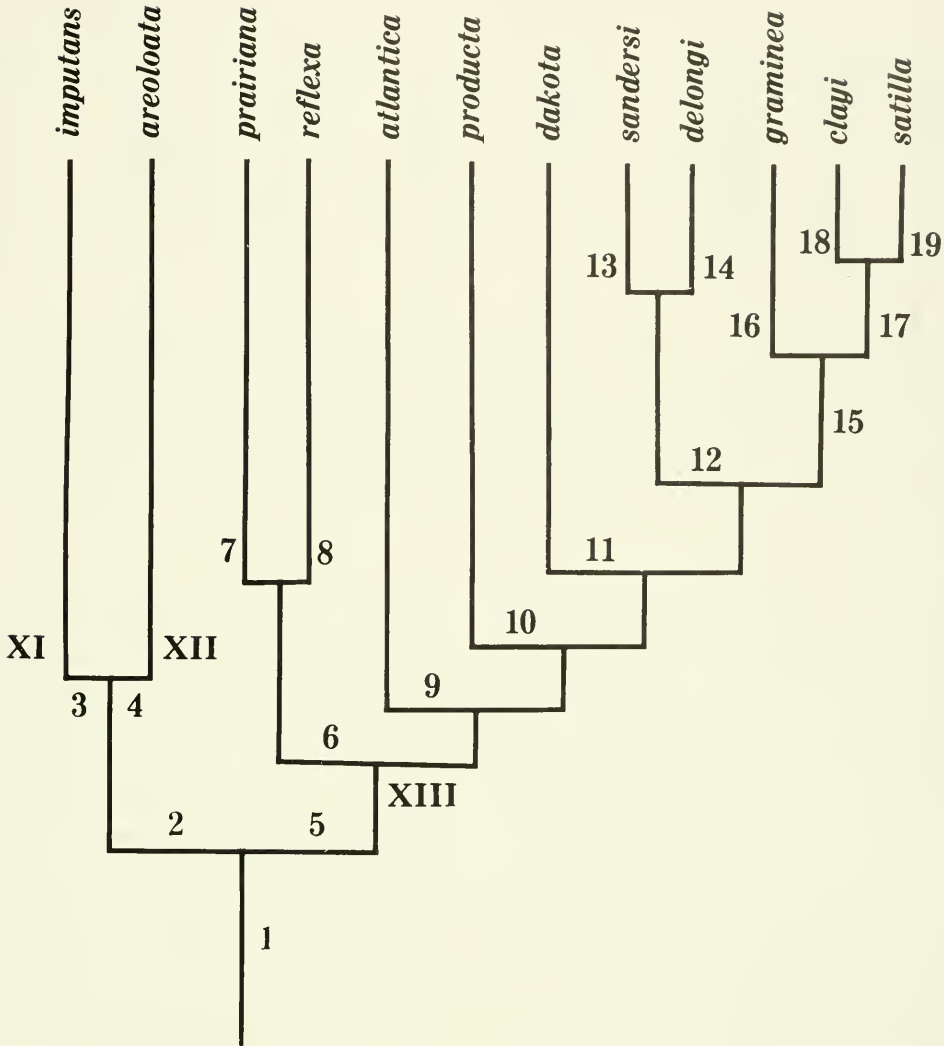
Fig. 60. Phylogeny of species of groups XI-XIII. Synapomorphies [s] and autapomorphies [au] are identified. In the plesiomorphic state (1) there may have been moderate aedeagal asymmetry, as in *inflata* (Fig. 61B). In the *imputans-areolata* lineage (2) [s] the unpaired processes are lateral, bearing a slitlike gonopore (Figs. 31B,C). In *imputans* (3) the ancestral articulation between aedeagus and connective was retained. This unique species is defined by a suite of apomorphies, including its black face, greenish dorsal pigmentation, and lack of dorsal markings, but lacks an autapomorphy. In *areolata* (Fig. 61C) [au] the aedeagus and connective have fused, and a conspicuous, black spot (Fig. 2F) is present in the corium (4). Because the *imputans* and *areolata* lineage is defined by several synapomorphies (see text), we have designated them as sister species, despite the important difference in the state of articulation between the aedeagus and connective. We hypothesize a second, independent fusion of aedeagus and connective that serves as a synapomorphy [s] defining group XIII (4). In the *prairiana-reflexa* lineage [s] the gonopore has become dorsal (Figs. 61D,E), as has the unpaired process (6). In *prairiana* (7) the traces of this fusion [au] are present as a transverse line (Fig. 6F) on the surface of the aedeagal shaft. The aedeagal configuration [au] is also unique (Fig. 61D). In *reflexa* (8) the gonopore [au] has become associated with the unpaired process (Fig. 61E). In *atlantica* one process has been lost, and [au] the aedeagus (Fig. 44A) has become highly asymmetrical (9). In *producta* [au] the gonopore has moved (10) to a lateral position (Fig. 61G), whereas in *dakota* (11) the gonopore remained dorsal (Fig. 44I), but the unpaired process has been lost. The symmetry of the *dakota* aedeagus is therefore apomorphic. In the *sandersi-delongi* lineage (12) the unpaired process has been retained but is present [s] as a lateral process that is closely appressed to the aedeagal shaft (Fig. 61F). In all three species of the final lineage (15), the unpaired process has essentially disappeared; instead, [s] the gonopore has become spiral, with [au] a narrow, basal portion (Fig. 44F) as in *graminea* (16), or [s] with a wider base (17) as in *clayi* and *satilla* (Figs. 44H,J). For discussion of the minor morphological divergences that define the sister species of the *sandersi-delongi* and *clayi-satilla* sets, see text.

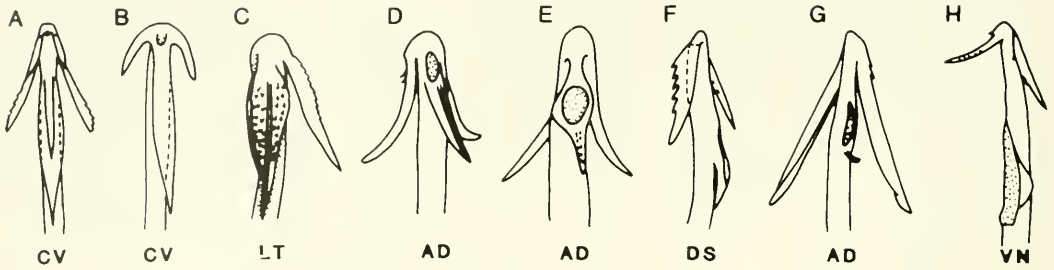Fig. 61. Postulated character transformation: phyletic twisting and modification of the *Flexamia* aedeagus. In *decora* (A) a plesiomorphic state exists in which the unpaired process is ventral and in the sagittal plane; the aedeagus is therefore symmetrical. In *inflata* (B) there is a small displacement of the unpaired process. In *areolata* (C) the unpaired process is lateral and bears the gonopore. In *prairiana* (D) the process is dorsal, as is the gonopore. In *reflexa* (E) the gonopore has become associated with the dorsal unpaired process. In *sandersi* (F) the unpaired process is reduced and appressed to the shaft. In *producta* (G) the process is reduced or absent and the gonopore is lateral. In *graminea* (H) the process has disappeared entirely, the apical processes are reduced, and the gonopore is spiral. Aspects: AD, anterodorsal; CV; caudoventral; DS, dorsal; LT, lateral; VN, ventral. Aedeagal structures redrawn from Young and Beirne (1958).

adapted to northeastern (*minima*) and west central (*zamora*) Mexican grasslands, to Chihuahuan (*bandarita*) and Sonoran (*doeringae*) montane grasslands of the Southwest, to the interdesert montane region of the Gila Mountains (*gila*), and to the tall-grass and mixed-grass prairie of the United States (*pectinata*). Also derived from the side-oats lineage were *jacala* (Mexico: host unknown) and *collorum* (Edwards plateau; host: *Bouteloua uniflora*), a close relative of side-oats grama). Clearly, most or all of the nodes in the *pectinata* lineage are Mexican or southwestern; none represent events that assuredly took place north of the Mexican–U.S. border.

A second lineage of the *pectinata* subtree resulted in the divergence of *mescalero,* a distinctive species that represents a host transfer to New Mexican muhly, *Muhlenbergia pauciflora*. Another branch of this lineage transferred to temperate *Bouteloua* grasslands of Mexico. One of the branches (*abbreviata* group) inhabited the mixed *Bouteloua* grasslands of Mexico and, by gradual adaptation, to similar grasslands of the United States. Another branch adapted to semiarid grasslands by colonizing bush muhlenbergia (*Muhlenbergia porteri*); divergence of this lineage led to the contemporary *canyonensis* (Sonoran) and *zacate* (Chihuahuan).

Consider next the *surcula-curvata* lineage. Both species possess the four aedeagal processes that Young and Beirne proposed as plesiomorphic; both species are *Buchloë* special-

ists. We propose that an ancient Mexican ancestral line adapted to *B. dactyloides,* which led to the present-day *surcula* and, later, to *curvata*. This divergence (Fig. 64) may have been mediated by climate. The grasslands of northeastern Mexico, where *surcula* may have arisen, have escaped major disturbance since the Cretaceous (Rosen 1978). This region has an extremely warm, temperate or subtropical climate and a Chihuahuan precipitation pattern, both of which differ immensely from the dry, temperate grasslands where *curvata* occurs today.

Another branch of the *curvata* subtree diverged, perhaps in Mexico or south Texas, leading to the *picta-pyrops* sister set. These species are *Aristida* specialists.

One of the major events in *Flexamia* phylogeny was marked by the fusion of the anteapical pair of aedeagal processes into a single, mesal process. The most primitive species in which this feature is retained are members of the *albida*, *serrata*, and *ritana* groups. Young and Beirne argued (and Ross concurred) that *slossonae*, *albida*, and *serrata* were related. We agree but consider their divergence to be an ancient one, given their entirely different climatic requirements (subtropical, prairie, and northern grasslands, respectively), and their retention of the *Spartopyge* habitus type. Perhaps the divergence of the *albida* lineage into four species, each with unique climatic adaptations, may have occupied a distinct stage in *Flexamia* evolution.
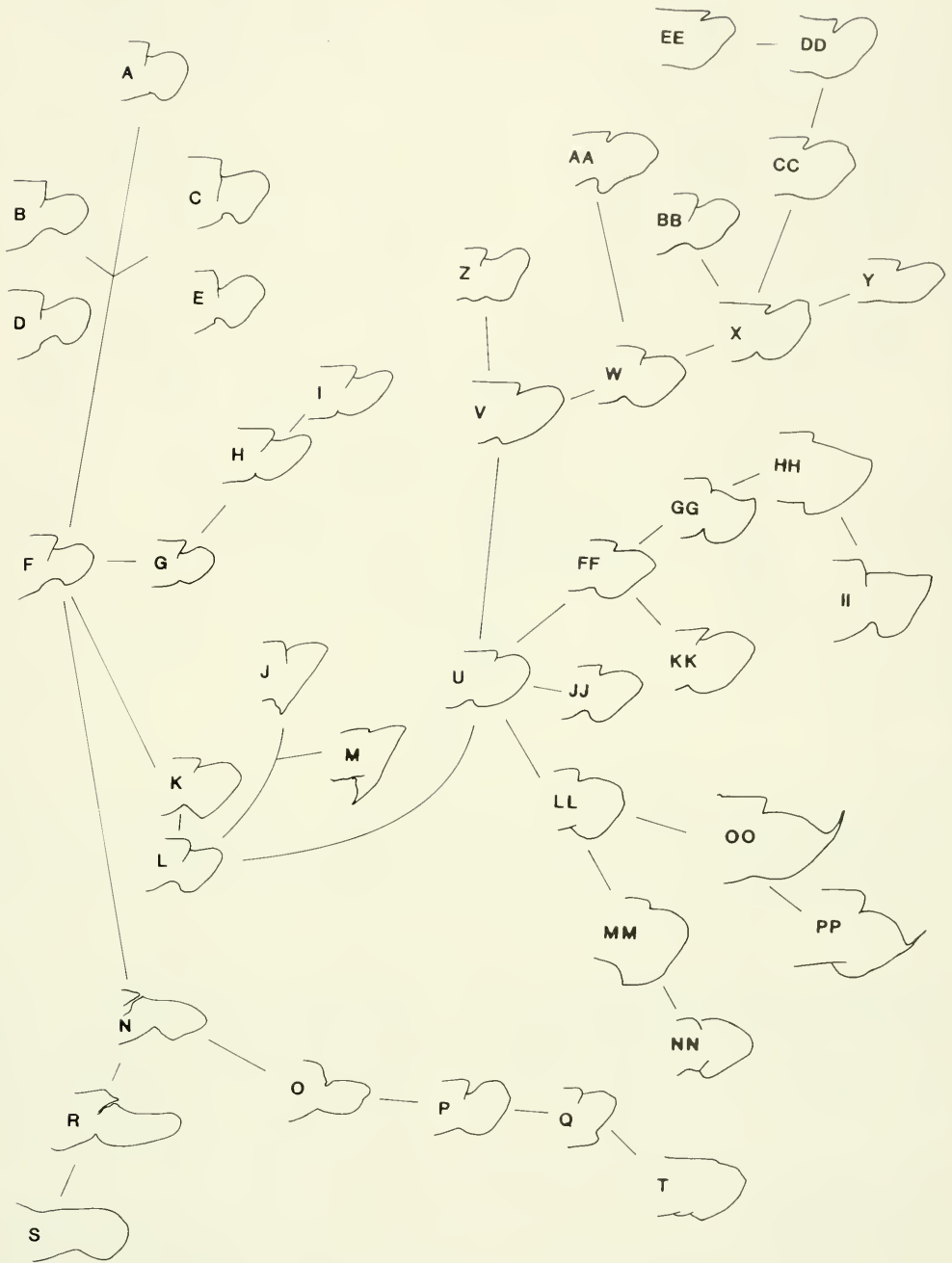
Fig. 62. Character transformation of the *Flexamia* pygofer. Diagrammed lineage was based in part on phylogeny of groups (see Figure 56). A, *collorum*; B, *mescalero*; C, *bandarita*; D, *jacala*; E, *gila*; F, *pectinata*; G, *doeringae*; H, *abbreviata*; I, *canyonensis*; J, *pyrops*; K, *curvata*; L, *surcula*; M, *picta*; N, *Spartopyge miranda*; O, *grammica*; P, *serrata*; Q, *albida*; R, *Alapus elongatus*; S, *Spartopyge mexicana*; T, *slossonae*; U, *ritana*; V, *imputans*; W, *prairiana*; X, *reflexa*; Y, *atlantica*; Z, *areolata*; AA, *producta*; BB, *dakota*; CC, *sandersi*; DD, *clayi*; EE, *graminea*; FF, *decora*; GG, *inflata*; HH, *texana*; II, *beameri*; JJ, *modica*; KK, *youngi*; LL, *arenicola*; MM, *arizonensis*; NN, *flexulosa*; OO, *stylata*; PP, *celata*. Some pygofers were redrawn from Young and Beirne (1958) and Lowry and Blocker (1987).
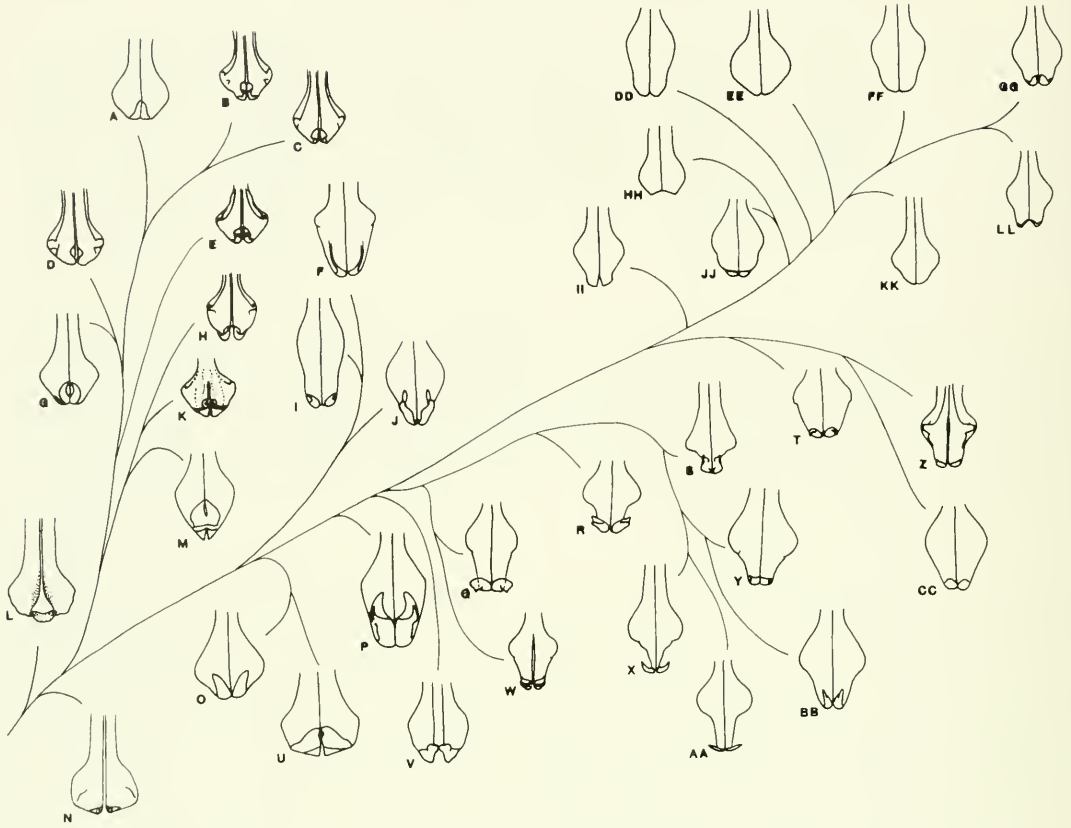
Fig. 63. Bases of first valvulae of *Flexamia* species. The depicted tree represents phylogeny presented in Figures 56–60. A, *doeringae*; B, *gila*; C, *bandarita*; D, *collorum*; E, *mescalero*; F, *curvata*; G, *pectinata*; H, *canyonensis*; I, *surcula*; J, *picta*; K, *zacate*; L, *Alapus elongatus*; M, *abbreviata*; N, *Spartopyge mexicana*; O, *albida*; P, *serrata*; Q, *decora*; R, *modica*; S, *arenicola*; T, *inflata*; U, *slossonae*; V, *ritana*; W, *youngi*; X, *celata*; Y, *arizonensis*; Z, *beameri*; AA, *stylata*; BB, *flexulosa*; CC, *texana* ; DD, *atlantica*; EE, *producta*; FF, *sandersi*; GG, *clayi*; HH, *reflexa*; II, *imputans*; JJ, *prairiana*; KK, *dakota*; LL, *graminea* .

Interestingly, there are present-day clues to the feeding strategies of this primitive complex. We suspect that *slossonae* and *albida* are habitat specialists, whereas *serrata* specializes on *Muhlenbergia richardsonis*. Ancestral *Flexamia* species in Mexican grasslands may have been general grass feeders; this strategy has been partially retained by some lineages, including those that retained the plesiomorphic striped habitus.

Perhaps the striped habitus is optimal for habitat specialists. Loss of the habitus occurred homoplastically several times; in at least one case (*serrata*), it accompanied host specialization in northern, temperate grasslands (on *Muhlenbergia richardsonis*). This event could actually have taken place far south of the current range of *serrata* during a glacial

maximum in the early Pleistocene. *Muhlenbergia richardsonis* not only occurs as far north as Wood Buffalo National Park in Canada, but also occurs in Mexico, presumably as a relict. Throughout much of the northern part of its range, this warm-season grass is an "island" surrounded by a sea of cool-season grasses. Such a condition is ideal for evolution of a specialist lineage from a more general ancestor; taxonomic distinctiveness has been recognized as an important force in determining insect species richness on plant hosts (Lawton and Schroder 1977). In any event, morphological evidence indicates that a subtree of *Flexamia* evolved on *Muhlenbergia*. The first event (Fig. 66) appears to have been the divergence of the *serrata* and *decora* lineages. The *decora* subgroup is
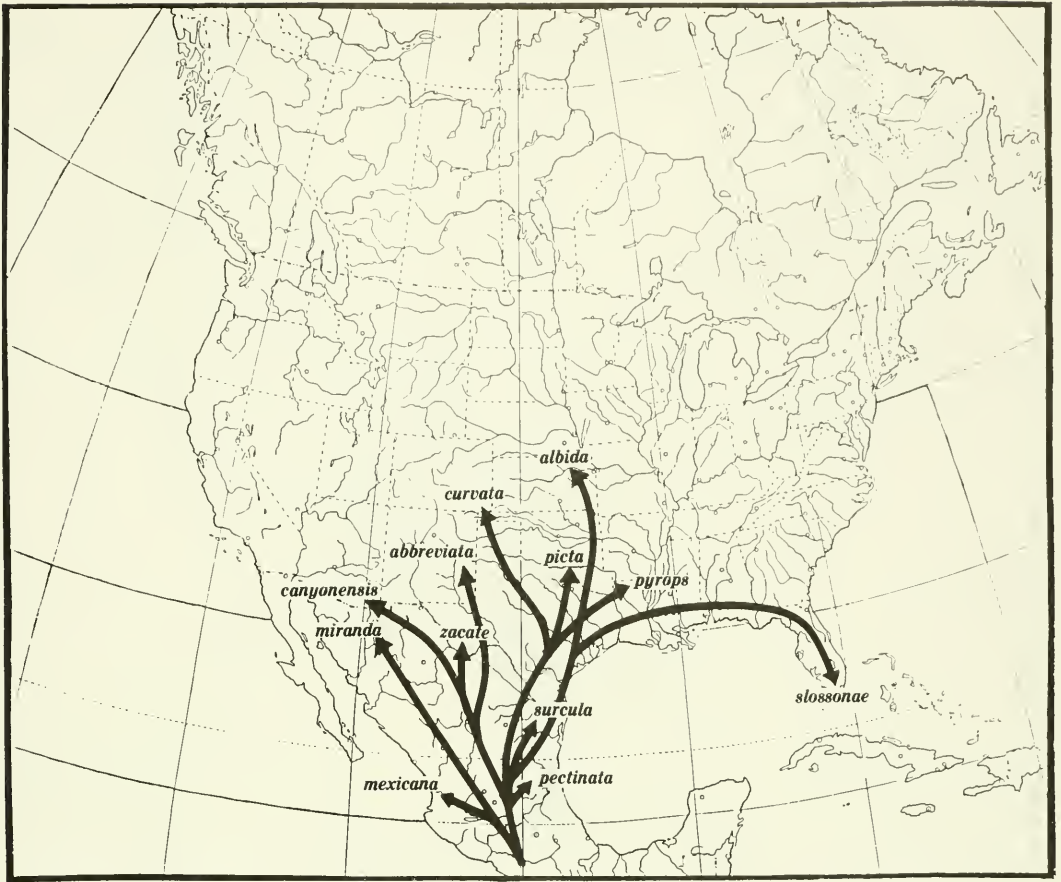
Fig. 64. Geographic interpretation of *Flexamia* phylogeny. Early evolution is postulated to be Mexican. The *Spartopyge* lineage diverged into *mexicana* and *miranda*. From this lineage *Flexamia* diverged. The first major node involved the divergence of the *pectinata* group, perhaps as a result of specialization on *Bouteloua curtipendula*. This divergence is hypothesized to have occurred in the grasslands of northeastern Mexico, a region thought to have remained stable over recent geologic history (Rosen 1978). Subsequent divergences, which occurred in the same general region of Mexico, were those of the *abbreviata-zacate* and *curvata-picta* lineages. The *abbreviata* lineage adapted to *Bouteloua* spp., the *curvata* group to *Buchloë dactyloides*, and the *picta* group to *Aristida* spp. The divergence of the *albida* lineage, characterized by a single, plesiomorphically ventral aedeagal process, may have occurred somewhat north of the Sierra Madre Orientale region, perhaps in Texan grasslands. Many contemporary species emerged from this lineage. The most plesiomorphic of these (members of the *albida* group) are relatively uncommon today; *albida* and *slossonae* do not appear to be strict host specialists, a feeding habit that we hypothesize to be plesiomorphic for the genus. Actual divergences in temperate zones may have occurred farther south than diagrammed, if they occurred during periods of glacial advance.

presumed to have divided by vicariance during glacial episodes into a Rocky Mountain-Canadian (*decora*) lineage, and a Great Basin lineage (*youngi*), both specialists on *M. richardsonis*. Alternatively, a second lineage developed, leading to a New Mexican montane lineage (*modica*) that transferred from *Muhlenbergia richardsonis* to *Muhlenbergia repens*. Further divergence led to *arenicola* (host: *Muhlenbergia pungens*) and to a set of sister species (*celata-stylata*) that specialized on *Muhlenbergia* or *Redfieldia* (and possibly other grasses of sandy grasslands), respectively. Finally, this line appears to have transferred from *Muhlenbergia* to the vast resource of *Bouteloua gracilis* in the plains region of New Mexico. This resource has been shared with *abbreviata*, which arrived in the New Mexican plains by an entirely different geographic route (i.e., Mexican mixed *Bouteloua*
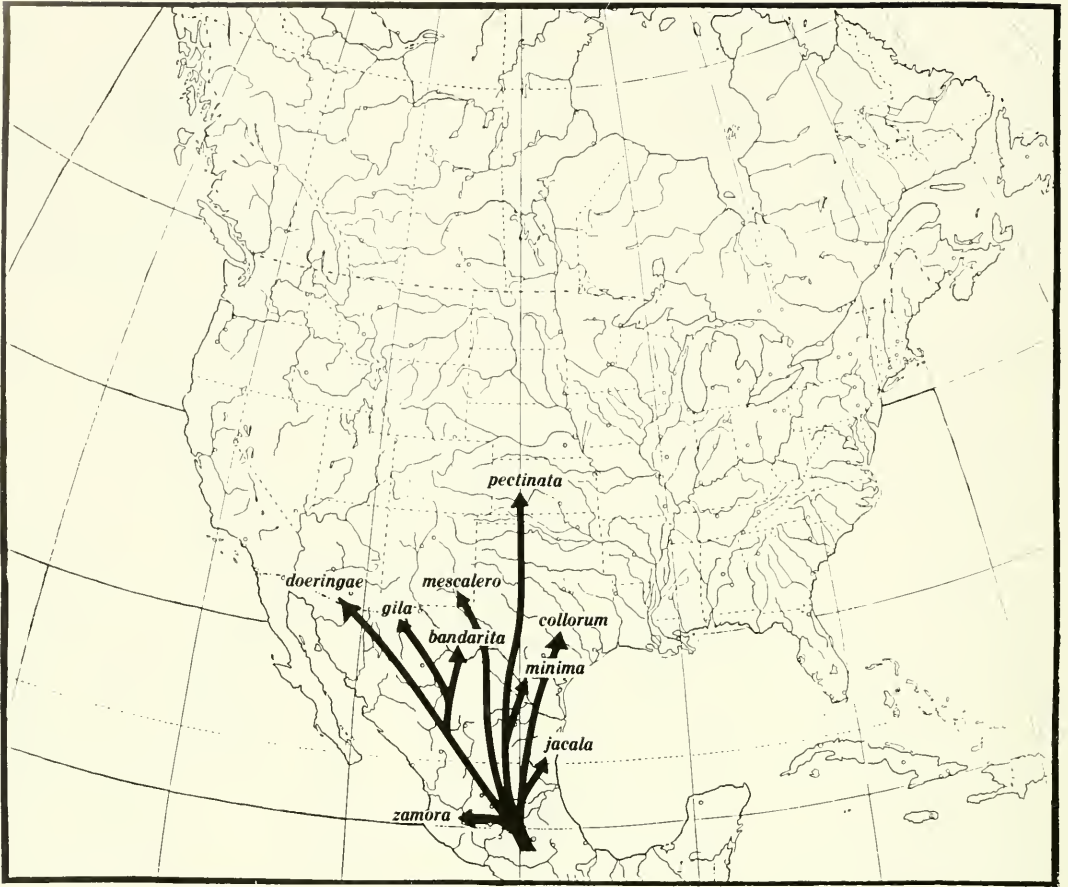
Fig. 65. Geographic interpretation of phylogeny of the *pectinata* group. A focal origin in grasslands of eastern Mexico is hypothesized. A western lineage comprised *gila*, *bandarita*, and *doeringae*. This lineage speciated exclusively on *Bouteloua curtipendula*. Morphological data suggest that *mescalero*, which apparently transferred to *Muhlenbergia pauciflora*, belongs on a deep branch. The subtree consisting of *zamora*, *minima*, and *pectinata* is closely related to the *doeringae* subtree; like all members of that subtree, *pectinata* specializes on *B. curtipendula* (side-oats grama). *F. collorum* may have been derived from a lineage on *B. curtipendula*, since its host is *B. uniflora*, which is closely related to side-oats grama. The host of *jacala* is unknown.

grasslands). (Interestingly, in contrast to *Athysanella* species [Hicks et al. 1988], both *Flexamia* blue grama specialists colonize this host throughout most of its range in New Mexico). A sister species, *arizonensis*, transferred to another dominant southwestern grass, *Aristida purpurea*. We emphasize that considerable climatic diversity exists today in the Southwest and no doubt has existed throughout the Pleistocene and Holocene as the result of elevational gradients (Axelrod and Raven 1985, Cole 1986, Cronquist 1978, Thompson and Mead 1982, VanDevender and Spaulding 1979). Therefore, evolutionary processes that might take place only over wide geographic

distances in regions of relatively constant elevation may be focused in small geographic areas in the Southwest.

Another lineage, possibly more closely allied to the *ritana* than *serrata* lineage, presumably diverged in grasslands of the southern plains. This is the *inflata* subgroup of the *flexulosa* group. One contemporary representative (*inflata*) exhibits one of the widest host ranges in the genus; largest populations occur on *Muhlenbergia asperifolia* in wetland areas. If this apparent preference indicates an ancestral *Muhlenbergia* host, it would be necessary to postulate a monumental subsequent widening of host range to pooid grasses or
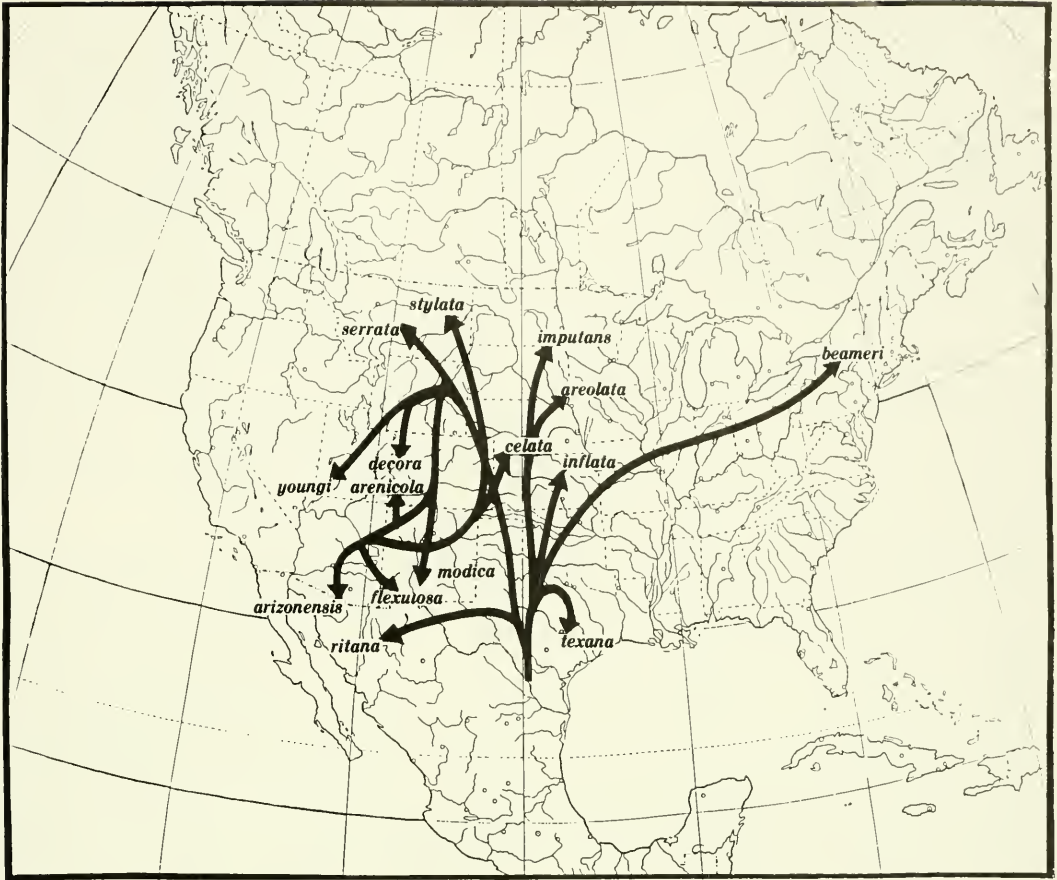
Fig. 66. Geographic interpretation of phylogeny of the *serrata*, *ritana*, *flexulosa*, *imputans*, and *areolata* groups. Texan grasslands may have been a focal area for initial divergence of lineages. *F. serrata* appears to be a *Muhlenbergia* specialist. The *ritana* group appears to have diverged in the Southwest. The contemporary distributions of the *albida*, *serrata*, and *ritana* groups suggest that they may have speciated by vicariant mechanisms or, in the case of *serrata*, by a combination of vicariance and host transfer. An eastern lineage consists of *inflata* and *beameri*. From a biogeographic perspective, it is most reasonable to propose an independent origin of *texana* and *beameri*, each from *inflata* or a closely related lineage. The present-day distribution of *inflata* suggests that it diverged in cool, temperate grasslands; Texas, of course, was cool during glacial maxima. In general, events postulated as northern in these reconstructions could have taken place much farther south during glaciations. The *imputans-areolata* lineage appears to have diverged in the prairie, on *Muhlenbergia cuspidata* and *Eragrostis spectabilis*, respectively. The western lineage of the *flexulosa* group may be related (see Fig. 59) to the *serrata* group; if this association can be confirmed, the derivation of the *decora* set of sister species from the *serrata* lineage would make an attractive hypothesis from a biogeographic standpoint, since all of the species (including *youngi*) specialize on *Muhlenbergia richardsonis*. Derivation of *modica* (host: *Muhlenbergia repens*) and *arenicola* (host: *Muhlenbergia pungens*) represents further evolution that occurred by host transfers within *Muhlenbergia*. The derivation of *flexulosa* and *arizonensis* by host transfer may have been a consequence of the regional abundance (in New Mexico and eastern Arizona) of their hosts, *Bouteloua gracilis* and *Aristida purpurea*, respectively; presumably, the region was colonized from the north. Finally, derivation of *celata* (host: *Redfieldia flexuosa* and perhaps other sandhill grasses) and *stylata* (hosts: *Muhlenbergia* spp.) is hypothesized to have followed a high-plains route around the eastern edge of the high Rocky Mountains.
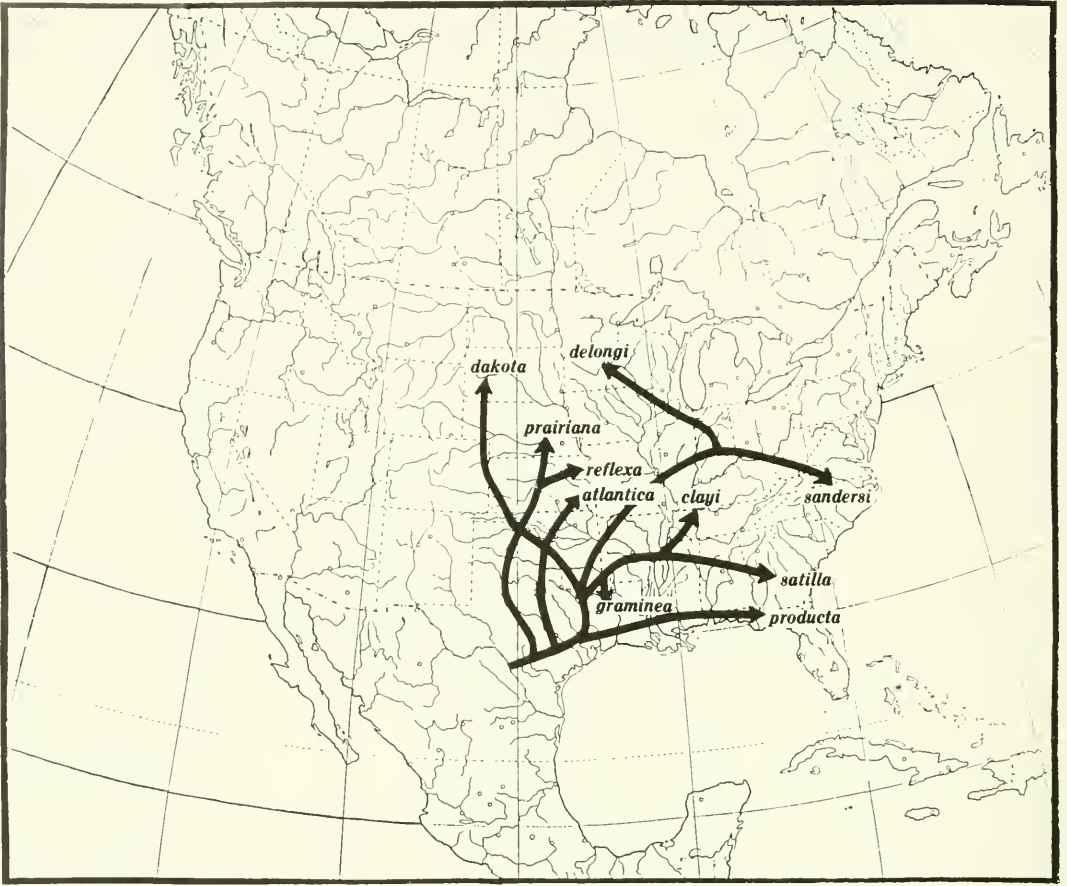
Fig. 67. Geographic interpretation of the phylogeny of the *prairiana* group. Although present-day distributions and host preferences do not offer obvious hypotheses for speciation mechanisms, an origin for the *prairiana* group in Texan grasslands is hypothesized. From this region *prairiana* presumably moved northward in postglacial episodes, where it adapted to little bluestem (*Schizachyrium scoparium*) or other andropogonoid grasses. In the tall-grass prairie, *reflexa* diverged from this lineage; this species often seems to be associated with big bluestem (*Andropogon gerardii*), particularly in glades of the eastern United States. *F. atlantica* may have transferred in postglacial times from chlorodoid grasses, on which it predominates in the Southwest, to switchgrass, *Panicum virgatum*. This host has been a conduit for colonization by *atlantica* of the eastern United States, including the Atlantic coastal prairies, where its host achieves high importance. Derivation of *sandersi* may have occurred by transfer to *Andropogon virginicus*, the first colonist in early fire succession in the Southeast. From this lineage, presumably post-Wisconsinan, *delongi* may have diverged by colonization of little bluestem in the glaciated area northwest of Illinois. Specialization on *Schizachyrium scoparium* and subsequent divergence led to *dakota* in the dry prairies of the plains, to *graminea* in Texas and northward through the tall-grass prairie, and to a lineage of eastern species. These species, also residents of andropogonoid grasses, are residents of the Gulf Coast (*satilla*), or the Appalachian mountains to Maine and cool, temperate savannas of Illinois and Ohio (*clayi*).

Juncus. It may be more likely that the currently observed host range breadth represents simply a retention of plesiomorphic generalism. In any event, this lineage has spawned two additional species: *texana* (south central Texas) and *beameri* (west slope of the Adirondack Mountains, New York). The circumstances surrounding these divergences are unclear, since we have no data on their host relationships.

After divergence of *inflata*, another lineage diverged in the prairie, leading to *imputans* (probable host: *Muhlenbergia cuspidata*) and *areolata* (host: *Eragrostis spectabilis*) on one hand, and to the *prairiana* group on the other.

All speciation events of the *prairiana* group (Fig. 67) occurred either in prairie, savanna, or southeastern grasslands. We hypothesize

an ancestor for this group that was adapted to both chloridoid and panicoid grasses. From such an ancestor, *prairiana* (host: *Schizachyrium* or *Bothriochloa*) and *reflexa* (host: *Andropogon gerardii*) were derived, as were *atlantica* (hosts: chloridoid grasses and/or *Panicum virgatum*), and *producta* (hosts· chloridoid grasses, or [possibly] a habitat specialist). Finally, specialization on *Schizachyrium scoparium* and/or *Andropogon virginicus* led (Fig. 67) to lineages that adapted to the most xeric of *Andropogon* habitats (*dakota*, a *Schizachyrium* specialist of the western Great Plains), *graminea* (a *Schizachyrium* specialist of the tall-grass prairie), and the *sandersi-delongi* and *satilla-clayi* sister pairs of eastern andropogonoid grasslands.

Stages of Speciation

Mayr (1942) believed that at any given time all stages of evolution should be observable. We believe that this is indeed the case in the genus *Flexamia*. We recognize at least 10 levels in the process of speciation in *Flexamia*:

1. Nonisolated ephemeral populations: (i) Many populations of *Flexamia inflata* appear to be ephemeral. These populations often occur on pooid grasses such as *Poa* or *Festuca*; presence of immature insects confirms oviposition; (ii) *F. abbreviata* colonizes *Muhlenbergia richardsonis* in the Sacramento Mountains of New Mexico and *M. reverchonii* in the Edwards Plateau of Texas, although in the latter case we have not confirmed oviposition.

2. Nonisolated stable populations: (i) *F. inflata* consistently colonizes path rush (*Juncus tenuis*) in Illinois and Maryland; populations, including immatures, are found regularly on that host. This is an especially interesting case, since it may represent an interfamily transfer by a species that has limited oligophagy. (ii) *Flexamia atlantica* regularly colonizes large plantings of weeping love grass (*Eragrostis spectabilis*) and bermudagrass (*Cynodon dactylon*) in Oklahoma and Texas. (iii) Similarly, *producta* colonizes bermudagrass and *Zoysia japonica* in Maryland. These are essentially "natural experiments" that may mimic to a large degree, but in a shorter geologic time period, the effect of radical changes in the dominance hierarchy of grasses induced by cyclic climatic change.

3. Disjunct populations that have not diverged morphologically: In the following

cases we have found no morphological variation associated with disjunct populations. (i) A disjunct population of *dakota*, a specialist on *Schizachyrium scoparium* in the western Great Plains, occurs on that host in the Loess Hills of western Iowa. (ii) *Flexamia reflexa* occurs (always, it seems, in association with big bluestem, *Andropogon gerardii*) in isolated grassland islands in the eastern deciduous forest as far east as the Soldier's Delight serpentine barrens in Baltimore County, Maryland.

4. Isolated stable populations with minor morphological divergence: In each of the following cases the populations may or may not represent biological species. (i) Two disjunct populations (Nebraska Sand Hills and Four Corners or Anasazi populations) of *arenicola* have been discovered; the unpaired, aedeagal processes of the Anasazi population always break, whereas the processes of the Sand Hills population rarely break. Other characters have not been found to separate these populations, each of which specializes on *Muhlenbergia pungens*. The host population is also separated into disjunct populations. (ii) The Mammoth Lakes population of *youngi*, probably isolated in eastern California in a region rich in endemics, has diverged somewhat from the population in the eastern Great Basin. (iii) Populations of *prairiana* on *Bothriochloa* in the Southwest have begun to diverge from the prairie *Schizachyrium* populations, perhaps as the result of phenological isolation. In this case divergence of female rather than male structures may signal the emergence of a new species.

5. Recent (Holocene) speciations: (i) The separation of *delongi* from the *sandersi* lineage may represent a postglacial transfer from *Andropogon virginicus* to *Schizachyrium scoparium* in the glaciated region of the northern prairie. (ii) The divergence of *clayi* and *satilla* may reflect phenological isolation between Gulf Coast and Appalachian populations.

6. Pleistocene speciations: Biological and biogeographic circumstances strongly suggest that *decora* and *youngi* represent vicariant populations of a common lineage that diverged during Pleistocene climatic cycles, retaining *Muhlenbergia richardsonis*.

7. Vicariance and semiisolation: In the case of Mexican and Southwestern grasslands, speciation was perhaps achieved by vicariance

during long periods of semiisolation. It is possible, in the case of certain species, that there may have been a punctuated infusion of genes into semiisolated populations as the climate became more mesic (Milstead 1960) and the distance between host stands of side-oats grama decreased. In any event the emergence of *gila, doeringae, bandarita, zamora, minima*, and *pectinata*, closely related species that appear to partion the range of side-oats grama, must have entailed different speciation mechanisms than those described above and are clearly enforced today by phenological isolation.

8. *Distinct species with obvious sisters:* We consider the sister pairs of *picta-pyrops, curvata-surcula, canyonensis-zacate*, and *prairiana-reflexa* to be obvious sisters that occur in ambiguous circumstances that suggest no particular age for their divergence. In some cases (*surcula-curvata* [tropical/temperate] and *zacate-canyonensis* [Chihuahuan/Sonoran]) the biogeographic circumstances for the divergences are clear.

9. *Species with distant sisters:* We consider the *albida-slossonae* sister pair to represent a historically remote divergence. *Flexamia slossonae* is a subtropical species that has many autapomorphies separating it from other *Flexamia* species. However, common characters of habitus and male genitalia leave no doubt that it is a sister to the tall-grass prairie species *albida*.

10. *Orphans:* The characteristics of *grammica* are sufficiently unique that it must be considered an orphan within the genus. In the absence of a contemporary link, the relationships to other extant species of the genus are obscure.

From the above examples we feel that our experience with *Flexamia* elegantly confirms Mayr's hypothesis.

CONCLUSIONS

The initial choice of *Flexamia* as a model for the study of the role of host plants in insect evolution was a fortuitous one. Whereas some speciation events in *Flexamia* must have occurred by host transfer, others surely occurred by vicariance. Further, there is a tendency of individuals representing advanced lineages to be reduced in size and complexity, and to be more highly specialized in their host

choice than their ancestors. There is therefore an immense stake in arriving at a well-substantiated phylogenetic hypothesis for the genus that is supported by independent lines of evidence. In particular, if advances in the study of molecular evolution prove to be adaptable to the study of small insects, we believe that *Flexamia* would provide an excellent model for study. Because the knowledge of *Flexamia* hosts is now adequate, obtaining live material of most species for such a study would be an achievable task. The rewards of further detailed studies would be many but would include, especially, important insights into the evolution of life-history strategies of sap-sucking insects.

When we began our studies of *Flexamia*, whose species number had remained relatively constant for a number of years, we did not dream that there were many remaining species awaiting discovery. It is difficult for us to guess, given the results reported here, how far we have fallen short, even now, of a complete inventory. Our discovery of the role of climate in inducing and reinforcing cicadellid speciation makes it clear that the biogeographically rich areas of the Southwest may well have many interesting stories that still await us.

In particular there may well be Mexican species awaiting discovery. For example, our phylogenetic hypothesis suggests that there may have been at one time a species with the plesiomorphic dorsal stripes of *Spartopyge, grammica*, and *albida*, but which possessed a full complement of four aedeagal processes. Because of the compelling logic of all phylogenetic schemes for its existence, such a species seems so real to us that we have jokingly referred to it as "ancestris." Is it possible that this species, or a closely related descendant of it, may actually exist in an unexplored Mexican grassland? It is questions such as these that have driven us to return repeatedly to the grasslands of the Southwest, which prove to be every bit as full of enigmas as they are of answers.

spades. The early biological work of E. D. Ball, H. Osborn, D. M. DeLong, and R. H. Beamer is implicit in our work. H. H. Ross introduced us to the genus, framed many of the questions that we discuss, and left much unpublished material from his grasslands (GL) project. D. A. Young, whose 1958 monograph with B. P. Beirne continues to be an important tool for students of *Flexamia*, kindly permitted us to redraw many structures from drawings in his monograph. We are particularly pleased to acknowledge the advice and encouragement of P. W. Oman, given especially to the senior author during his early years at Beltsville. Further, a large fraction of USNM *Flexamia* had been collected and correctly determined by Oman; this material was extremely valuable in our study. Earlier studies on *Flexamia* at Beltsville were assisted by M. E. Coan, J. P. Kramer, and, in later years, J. E. Lowry, whose illustration of *serrata* is presented here as Figure 1. All other drawings were done by Debi Roney. Robert Almond and Edward Clark gave advice and assistance on the graphics. Host records were retrieved from a computerized index developed by D. E. Lynn. T. Mogel assisted with the scanning electron microscopy. Assistance with phylogenetic programs was provided by Mary Mickevich. We acknowledge further the assistance of G. W. Byers, P. S. Cwikla and C. P. Triplehorn, M. W. Nielson, and T. J. Henry and R. C. Froeschner, who made available the *Flexamia* collections of Kansas University, Ohio State University, Monte Bean Life Science Museum (Brigham Young University), and the United States National Museum, respectively. K. G. A. Hamilton made available the *Flexamia* material from the Canadian National Collection and provided a wealth of stimulating comments on the manuscript. M. Schauff made many useful comments on the manuscript. So many friends have helped in our field studies that all cannot be acknowledged. We are especially indebted, however, to Kelly Allred of New Mexico State University for continuing lessons on New Mexico agrostology. Charles T. Mason, Jr., assisted with grasses of Arizona. R. Chambers of the U.S. Soil Conservation Service drove us to the type locality of *collorum* and called our attention to the host. Mike Fleming of Big Bend National Park and Jim Walters of

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LITERATURE CITED

AXELROD, D. I., AND P. H. RAVEN 1985. Origins of the Cordelleran flora. J. Biogeogr. 12: 21–47.

BALL, E. D. 1899. Some new species of *Deltocephalus*. Canadian Entomol. 31: 188–192.

———. 1900. Some new Jassidae from the Southwest. Canadian Entomol. 32: 200–205.

———. 1905. Some new Homoptera from the South and Southwest. Biol. Soc. Washington, Proc. 18: 117–120.

BEAMER, R. H. 1936. New leafhoppers from the western United States (Homoptera–Cicadellidae). Canadian Entomol. 68: 252–257.

BEAMER, R. H., AND L. D. TUTHILL. 1934. Some new species and a new genus of deltocephaloid leafhoppers (Homoptera, Cicadellidae). J. Kansas Entomol. Soc. 7: 1–22.

———. 1935. A monograph of the genera *Alapus* and *Hebecephalus* (Cicadellidae, Homoptera). Univ. Kansas Sci. Bull. 22: 527–547.

COLE, K. L. 1986. The lower Colorado River Valley: a Pleistocene desert. Quaternary Res. 25: 392–400.

CRONQUIST, A. 1978. The biota of the Intermountain Region in geohistorical context. Great Basin Nat. Mem. 2: 3–15.

CRUMB, S. E. 1915. Some new species of Jassoidea. Ann. Amer. Entomol. Soc. 8: 189–199.

CWIKLA, P. S., AND H. D. BLOCKER. 1981. An annotated list of the leafhoppers (Homoptera: Cicadellidae) from tallgrass prairie of Kansas and Oklahoma. Trans. Kansas Acad. Sci. 84: 89–97.

DELONG, D. M. 1926. A monographic study of the North American species of the genus *Deltocephalus*. Ohio State University, Univ. Studies 2: 1–129.

———. 1935. Some new species of deltocephaloid leafhoppers (Homoptera, Cicadellidae). Ann. Amer. Entomol. Soc. 28: 154–159.

_____. 1937. Some new deltocephaloid leafhoppers (Ho- moptera, Cicadellidae) from Illinois. Pan-Pacific Entomol. 13: 32–34.

_____. 1948. The leafhoppers or Cicadellidae (Eurymeli- nae–Balcluthinae) of Illinois. Illinois Nat. Hist. Surv. Bull. 24: 93–376.

DeLong, D. M., and J. S. Caldwell. 1937. Check list of the Cicadellidae (Homoptera) of America, north of Mexico. pp. 1–93.

DeLong, D. M., and R. V. Hershberger. 1947. The genus *Flexamia* (Homoptera, Cicadellidae) in Mexico. Bull. Brooklyn Entomol. Soc. 42: 136–139.

DeLong, D. M., and D. J. Knull. 1945. Check list of the Cicadellidae (Homoptera) of America, north of Mexico. Ohio State University, Grad. School Studies, Biol. Sci. Ser. No. 1. 102 pp.

DeLong, D. M., and J. P. Sleesman. 1929. New genera and subgenera from the genus *Deltocephalus*. Ann. Entomol. Soc. Amer. 22: 81–114.

Fox, L. R., and P. A. Morrow. 1981. Host specialization: species property or local phenomenon? Science 211: 888–893.

Gould, F. W. 1975. The grasses of Texas. Texas A & M University Press, College Station. 653 pp.

Gould, F. 1979. The genus *Bouteloua* (Poaceae). Ann. Missouri Bot. Garden 66: 348–413.

Hamilton, K. G. A., and H. H. Ross. 1975. New species of grass-feeding deltocephaline leafhoppers with keys to the Nearctic species of *Palus* and *Rosenus*. Canadian Entomol. 107: 601–611.

Harrington, H. D. 1954. Manual of the plants of Colo- rado. Sage Books, Denver. 666 pp.

Hicks, A. L., R. F. Whitcomb, and H. D. Blocker. 1988. Why are there so many species of *Athysanella?* Pages 397–403 *in* C. Vidano, ed., Proc. 6th Auchenorrhyncha Meeting, Turin, Italy, 7–11 Sept. 1987.

Hitchcock, A. S. 1971. Manual of the grasses of the United States. 2d ed. Revised by A. Chase. Vols. I, II. Dover Publications Inc., New York.

Jepson, W. L. 1925. A manual of the flowering plants of California. Associated Students Store, Berkeley, California. 1,238 pp.

Johnston, I. M. 1943. Plants of Coahuila, eastern Chi- huahua, and adjoining Zacatecas and Durango, II. J. Arnold Arboretum 24: 375–421.

Johnston, M. C. 1963. Past and present grasslands of southern Texas and northeastern Mexico. Ecology 44: 456–466.

Kearney, T. H., and R. H. Peebles. 1960. Arizona flora. 2d ed., with suppl. University of California Press, Berkeley and Los Angeles. 1,085 pp.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Special Publications, American Geographical Society, Washington. 116 pp.

Lawton, J. H., and D. Schroder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature 265: 137–140.

Lesueur, H. 1945. The ecology of the vegetation of Chi- huahua, Mexico, north of parallel twenty-eight. Univ. of Texas Publ. No. 4521. Pages 9–92.

Linnavuori, R. 1959. Revision of the Neotropical delto- cephalinae and some related subfamilies (Ho- moptera). Ann. Zool. Soc. 'Vanamo' 20: 89.

Linnavuori, R. E., and D. M. DeLong. 1978. Seventeen new species and three new genera of Central and South American Deltocephalini (Homoptera: Ci- cadellidae). Brenesia 14–15: 195–226.

Lonard, R. I., and F. W. Judd. 1980. Phytogeography of South Padre Island, Texas. Southw. Nat. 25: 313–322.

Lowry, J. E., and H. D. Blocker. 1987. Two new species of *Flexamia* from the Nebraska Sand Hills (Ho- moptera: Cicadellidae: Deltocephalinae). Proc. Entomol. Soc. Washington 89: 57–60.

Lynn, D., and R. F. Whitcomb. 1986. A computerized file for cicadellid host acquisitions. Pages 269–272 *in* M. R. Wilson and L. R. Nault, eds., Proc. 2d Int. Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Inst. En- tomol., London.

MacArthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York. 334 pp.

McGregor, R. L., coord. 1977. Atlas of the flora of the Great Plains. Iowa State University Press, Ames. 600 pp.

Mickevich, M. F., and J. S. Farris. 1984. PHYSYS docu- mentation. Maryland Center for Systematic Ento- mology, Entomology Department, University of Maryland, College Park.

Milstead, W. W. 1960. Relict species of the Chihuahuan Desert. Southw. Nat. 2: 75–88.

Morden, C. W. 1985. A biosystematic study of the *Muh- lenbergia repens* complex (Poaceae: Era- grostideae). Unpublished dissertation, Texas A & M University, College Station.

Morden, C. W., and S. L. Hatch. 1987. Anatomical study of the *Muhlenbergia repens* complex (Poaceae: Chloridoideae: Eragrostideae). Sida 12: 347–359.

Muller, C. H. 1947. Vegetation and climate of Coahuila, Mexico. Madroño 9: 1–32.

Oman, P. W. 1949. The Nearctic leafhoppers (Ho- moptera: Cicadellidae). Mem. Washington Ento- mol. Soc., Mem. 3. 253 pp.

Osborn, H. 1907. Descriptions of new forms of Jassidae. Proc. Davenport Acad. Sci. 10: 163–166.

_____. 1909. Notes on Guatemalan Hemiptera with de- scriptions of a few new species. Ohio. Nat. 9: 457–466.

_____. 1928. The leafhoppers of Ohio. Ohio Biol. Surv. 3, Bull. 14: 199–374.

Osborn, H., and E. D. Ball. 1897a. Studies on the life histories of grass feeding Jassidae. Iowa Agric. Expt. Sta. Bull. 34: 612–640.

_____. 1897b. Contributions to the hemipterous fauna of Iowa. Proc. Iowa Acad. Sci. 4: 172–234.

_____. 1898. Studies of North American Jassoidea. Proc. Davenport Acad. Nat. Sci. 7: 45–100.

Pohl, R. W. 1966. The grasses of Iowa. Iowa State J. Sci. 40: 341–573.

_____. 1968. How to know the grasses. Wm. C. Brown, Dubuque, Iowa. 244 pp.

Rosen, D. E. 1978. Vicariant patterns and historical ex- planation in biogeography. Syst. Zool. 1978: 159–188.

Ross, H. H. 1965. Pleistocene events and insects. Pages 583–596 *in* H. E. Wright and D. G. Frey, eds.,

The Quaternary of the United States. Princeton University Press, Princeton, New Jersey.

_____. 1970. The ecological history of the Great Plains: evidence from grassland insects. Pages 225–240 *in* W. Dort, Jr., and J. K. Jones, Jr., eds., Pleistocene and Recent environments of the Central Great Plains. Department of Geology, University of Kansas Special Publications 3. The University Press of Kansas. Lawrence/Manhattan/Wichita.

ROSS, H. H., AND T. A. COOLEY. 1969. A new Nearctic leafhopper of the genus *Flexamia* (Hemiptera: Cicadellidae). Entomol. News 80: 246–248.

RZEDOWSKI, J. 1966. Vegetación del estado de San Luis Potosí. Acta Cient. Potos. 5: 5–291.

_____. 1973. Geographical relationships of the flora of Mexican dry regions. Pages 61–72 *in* Vegetation and vegetational history of northern Latin America. Elsevier Scientific Company, Amsterdam.

_____. 1975. An ecological and phytogeographical analysis of the grasslands of Mexico. Taxon 24: 67–80.

_____. 1983. Vegetación de Mexico. Editorial Limusa, Mexico, D. F. 432 pp.

SHREVE, F. 1939. Observations on the vegetation of Chihuahua. Madroño 5: 1–48.

_____. 1942. Grassland and related vegetation in northern Mexico. Madroño 6: 190–198.

STEYERMARK, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames. 1,725 pp.

STUBBENDIECK, J., S. L. HATCH, AND K. J. HIRSCH. 1986. North American range plants. 3d ed. University of Nebraska Press, Lincoln. 465 pp.

THOMPSON, R. S., AND J. I. MEAD. 1982. Late Quaternary environments and biogeography in the Great Basin. Quaternary Res. 17: 39–55.

TRIPLEHORN, B. W., AND L. R. NAULT. 1985. Phylogenetic classification of the genus *Dalbulus* (Homoptera: Cicadellidae), and notes on the phylogeny of the Macrostelini. Ann. Entomol. Soc. Amer. 78: 291–315.

VAN DEVENDER, T. R., AND T. L. BURGESS. 1985. Late Pleistocene woodlands in the Bolson de Mapimi: a refugium for the Chihuahuan Desert biota? Quaternary Res. 24: 346–353.

VAN DEVENDER, T. R., AND W. G. SPAULDING. 1979. Development of vegetation and climate in the south-western United States. Science 204: 701–710.

WELSH, S. L., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS. 1987. A Utah flora. Great Basin Nat. Mem. 9. 1–894.

WHITCOMB, R. F. 1957. Host relationships of some grass-inhabiting leafhoppers. Unpublished thesis, University of Illinois. 37 pp.

_____. 1986. North American forests and grasslands: biotic conservation. Pages 163–176 *in* D. A. Saunders, G. W. Arnold, A. A. Burbridge, and A. J. M. Hopkins, eds., Nature conservation: the role of remnants of native vegetation. Surrey Beatty and Sons, Sydney.

WHITCOMB, R. F., A. L. HICKS, H. D. BLOCKER, AND J. P. KRAMER. 1988. Host specificity: a major mechanism enhancing insect diversity in grasslands. Paper 11.06 *in* A. Davis and G. Stanford, eds., The prairie: roots of our culture; formulation of our economy. Proc. 10th No. Amer. Prairie Conf., Denton, Texas, 1986. Native Prairies Assoc., Wheatland, Texas.

WHITCOMB, R. F., A. L. HICKS, D. E. LYNN, K. ALLRED, AND H. D. BLOCKER. 1987. Geographic variation in host relationships of leafhoppers (Homoptera: Cicadellidae) in North American grasslands. Pages 293–325 *in* M. R. Wilson and L. R. Nault, eds., Proc. 2d Int. Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Inst. Entomol., London.

WHITCOMB, R. F., J. KRAMER, M. E. COAN, AND A. L. HICKS. 1986. Ecology and evolution of leafhopper-grass host relationships in North American grasslands. Curr. Top. Vector Res. 4: 125–182.

WRIGHT, H. E., JR. 1970. Vegetational history of the Central Plains. Pages 157–172 *in* W. Dort, Jr., and J. K. Jones, Jr., eds., Pleistocene and Recent environments of the central Great Plains. Department of Geology, University of Kansas Special Publications 3. The University Press of Kansas. Lawrence/Manhattan/Wichita.

YOUNG, D. A., JR., AND B. P. BEIRNE. 1958. A taxonomic revision of the leafhopper genus *Flexamia* and a new related genus. U.S. Dept. Agric. Tech. Bull. 1173: 1–53.

APPENDICES

APPENDIX I. Specimens examined[1].

Species	Holotype	Paratype(s)	BARC	CNC	KU	OSU	USNM
minima	OSU(h)	none	0	0	0	1	8
zamora	OSU(h)	OSU(p)	0	0	0	9	0
pectinata	USNM(c)	USNM(c)	57	5	150	45	75
gila	USNM(h)	p[2]	9	0	0	0	0
bandarita	USNM(h)	p[2]	5	0	0	6	0
doeringae	KU(h)	USNM(p)	35	0	68	24	91
collorum	USNM(h)	p[2]	81	0	0	0	0
jacala	USNM(h)	none	0	0	0	0	1
mescalero	USNM(h)	p[2]	26	0	0	0	0
abbreviata	USNM(c)	USNM(c)	765	141	661	74	409
zacate	USNM(h)	p[2]	96	0	0	0	0
canyonensis	USNM(h)	USNM(p)	9	0	0	0	2
surcula	OSU	OSU	72	0	10	57	37
curvata	OSU	OSU	560	81	209	77	107
grammica	USNM(l)	KU(p)	47	64	164	48	109
picta	OSU(h)	USNM(c)	285	107	202	135	112
pyrops	KU(l)	KU(c)	56	39	56	83	162
albida	USNM(c)	USNM(c)	46	1	7	17	19
slossonae	USNM(h)	none	12	0	50	0	18
serrata	KU(h)	KU(p)	56	98	20	0	14
ritana	KU(h)	USNM(p)	0	0	17	0	5
arizonensis	USNM	USNM(p)	177	11	114	20	94
flexulosa	USNM(l)	USNM(c)	380	211	254	51	353
arenicola	USNM(h)	USNM(p)	91	0	0	0	5
celata	USNM(h)	USNM(p)	49	0	4	0	5
stylata	USNM(l)	USNM(c)	83	67	66	9	70
decora	KU	USNM(p)	95	246	177	3	28
youngi	USNM	p[2]	30	0	5	0	0
modica	KU	USNM(p)	377	0	110	3	8
inflata	USNM(c)	USNM(c)	665	103	257	146	155
beameri	KU	USNM(p)	0	0	7	0	0
texana	USNM	USNM(p)	0	0	0	0	10
imputans	OSU(c)	OSU(c)	4	0	10	11	19
areolata	USNM(l)	USNM(c)	37	51	42	51	88
prairiana	OSU	OSU	612	44	193	23	172
reflexa	USNM	USNM(c)	25	1	1	8	26
atlantica	OSU	OSU(p)	378	17	8	12	44
dakota	USNM(h)	USNM(p)	209	3	1	0	2
producta	(BNM)	USNM(c[3])	4	5	136	117	267
sandersi	OSU(h)	OSU(h[4])	45	3	60	31	126
delongi	(INHS)	none	0	26	1	39	13
graminea	OSU(h)	none	176	28	105	10	190
clayi	USNM(h)	USNM(p)	148	9	115	47	3
satilla	CNC(h)	CNC(p)	0	2	2	0	0

[1]Numbers reflect content of collection before redistribution at end of study. Type distribution occurred after this enumeration (c = cotype; b = holotype; l = lectotype; p = paratype). Parentheses = specimen not examined.
[2]See text for distribution of paratypes.
[3]Cotype of *visenda* (= *producta*).
[4]Holotype of *bidentata* (= *sandersi*).

APPENDIX II. PART I. Character matrix for PHYSYS.

DISTIN	SIMPLE	ABSENTP	?	SINUATC	THICK	1	ELONGA
SHORTL	TAPER	ABSNT	FLAREDG	APODNOX	APOPRIM	2	ELONGA
CONNAR	FORCEPY	PRIMPL	DEEPST	ABSTR	BRFACE	3	ELONGA
DISTIN	SIMPLE	ABSENTP	?	LEFTC	THICK	1	MEXICAN
SHORTL	TAPER	ABSNT	APICALG	APODEXP	APOPRIM	2	MEXICAN
CONNAR	PRIMPY	PRIMPL	PARALST	PRESTR	CONBLF	3	MEXICAN
DISTIN	SIMPLE	ABSENTP	?	LEFTC	THIN	1	MIRAND
SHORTL	TAPER	ABSNT	APICALG	APODEXP	APOPRIM	2	MIRAND
CONNAR	CNSTRPY	PRIMPL	EXCVST	PRESTR	CONBLF	3	MIRAND
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	MINIMA
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APOPARL	2	MINIMA
CONNAR	BULBPY	ACUTPL	TOOTHST	ABSTR	BRFACE	3	MINIMA
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	ZAMORA
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APOPARL	2	ZAMORA
CONNAR	BULBPY	LNGBRPL	OUTRST	ABSTR	BRFACE	3	ZAMORA
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	PECTIN
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APOPARL	2	PECTIN
CONNAR	BULBPY	RECTPL	TOOTHST	ABSTR	BRFACE	3	PECTIN
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	BANDAR
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APORECU	2	BANDAR
CONNAR	BULBPY	LNGBRPL	INNRST	ABSTR	BRFACE	3	BANDAR
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	GILA
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APORECU	2	GILA
CONNAR	BULBPY	LNGBRPL	INNRST	ABSTR	BRFACE	3	GILA
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	DOERIN
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APOPARL	2	DOERIN
CONNAR	BULBPY	RECTPL	PROCST	ABSTR	CONBLF	3	DOERIN
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	COLLOR
SHORTL	TAPER	ABSNT	FLAREDG	APODEXP	APORECU	2	COLLOR
CONNAR	BUDPY	SHORTPL	TOOTHST	ABSTR	BRFACE	3	COLLOR
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	JACALA
SHORTL	TAPER	ABSNT	FLAREDG	APODNOX	APORECU	2	JACALA
CONNAR	BULBPY	LNGBRPL	?	ABSTR	BRFACE	3	JACALA
DISTIN	CAPITAT	ABSENTP	?	LEFTC	THIN	1	MESCAL
SHORTL	TAPER	ABSNT	FLAREDG	APODNOX	APOCLOS	2	MESCAL
CONNAR	BULBPY	LNGROPL	DEEPST	ABSTR	BRFACE	3	MESCAL
DISTIN	SHORTPR	ABSENTP	?	STRAIT	LESTHIC	1	ABBREV
LONGERL	UNTAPER	ABSNT	SLITG	APODEXP	APOPARL	2	ABBREV
CONNAR	PRODPY	LOBATPL	INCISST	ABSTR	BRFACE	3	ABBREV
DISTIN	FLARED	ABSENTP	?	LEFTC	THICK	1	CANYON
SHORTL	TAPER	ABSNT	MIDLENG	APODNOX	APORECU	2	CANYON
CONNAR	PRODPY	LOBATPL	LONGST	ABSTR	BRFACE	3	CANYON
DISTIN	FLARED	ABSENTP	?	LEFTC	THIN	1	ZACATE
SHORTL	TAPER	ABSNT	SLITG	APODNOX	APORECU	2	ZACATE
CONNAR	PRODPY	LOBATPL	PROJST	ABSTR	BRFACE	3	ZACATE
DISTIN	ASYMPR	ABSENTP	?	LEFTC	THICK	1	GRAMMI
SHORTL	TAPER	SERRATE	BIPROVG	APODNOX	APOWING	2	GRAMMI
CONNAR	NARRPY	SQUATPL	ROUNDST	PRESTR	CONBLF	3	GRAMMI
DISTIN	LONGPR	SUBAPP	?	STRAIT	LESTHIC	1	SURCUL
LONGERL	UNTAPER	ENTIRE	BIPROVG	APODNOX	APOFORK	2	SURCUL
CONWIDE	SHORTPY	SHORTPL	BOXST	ABSTR	BRFACE	3	SURCUL
DISTIN	LONGPR	DISTALP	?	STRAIT	LESTHIC	1	CURVAT
LONGERL	UNTAPER	ENTIRE	BIPRSLG	APODEXP	APOFORK	2	CURVAT
CONNAR	SHORTPY	SHORTPL	WIDINST	ABSTR	BRFACE	3	CURVAT
INDIST	FLANGED	SUBAPP	?	STRAIT	THIN	1	PICTA
LONGSTL	UNTAPER	SERRATE	SUBAPIG	APODNOX	APOFORK	2	PICTA
CONNAR	ANGLPY	TAPERPL	SERRST	ABSTR	CONBLF	3	PICTA
INDIST	FLANGED	APPOSP	?	SINUATC	THIN	1	PYROPS
LONGSTL	UNTAPER	SERRATE	SUBAPIG	APODNOX	APOFORK	2	PYROPS
CONNAR	ANGLPY	REDUCPL	EXTHST	ABSTR	TOOTHF	3	PYROPS

Appendix II. Part I continued.

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DISTIN    BIFURC   FUSEDP   SAGGITV  LESSC    THICK      1 ALBIDA
SHORTL    TAPER    SERRATE  SUBVNPG  APODEXP  APOCLUB    2 ALBIDA
CONWIDE   WIDEPY   TAPERPL  TTHEXST  PRESTR   CONBLF     3 ALBIDA
PARTLY    BIFURC   FUSEDP   SAGGITV  RIGHTC   THICK      1 SLOSSO
SHORTL    UNTAPER  ENTIRE   SYMSLTG  APODNOX  APOWING    2 SLOSSO
CONPAFU   UNDIFPY  ACUTPL   TRILBST  PRESTR   CONBLF     3 SLOSSO
DISTIN    BIFURC   FUSEDP   SAGGITV  STRAIT   THICK      1 SERRAT
SHORTL    UNTAPER  ENTIRE   SUBVNPG  APODEXP  APOCLUB    2 SERRAT
CONWIDE   IRREGPY  CLEAVPL  LOBEDST  ABSTR    CONBLF     3 SERRAT
DISTIN    LYRIFO   FUSEDP   SAGGITV  LESSC    THICK      1 RITANA
SHORTL    UNTAPER  ENTIRE   SUBVNPG  APODNOX  APOCLAW    2 RITANA
CONNAR    OVATEPY  TAPERPL  ANGLST   REDUSTR  CONBLF     3 RITANA
DISTIN    SYMMET   SHORTV   SAGGITV  LESSC    LESTHIC    1 ARENIC
LONGERL   UNTAPER  ENTIRE   SUBAPIG  APODNOX  APOAWAY    2 ARENIC
CONNAR    ROUNDPY  INCISPL  NOTCHST  ABSTR    CONBLF     3 ARENIC
DISTIN    SYMMET   SHORTV   SAGGITV  STRAIT   LESTHIC    1 CELATA
LONGERL   UNTAPER  ENTIRE   SUBAPIG  APODNOX  APOPARL    2 CELATA
CONWIDE   THSTYPY  INCISPL  NOTCHST  ABSTR    CONBLF     3 CELATA
DISTIN    ASYMME   TWISTV   DISPLCV  RIGHTC   LESTHIC    1 STYLAT
LONGERL   UNTAPER  ENTIRE   SUBAPIG  APODNOX  APOTHIC    2 STYLAT
CONBROD   STYLPY   SQUARPL  BINOTST  ABSTR    CONBLF     3 STYLAT
DISTIN    SYMMET   SHORTV   SAGGITV  STRAIT   LESTHIC    1 ARIZON
LONGERL   UNTAPER  ENTIRE   SUBAPIG  APODNOX  APOFORK    2 ARIZON
CONNAR    VNPRPY   MINUTPL  SQUARST  ABSTR    CONBLF     3 ARIZON
DISTIN    SYMMET   SHORTV   SAGGITV  LEFTC    LESTHIC    1 FLEXUL
LONGERL   UNTAPER  SERRATE  SUBAPIG  APODNOX  APOFORK    2 FLEXUL
CONNAR    CAUDPY   MINUTPL  MEDNST   ABSTR    CONBLF     3 FLEXUL
DISTIN    SYMMET   FUSEDP   SAGGITV  LEFTC    THICK      1 DECORA
SHORTL    TAPER    SERRATE  APPRG    APODNOX  APOAWAY    2 DECORA
CONBROD   LOBEDPY  INCISPL  BINOTST  ABSTR    CONBLF     3 DECORA
DISTIN    ASYMME   RECURVP  DISPLCV  LESSC    LESTHIC    1 YOUNGI
LONGERL   TAPER    SERRATE  APPRG    APODNOX  APOTHIC    2 YOUNGI
CONBROD   BROADPY  INCISPL  BINOTST  ABSTR    CONBLF     3 YOUNGI
DISTIN    ASYMME   DECURVP  DISPLCV  LEFTC    THICK      1 MODICA
SHORTL    TAPER    SERRATE  SUBAPIG  APODNOX  APOAWAY    2 MODICA
CONBROD   OVATEPY  DEEPL    NOTCHST  ABSTR    CONBLF     3 MODICA
DISTIN    ASYMME   DECURVP  DISPLCV  RIGHTC   THIN       1 INFLAT
LONGSTL   UNTAPER  ENTIRE   SUBAPIG  APODNOX  APOFORK    2 INFLAT
CONWIDE   BOATPY   TAPERPL  BINOTST  ABSTR    CONBRF     3 INFLAT
DISTIN    TWISTED  RECURVP  DISPLCV  RIGHTC   THIN       1 BEAMER
LONGSTL   UNTAPER  ENTIRE   APPRG    APODNOX  APOTHIC    2 BEAMER
CONBROD   SHIPPY   SHORTPL  BINOTST  ABSTR    CONBRF     3 BEAMER
DISTIN    TWISTED  TWISTV   DISPLCV  STRAIT   THIN       1 TEXANA
LONGSTL   UNTAPER  ENTIRE   APPRG    APODNOX  APOREDU    2 TEXANA
CONWIDE   SHIPPY   SHORTPL  BINOTST  ABSTR    CONBRF     3 TEXANA
DISTIN    TWISTED  ?        LATERLV  STRAIT   THIN       1 IMPUTA
LONGSTL   UNTAPER  SERRATE  LATSLTG  APODNOX  APOHOOK    2 IMPUTA
CONWIDE   LGOVPY   TAPERPL  LOBEDST  ABSTR    BLFACE     3 IMPUTA
FUSED     TWISTED  ?        LATERLV  LEFTC    LESTHIC    1 AREOLA
LONGERL   UNTAPER  SERRATE  LATSLTG  APODNOX  APOAWAY    2 AREOLA
CONWIDE   BIZARPY  TAPERPL  PROCST   ABSTR    BLFACE     3 AREOLA
BARELY    INVERT   ?        DORSALV  STRAIT   LESTHIC    1 PRAIRI
LONGERL   UNTAPER  SERRATE  DORSALG  APODNOX  APOPEN     2 PRAIRI
CONFUSE   ELLIPY   NARRPL   NAROWST  ABSTR    VARCONF    3 PRAIRI
FUSED     INVERT   ?        BASFUSV  STRAIT   LESTHIC    1 REFLEX
LONGERL   UNTAPER  SERRATE  PROFUSG  APODNOX  APOCLOS    2 REFLEX
CONFUSE   UPTNPY   NARRPL   NAROWST  ABSTR    VARCONF    3 REFLEX
FUSED     WINDSW   ?        FUSEDV   STRAIT   LESTHIC    1 ATLANT
LONGERL   UNTAPER  SERRATE  LATG     APODNOX  APOWIDE    2 ATLANT
CONFUSE   THINPY   NOTCHPL  NAROWST  ABSTR    VARCONF    3 ATLANT
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APPENDIX II. PART I continued.

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FUSED    INVTWO   ?        TINYV    STRAIT   THICK    1 PRODUC
FUSEDL   UNTAPER  SERRATE  FUSEDG   APODNOX  APOPARL  2 PRODUC
CONFUSE  VNTLBPY  BOTTLPL  NAROWST  ABSTR    VARCONF  3 PRODUC
FUSED    INVTWO   ?        FUSEDV   STRAIT   THICK    1 DAKOTA
FUSEDL   UNTAPER  SERRATE  DORFUSG  APODNOX  APOCLOS  2 DAKOTA
CONFUSE  POSTPY   BOTTLPL  NAROWST  ABSTR    BRFACE   3 DAKOTA
FUSED    FUSPR    ?        REDUCV   STRAIT   THICK    1 SANDER
FUSEDL   UNTAPER  SERRATE  APPRSDG  APODNOX  APOWIDE  2 SANDER
CONFUSE  HIGHPY   NOTCHPL  NAROWST  ABSTR    BRFACE   3 SANDER
FUSED    FUSPR    ?        REDUCV   STRAIT   THICK    1 DELONG
FUSEDL   UNTAPER  SERRATE  APPRSDG  APODNOX  APOWIDE  2 DELONG
CONFUSE  HIGHPY   NOTCHPL  NAROWST  ABSTR    BRFACE   3 DELONG
FUSED    ASKEW    ?        FUSEDV   STRAIT   THICK    1 GRAMIN
FUSEDL   SPIRALT  SERRATE  SPIRALG  APODNOX  APOPARL  2 GRAMIN
CONFUSE  THICKPY  RECURPL  NAROWST  ABSTR    BRFACE   3 GRAMIN
FUSED    ASKEW    ?        FUSEDV   LEFTC    THICK    1 CLAYI
FUSEDL   SPIRALT  SERRATE  WIDSPIG  APODNOX  APOCLOS  2 CLAYI
CONFUSE  UPLOBPY  RECURPL  NAROWST  ABSTR    BRFACE   3 CLAYI
FUSED    ASKEW    ?        FUSEDV   LEFTC    THICK    1 SATILL
FUSEDL   SPIRALT  SERRATE  WIDSPIG  APODNOX  APOCLOS  2 SATILL
CONFUSE  UPLOBPY  RECURPL  NAROWST  ABSTR    BRFACE   3 SATILL
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APPENDIX II. PART II. Hypothesized character transformation in *Flexamia*. Data for PHYSYS.

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AEDCONN;DISTIN-INDIST-PARTLY-BARELY-FUSED;              1 AEDCONN
AEDAPEX;SIMPLE-FLARED-CAPITAT,SHORTPR-[LONGPR-FLANGED,  1 AEDAPEX
BIFURC,LYRIFO,SYMMET-ASYMME-TWISTED-[INVERT-WINDSW,     2 AEDAPEX
[FUSPR-ASKEW],INVTWO]];                                 3 AEDAPEX
ANTEPR;ABSENTP-SUBAPP-DISTALP-APPOSP-[FUSEDP-DECURVP,   1 ANTEPRO
RECURVP,[LONGV-SHORTV-TWISTV]];                         2 ANTEPRO
VENTRALP;SAGGITV-DISPLCV-LATERLV-DORSALV-BASFUSV-REDUCV 1 VENTRLP
TINYV-FUSEDV;                                           2 VENTRLP
AEDCURV;LEFTC-LESSC-STRAIT-SINUATC-RIGHTC;              1 AEDCURV
AEDTHIC;THICK-LESTHIC-THIN;                             1 AEDTHIC
AEDLENG;SHORTL-LONGERL-LONGSTL-FUSEDL;                  1 AEDLENG
AEDTAPER;TAPER-UNTAPER-SPIRALT;                         1 AEDTAPER
AEDPRMG;ENTIRE-SERRATE;                                 1 AEDPRMG
GONOLOC;APICALG-FLARED-[SLITG-MIDLENG],[BIPROVG-[SUBVNPG- 1 GONOLOC
SYMSLTG],BIPRSLG,[SUBAPIG-APPRG,LATSLTG-DORSALG-[PROFUSG- 2 GONOLOC
[APPRSDG-SPIRALG-WIDSPIG],[FUSEDG-DORFUSG],LATG]]];     3 GONOLOC
APOAPEX;APODEXP-APODNOX;                                1 APOAPEX
APOARM;APOPRIM-[APOPARL-[APOCLAW-APOHOOK-APOPEN-APOCLOS- 1 APOARM
APOWIDE],[APOAWAY-APOTHIC-APOREDU],APOFORK,[APOCLUB-    2 APOARM
APOWING],APORECU];                                      3 APOARM
CONKEEL;CONNAR-CONWIDE-CONBROD-CONPAFU-CONFUSE;         1 CONKEEL
PYGMAL;PRIMPY-FORCEPY-[CNSTRPY-[NARRPY-IRREGPY-WIDEPY-  1 PYGMAL
UNDIFPY],[BULBPY-BUDPY,PRODPY,[SHORTPY-ANGLPY,[OVATEPY- 2 PYGMAL
[LOBEDPY-[BOATPY-SHIPPY],BROADPY],[ROUNDPY-[VNPRPY-CAUDPY], 3 PYGMAL
[STYLPY-THSTPY]],[LGOVPY-BIZARPY,[ELLIPY-VNTLBPY,[UPTNPY- 4 PYGMAL
POSTPY,THINPY,[HIGHPY-UPLOBPY-THICKPY]]]]]]]];          5 PYGMAL
PLATES;PRIMPL-[LNGBRPL-RECTPL,SHORTPL],SQUATPL,[LNGROPL- 1 PLATES
LOBATPL-REDUCPL],[TAPERPL-[NARRPL-BOTTLPL-NOTCHPL-RECURPL], 2 PLATES
ACUTPL,[CLEAVPL-[INCISPL-SQUARPL,[DEEPL-MINUTPL]]]];    3 PLATES
STERNUM;PARALST-EXCVST-ROUNDST,[TOOTHST-[OUTRST-DEEPST], 1 STERNUM
[INNRST-PROCST],[INCISST-LONGST-PROJST],[BOXST-WIDINST, 2 STERNUM
[SERRST-EXTHST]]],[TTHEXST-TRILBST,LOBEDST-[ANGLST-     3 STERNUM
[NOTCHST-BINOTST],[PROCST-NAROWST],[SQUARST-MEDNST]]]; 4 STERNUM
DORSVIT;PRESTR-REDUSTR-ABSTR;                           1 DORSVIT
FACE;CONBLF-TOOTHF,[CONBRF-BRFACE],[VARCONF-BLFACE];    1 FACE
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APPENDIX II. PART III.

Character Codes of *Flexamia* Species:
Code Identification*
P = plesiomorphic; A = apomorphic

1. AEDCONN: Articulation (P) or fusion
(A) of aedeagus and connective: DISTIN (P)
(Figs. 6A,B,C,E); INDIST (Fig. 6D); BARE-
LY (Fig. 6F); PARTLY (Y&B Fig. 9B) FUSED
(Fig. 6G).

2. AEDAPEX: Morphology of aedeagal
apex which may be simple, without processes
or special structures (P), or with paired pro-
cesses (A): SIMPLE (P) (Figs. 55C,F);
FLARED (Figs. 12A–H); CAPITAT (Figs.
12I,22); SHORTPR (Fig. 7H); ASYMPR (Fig.
7E); LONGPR (Figs. 7F,G); FLANGED
(Figs. 7K,L); BIFURC (Figs. 7A–C); LYRIFO
(Fig. 7D); SYMMET (Figs. 31G,K);
ASYMME (Figs. 31E,H,M); TWISTED
(Fig. 31A); INVERT (Figs. 44D,G);
WINDSW (Fig. 44A); INVTWO (Fig. 44I);
FUSPR (Fig. 44B); ASKEW (Figs. 44F,H).

3. ANTEPR: Anteapical processes, which
are absent (P), present as paired processes, or
fused (A) into a single process: ABSENTP
(Figs. 55C,F); SUBAPP (Fig. 7G); DISTALP
(Fig. 7F); APPOSP (Fig. 7L); FUSEDP (Figs.
7A–D); LONGV (Fig. 31G); RECURVP
(Fig. 38A); DECURVP (Fig. 31E); SHORTV
(Figs. 31I–L); TWISTV (Fig. 31A).

4. VENTRLP: Phyletic twisting of the un-
paired ventral process (see 3. ANTEPR),
which was (P) symmetrically situated on the
ventral surface of the aedeagus, but moved to
the dorsum, and was (A) ultimately lost
(Fig. 61), presumably by fusion: SAGGITV
(Fig. 61A); DISPLCV (Fig. 61B); LATERLV
(Fig. 61C); DORSALV (Fig. 61D); BASFUSV
(Fig. 61E); REDUCV (Fig. 61F); TINYV
(Fig. 61G); FUSEDV (Fig. 61H).

5. AEDCURV: Curvature (lateral aspect) of
the aedeagus, which may be curved sinistrad
(P), without curvature, sinuate, or curved
dextrad (A): LEFTC (Figs. 7I,J); LESSC
(Y&B Figs. 10B,11A); STRAIT (Fig. 7H);
SINUATC (Y&B Fig. 2B); RIGHTC (Fig.
40A).

6. AEDTHIC: Thickness (lateral aspect) of
the aedeagus, which may be thick (P), less
thick, or thin (A); THICK (Fig. 7J); LES-

THICK (Fig. 38A); THIN (Figs. 16A, 17A,
18A).

7. AEDLENG: Length of the aedeagus,
which may be short (P), longer, even longer,
or, finally (A), fused with the connec-
tive: SHORTL (Figs. 16A,7I,J); LONGERL
(Fig. 6B); LONGSTL (Fig. 6D); FUSEDL
(Fig. 6G).

8. AEDTAPR: Form of the aedeagal shaft
which may be tapered (P), untapered, or, ulti-
mately (A), tapered in association with a spiral
gonopore: TAPER (Figs. 7I,J); UNTAPER
(Fig. 7H); SPIRALT (Fig. 6G).

9. AEDPRMG: Form of the margins of the
paired, apical, aedeagal processes which, if
present, may have entire (P) or serrate mar-
gins (A): ABSNT (absent); ENTIRE (Figs.
7F,G); SERRATE (Figs. 44B–D).

10. GONOLOC: Form and position of the
gonopore. In the plesiomorphic condition,
this structure was apical and subcircular or
ovate. In early stages in transformation the
gonopore was subapical on the ventral sur-
face. In the *flexulosa* group the gonopore may
have reversed its distad movement from the
aedeagal apex and returned to the apex, or
nearly so; but in *imputans* and *areolata* the
gonopore became associated with the un-
paired process, which had moved to a lateral
position on the aedeagal shaft. In *prairiana*
the gradual twisting (see 4. VENTRLP) of the
processes had stabilized with the gonopore in
a dorsal, anteapical position. Transformation
from this condition involved association with
the unpaired process and movement with the
process as it became appressed to the aedea-
gal shaft and, eventually, fused with the shaft.
Ultimately, the fusion led to an elongate
structure that winds around the shaft in a
helical configuration: APICALG (Y&B Fig.
32B); FLAREDG (Figs. 12A–H); SLITG (Fig.
7H); MIDLENG (Fig. 6C); BIPROVG
(Fig. 7G); SUBVNPG (Fig. 7B); SYMSLTG
(Fig. 7C); BIPRSLG (Fig. 7F); SUBAPIG
(Figs. 31E,J,M); APPRG (Fig. 31A); LAT-
SLTG (Fig. 61C) DORSALG (Fig. 44G)
PROFUSG (Fig. 44D); APPRSDG (Fig. 44B)
SPIRALG (Fig. 44F); WIDSPIG (Figs
44H,J); FUSEDG (Fig. 44E); DORFUSC
(Fig. 44I); LATG (Fig. 44A).

11. APOAPEX: Apices of the apodema
arms may be expanded (P) or not expandec
(A): APODEXP (Fig. 6B); APODNOX (Figs
6A,D,E).

12. APOARM: In dorsal aspect the apodemal arms in the plesiomorphic condition were parallel to the aedeagal shaft. Transformations from this state (A) involved several lines of development, some of which involved reduction of the arms, or direction of the apices toward or away from the sagittal plane: APOPRIM (Y&B Fig. 32B); APOPARL (Fig. 6B); APOCLAW (Y&B Fig. 11B); APOHOOK (Y&B Fig. 21B); APOPEN (Fig. 6F); APOCLOS (Y&B Fig. 28C); APOWIDE (R&C Fig. 2); APOAWAY (Y&B Fig. 14B); APOTHIC (Fig. 40B); APOREDU (Y&B Fig. 16B); APOFORK (Figs. 6A,D,E); APOCLUB (Fig. 8B); APOWING (Y&B Fig. 27B); APORECU (Figs. 6C, 16B, 17B, 19B, 20B).

13. CONKEEL: In lateral aspect the dorsal keels of the connective may be narrow (P), widened, or very much widened. Alternatively (A), the connective fused with the aedeagus, a process that resulted in the loss of an independent identity for the keels: CONNAR (Figs. 16A, 17A, 18A); CONWIDE (Y&B Fig. 12A); CONBROD (Fig. 40A); CONPAFU (Y&B Fig. 9B); CONFUSE (Fig. 6G).

14. PYGMAL: The male pygofer, plesiomorphically, was apparently undifferentiated. From this state a defined posterior lobe differentiated, as in *Spartopyge miranda*. Several lines of development (A) are postulated (Fig. 62): PRIMPY (Fig. 62S); FORCEPY (Fig. 55G); UNDIFPY (Fig. 62T); CNSTRPY (Fig. 62N); BULBPY (Figs. 62C-G); BUDPY (Fig. 62A); PRODPY (Figs. 62H,I); NARRPY (Fig. 62O); IRREGPY (Fig. 62P); SHORTPY (Figs. 62K,L); ANGLPY (Fig. 62M); WIDEPY (Fig. 62Q); OVATEPY (Fig. 62U); ROUNDPY (Fig. 62LL); STYLPY (Fig. 62OO); THSTYPY (Fig. 62PP); LOBEDPY (Fig. 62FF); BROADPY (Fig. 62KK); BOATPY (Fig. 62GG); SHIPPY (Figs. 62HH,II); LGOVPY (Fig. 62V); BIZARPY (Fig. 62Z); ELLIPY (Fig. 62W); VNTLBPY (Fig. 62AA); UPTNPY (Fig. 62X); POSTPY (Fig. 62BB) THINPY (Fig. 62Y); HIGHPY (Fig. 62CC); UPLOBPY (Fig. 62DD); THICKPY (Fig. 62EE) CAUDPY (Fig. 62NN); VNPRPY (Fig. 62MM)..

15. PLATES: The male plates, plesiomorphically, were apparently long and relatively wide. The broad aspect of the plates was retained in the *pectinata* group, but in subsequent lineages tended to be modified to become tapered. In the *flexulosa* group the tapered plates became notched to accommodate dorsally produced pygofers; in *arizonensis* and *flexulosa* this tendency is maximized. In the *prairiana* group the tapered design was modified by narrowing of the apical third of the plates, by the development of small apical notches, and by the plates ultimately becoming recurved: PRIMPL (Fig. 54C); SQUATPL (Fig. 8F); LNGROPL (Fig. 11I); LNGBRPL (Fig. 11B); RECTPL (Figs. 11C,F); SHORTPL (Fig. 11G); LOBATPL (Fig. 8E); REDUCPL (Fig. 9B); TAPERPL (Fig. 8A); NARRPL (Fig. 45A); BOTTLPL (Fig. 45E); NOTCHPL (Fig. 45C); RECURPL (Fig. 45H); ACUTPL (Fig. 8B); CLEAVPL (Fig. 8C); MINUTPL (Figs. 33A,B); INCISPL (Figs. 33C,D,E); SQUARPL (Fig. 34E); DEEPL (Fig. 33F).

16. STERNUM: The sternum VII was apparently plesiomorphically excavated. From this condition several lines of development (A) ensued. Many of these lines involved two pairs of teeth separated by an incision on the posterior margin of the sternum. In the *pectinata* group the development of the inner or outer sets of teeth relative to one another is an important character in species discrimination. In the *flexulosa* and *prairiana* groups, at a time that aedeagal evolution was proceeding rapidly, the sternum VII became a relatively stable apomorphy that underwent minimal transformation: PARALST (Y&B Fig. 32E); EXCVST (Y&B Fig. 33F); ROUNDST (Fig. 10F); TOOTHST (Figs. 14A,C,G); OUTRST (Fig. 14B); DEEPST (Fig. 14H); INNRST (Figs. 14D,E); PROCST (Fig. 14F); INCISST (Fig. 10E); LONGST (Fig. 10I); PROJST (Fig. 10L); BOXST (Fig. 10J); WIDINST (Fig. 10K); SERRST (Fig. 10G); EXTHST (Fig. 10H); TTHEXST (Fig. 10A); TRILBST (Fig. 10B); LOBEDST (Fig. 10C); ANGLST (Fig. 10D); NOTCHST (L&B Figs. 1F, 2F); BINOTST (Fig. 10R); PROCST (Fig. 10Q); NAROWST (Fig. 10S); SQUARST (Y&B Fig. 17F); MEDNST (Fig. 10M).

17. DORSVIT: Species of the genus *Spartopyge* possess conspicuous dorsal stripes (P) that appear to be homologous with the stripes in *albida*, *slossonae*, *ritana*, and *grammica*. The loss of stripes (A) is presumed to be homoplastic: PRESTR (Figs. 2A–C, 54A); REDUSTR (Fig. 2D); ABSTR (Figs. 2E,F).

18. FACE: The plesiomorphic face of *Flex-amia* (and its ancestor *Spartopyge*) is presumed to be pale, with a conspicuously contrasting, black interocular band. In later lineages this habitus aspect was modified, as the interocular band became brown rather than black, as the distinction between the line and the remainder of the face became blurred, and, finally (A), as the face became essentially brown. In some transitional species, such as *prairiana*, the face varies widely from pale with a contrasting, brown interocular line to brown to (occasionally) nearly entirely black. We presume that loss of the plesiomorphic face condition, as with dorsal stripes, probably occurred in several lines: CONBLF (Figs. 3A,B,E,F,G); TOOTHF (*pyrops:* see text); BRFACE (Fig. 3H); CONBRF (contrasting brown face) VARCONF (variable contrast); BLFACE (Fig. 3C).

APPENDIX III

NOTES

PLANT NAMES.—*Andropogon gerardii* Vitman, big bluestem; *Andropogon virginicus* L., broomsedge; *Aristida dichotoma* Michx. var. *curtisii* Gray; *Aristida purpurea* Nutt.; *Bouteloua curtipendula* (Michx.) Torr., sideoats grama; *Bouteloua eriopoda* (Torr.) Torr., black grama; *Bouteloua gracilis* (Willd. ex H. B. K.) Lag. ex Griffiths, blue grama; *Bouteloua hirsuta* Lag., hairy grama; *Bouteloua pectinata* Featherley, tall grama; *Bouteloua uniflora* Vasey, Nealley grama; *Buchloë dactyloides* (Nutt.) Engelm., buffalograss; *Calamovilfa gigantea* (Nutt). Scribn. & Merr., big sandreed; *Calamovilfa longifolia* (Hook.) Scribner., prairie sandreed; *Cynodon dactylon* (L.) Pers., bermudagrass; *Distichlis spicata* (L.) Greene, salt grass; *Eragrostis curvula* (Schrad.) Nees, weeping lovegrass; *Eragrostis pectinacea* (Michx.) Nees, tufted lovegrass; *Eragrostis spectabilis* (Pursh) Steud., purple lovegrass; *Juncus tenuis* Willd., poverty rush; *Leptoloma cognatum* (Shult) Chase, fall witchgrass; *Muhlenbergia asperifolia* (Nees & Mey.) Paradi, scratchgrass; *Muhlenbergia cuspidata* (Torr. in Hook.) Rydb., plains muhly; *Muhlenbergia pauciflora* Buckley, New Mexican muhly; *Muhlenbergia porteri* Scribn. ex Beal, bush muhly; *Muhlenbergia pungens* Thurb., sand muhly; *Muhlenbergia repens* (Presl.) A. S. Hitchc., creeping muhly; *Muhlenbergia reverchonii* Vasey & Scribn., seep muhly; *Panicum capillare* L., witchgrass; *Panicum virgatum* L., switchgrass; *Poa pratensis* L., Kentucky bluegrass; *Redfieldia flexuosa* (Thurb.) Vasey, sand blowout grass; *Schizachyrium scoparium* (Michx.) Nash, little bluestem; *Sporobolus virginicus* (L.) Kunth., seashore dropseed; *Zoysia japonica* Steudl., zoysia grass.

PLANT RANGES.—Plant ranges were mapped using published range maps (Pohl 1968; Hitchcock 1971; McGregor 1977; Stubbendieck et al. 1986) and/or various floras (Gould 1975; Harrington 1954; Jepson 1925; Johnston 1943, 1963; Kearny and Peebles 1960; Küchler 1964; Lesueur 1945; Lonard and Judd 1980; Muller 1947; Rzedowski 1966, 1973, 1975, 1983); Shreve 1939, 1942; Steyermark 1963; Pohl 1966; and Welsh et al. 1987).

INSECT RANGES.—Occurrence of specimens was mapped on maps of the United States or North America (Goode Base Map, Department of Geography, University of Chicago, was used as a base). Specimens examined from the collections listed below were mapped. Canadian and Mexican records are mapped by locality; U.S. records were mapped by county to avoid extensive overlap of symbols. Some records from the collections of the Illinois State Natural History Survey (as reported in DeLong 1948), and the Kansas State University Collection were also mapped.

OTHER RECORDS.—Not all "records" were mapped. We refrained from mapping specimens that in our judgment represented possible or probable errors. These records included the following record for *clayi:* "Colfax, Cal., 8-7-30," from the OSU collection. Since *clayi* is a common Ohio species, but apparently does not occur west of the Mississippi River, this record is probably in error. Three records for *picta* seem questionable. Perhaps "Coronado N.F., Pena Blanca Resort, Arizona, 19 Aug. 1970, Harris and Harris, GL2019" (CNC) is valid. However, "Panama City, C. Z., July 23, 1920" (OSU), and "Mina, Mineral Co. Nevada, Aug. 20, 1955, GL274, Galloway" (CNC) seem less likely to be correct. For other unusual records, see discussion under *decora, areolata,* and *graminea.*

In all studies, some specimens (usually fe-
males) remain unidentified at the end of the
study. One record of this kind is intriguing.
The label "Cowan, Manitoba, 8 Aug., 1946,
R. H. Beamer" (KU) is affixed to a single
female that we cannot name. See field
notes (later in this appendix) concerning this
record.

COLLECTIONS UTILIZED.—We examined the
Flexamia collections of the United States Na-
tional Museum (USNM), Ohio State Univer-
sity (OSU), University of Kansas (KU), and
the Canadian National Collection (CNC). Our
own collection (Beltsville Agricultural Re-
search Center [BARC]) contains, in addition
to mounted specimens, a large inventory of
unmounted but accessioned (Lynn and Whit-
comb 1987) specimens. The inventories given
in Appendix I are summations of cleared and
uncleared specimens. We feel that the risk of
misdeterminations of uncleared specimens is
very low, with some important caveats. Fe-
males of the *prairiana* and *flexulosa* groups
must be cleared for determination, and males
of the *prairiana* group should be cleared. In
many cases large series were available, in
which case we cleared several specimens and
tentatively identified others by inference. For
these reasons the numbers given probably are
an accurate reflection of the relative abun-
dance of each species. We attempted to curate
the collections examined and to supplement
them, where possible, with additional mate-
rial.

IPL ACCESSIONS.—The BARC collection is
largely computerized (Lynn and Whitcomb
1987); collection records are given in terms of
the accession number in this system. Collec-
tion methods have been described (Whit-
comb et al. 1986, 1987).

ORIGINAL BEAMER FIELD NOTES.—Relevant
excerpts from field notes written by Mrs.
Lucy D. Beamer on:

ritana. "08-18-35. Santa Rita Mts., Ariz. (E.
side) 11:30–5 PM. mild, fair to cloudy . . . Dr.
Ball, RHB (R. H. Beamer) and Jack climbed
the trail up the mountain. Just as they were
abandoning the search RHB took a new spe-
cies of *Gladionura* or *Athysanella* which Dr.
Ball is naming. Worked for a good while, fi-
nally had 30 or 40 of them. Before this only 3
specimens had been taken." There are no ex-
plicit references to *Flexamia*, or to the exact
collecting location. The *Athysanella* species
mentioned was presumably *A. (Gladionura)
furculata.*

beameri. "07-26-46. Otter Lake, New York
(5 miles west). Collected just inside Adiron-
dack Park on Highway 365 at one of the first
little lakes. R. [R. H. Beamer] swept tiny
sedges along the shore—took 80 or so of a tiny
fulgorid he thought was *Bakerella* sp. Later
not so sure." Again, there was no explicit men-
tion of *Flexamia*.

Unidentifiable female. "08-07-37. Cowan,
Manitoba (3 miles north). R. swept in the tall
green grass growing up through the heavy mat
of fallen grass which surrounds a lake for fifty
or a hundred yards in all directions. Found
interesting cicadellid—long wings—proba-
bly belonging to the genus *Polyamia*. Their
wings were ruffed even when he took them."
We have been unable to find other specimens
from this collection in the KU collection.