

Evolutionary Differentiation:
Differentiating Gold-banded Skippers—
Autochton cellus and More
(Lepidoptera: HesperIIDae: Pyrginae)

JOHN M. BURNS

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 405

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ABSTRACT

Burns, John M. Evolutionary Differentiation: Differentiating Gold-banded Skippers—*Autochton cellus* and More (Lepidoptera: Hesperidae: Pyrginae). *Smithsonian Contributions to Zoology*, number 405, 38 pages, 90 figures, 3 tables, 1984.—In the Smithsonian monograph of 1936 on the gold-banded skipper, *Autochton cellus* (Boisduval and Le Conte), Clark wrote, "This butterfly appears to be unusually uniform in its characters . . . throughout its range" and "there are no variations of geographical significance in this butterfly." Actually, there is important geographic variation both in biologic characters (population dispersion, temporal distribution, and larval foodplants) and in morphologic characters (size, facies, and especially male and female genitalia). (Clark was misled particularly by two males from Arizona or northern Mexico erroneously labelled Pennsylvania.) Genitalic differences indicate two major differentiates in *A. cellus* over its wide range from New Jersey southwest to southwestern Colorado and Arizona and thence southeast to El Salvador: one differentiate occurs mostly in hilly country of the southeastern United States (rarely in adjacent coastal plain); the other, in montane parts of the southwestern United States, Mexico, and northern Central America. A large intervening gap is slightly reduced by a very few populations in central and western Texas whose genitalic variation reflects extensive interbreeding between the differentiates in the recent past.

Genitalic differences within *A. cellus* are likely nonadaptive. Because they are "constant" through each widespread and discontinuously distributed differentiate, they probably arose in a small isolate, became fixed, and thereafter were carried wherever the isolate went. The basic differentiation process was probably rapid and random. Overlays of finer geographic differentiation mediated by selection and involving various "external" characters (such as size and temporal distribution) developed more slowly later on. These views mesh with some expressed by "punctrockers," those paleontologists who have shaken phyletic gradualism and evolutionary theory generally with notions of punctuated equilibria and hierarchy.

The mother differentiate within *A. cellus* is the one now ranging from the Southwest through Mexico to Central America and the daughter differentiate, the one now occurring in the eastern United States. Presumably the founding of a miniisolate somewhere off the northeastern frontier of the mother differentiate started the sequence of isolation, basic differentiation, range expansion, secondary contact, compatible hybridization, and, finally, loss of contact in very recent time. This sort of thing has happened before with somewhat different results: the mother differentiate more or less coexists with a superficially similar but genitalically distinct sibling (*A. sierramadror*, new species) in the Sierra Madre Oriental of Mexico.

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Evolutionary Differentiation: Differentiating Gold-banded Skippers— *Autochton cellus* and More (Lepidoptera: Hesperiiidae: Pyrginae)

John M. Burns

Introduction

Anyone with any grasp of evolutionary dynamics who reads the Smithsonian monograph on the gold-banded skipper, *Autochton cellus* (Boisduval and Le Conte), will question certain remarks on variation (Clark, 1936:13, 14):

This butterfly appears to be unusually uniform in its characters, both locally and throughout its range. . . .

So far as we have been able to determine there are no variations of geographical significance in this butterfly. . . .

Some of Clark's assembled wealth of information points in an opposite direction (1936:10–11):

The known range of this butterfly—from New York to Florida, about Kerrville, Tex., and from southern Arizona southward to Guatemala—is curiously discontinuous.

Furthermore, though it is generally common in Mexico and in the mountains of southern Arizona, in the eastern States, though widely distributed, it is very local, occurring at widely separated stations almost exclusively in hilly or mountainous regions where it is found in small numbers—indeed from many localities there is only a single record. It is true that its habits are such as to cause

it easily to be overlooked, yet if it were anywhere really numerous in the eastern States, or if it were generally distributed, this certainly would be reflected in the records.

Most of the specimens in collections are from Arizona or Mexico. No collection contains a long series of eastern specimens, nor more than a very few eastern examples from any one locality.

In other words, here is a widespread skipper that is missing from much of the middle of its range and sharply different with respect to distribution and abundance in the two main (ecologically divergent) regions it does inhabit. This suggests a classic evolutionary pattern involving differentiation on either side of a major distributional gap.

Though Clark did think it biologically significant that *A. cellus* is common and more generally distributed in montane Arizona and Mexico, while it is infrequent and local in the eastern United States, he saw this not as one possible aspect of geographic differentiation but as evidence of recurrent movement from a continuing source area to an unstable derivative range (Clark, 1936:11):

The explanation of the distribution of the gold-banded skipper would seem to be that its true habitat is in Mexico and the mountains of southern Arizona, where it is locally a common permanent resident. In the eastern States it is

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a casual resident of erratic and fortuitous occurrence, maintaining its foothold by virtue of constant new arrivals from the southwest coupled with redistribution from local more or less permanent centers; though constantly present, it cannot properly be regarded as an endemic species in this area.

Many of Clark's observations on eastern populations, and mine on Arizona populations, imply that *A. cellus* is too sedentary to colonize easily or often over great distances. Despite the fact that records more recent than Clark's diminish the gaps in midrange—e.g., Freeman (1951) reported *A. cellus* from Arkansas and west Texas, and Mather and Mather (1958), from Alabama and Mississippi—glaring gaps do exist. Instead of dismissing geographic differentiation, I would look harder for it.

How? First, by probing a few traditional characters. Clark (1936) neither scanned superficial appearance systematically nor examined those most respected of species-specific structures, the genitalia. Granted, male genitalia had already been figured by Godman and Salvin (1894), Skinner and Williams (1922), and Lindsey, Bell, and Williams (1931). But Godman and Salvin's model came from Mexico (or possibly southeastern Arizona); Skinner and Williams's, from southeastern Arizona (Mount Graham); and Lindsey, Bell, and Williams merely reprinted the Skinner and Williams figure. Long after Clark's monograph, Evans (1952) published a caricature of male genitalia. From what I know now about the genitalia of *A. cellus*, I can state categorically that Evans's model also came from Arizona or Mexico. (Odds strongly favored this, anyway: the British Museum material that Evans used contained, by his own count, 67 males from Arizona and Mexico but only seven from the eastern United States.) All along, workers have ignored female genitalia and have assumed that the few males figured represented the species adequately. But, as noted above, those figured males hail from a limited part of the total range; and, as intimated, the genitalia vary geographically (in both sexes). So does a minor feature of facies.

I have demonstrated suspected differentiation in *A. cellus* without resorting to molecular characters. Though the use of isozymes permits much finer analysis of spatial differentiation (see, e.g., Webster and Burns, 1973; Burns, 1975a), it requires large samples of fresh material from diverse localities, which would have prolonged work on these skippers indefinitely. Detailed comparison of genitalia can take long enough. Late in this study, when I thought I was closing the circle, what should have been just another routine genitalia dissection propelled me tangentially toward a sibling species that is superficially and phylogenetically much closer to *A. cellus* than is *A. pseudocellus* (Coolidge and Clemence). It is quasi setbacks like this that keep a researcher going or drive him to distraction.

MATERIAL AND ACKNOWLEDGMENTS

For this project I examined a total of 529 adult specimens: 126 (88 ♂, 38 ♀) from the eastern United States, 21 (10 ♂, 11 ♀) from Texas, 229 (184 ♂, 45 ♀) from the southwestern United States, 136 (107 ♂, 29 ♀) from Mexico, 7 (7 ♂) from Guatemala, and 10 (9 ♂, 1 ♀) from El Salvador. My thanks to the following people and places for lending material: Lee D. Miller and the Allyn Museum of Entomology, Sarasota, Florida (AME); Frederick H. Rindge and the American Museum of Natural History, New York (AMNH); Julian P. Donahue and the Los Angeles County Museum of Natural History, California (LACM); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (where the USNM collections are held); Jerry A. Powell and the Essig Museum of Entomology, University of California, Berkeley (UCB); Charles V. Covell, Jr., and the Department of Biology, University of Louisville, Kentucky; Linda Butler and the Department of Entomology, West Virginia University, Morgantown; Charles T. Bryson; Roy O. Kendall; Robert L. Langston; C. Don MacNeill; Bryant Mather; and

Ray E. Stanford. Thanks, too, to Covell, Richard B. Dominick, Oliver S. Flint, Jr., J. Richard Heitzman, Kendall, MacNeill, Miller, Powell, and Stanford for various information from personal records and observations.

A National Science Foundation graduate fellowship incidentally produced a sample of *A. cellus* in 1958, and NSF grant GB-37832 directly supported extensive study and illustration of this skipper in field and laboratory in 1974–1975. Both times, the Southwestern Research Station of the American Museum of Natural History made an ideal base for field operations, thanks to Mont A. Cazier (earlier) and Vincent D. Roth (later).

Photographs are by A.H. Coleman (Figures 4–17) and Victor E. Krantz (Figures 18, 58–73); drawings, by Robin S. Lefberg (Figures 20–36, 38–55) and George L. Venable (Figures 56, 57, and 74–89). Lefberg also did many of the KOH-dissections of genitalia; her dissection numbers (the X-rated series), as well as mine (JMB), appear in legends of genitalia figures in parentheses. Lee-Ann C. Hayek facilitated statistical calculations. Bernice G. Schubert and Richard S. Cowan determined pressed leguminous foodplants. My wife, Sarah N. Burns, helped collect the skippers, search distributional literature, record data, and proof the manuscript. C. Don MacNeill, Wayne N. Mathis, and W. Donald Duckworth reviewed it critically. Thank you one and all.

Differentiation in *Autochton cellus* (Boisduval and Le Conte)

I concur with the synonymy for *A. cellus* given by dos Passos (1964:26) and find the few synonyms he lists of no real help in conveying geographic differentiation within this species.

SPATIAL DISTRIBUTION

Autochton cellus occurs between roughly 14° and 40°N latitude and 75° and 112°W longitude in a <-shaped distribution whose upper arm is broken (Figure 1). The break—a lack of material from Louisiana, Oklahoma, and most of

Texas—leaves the skipper mainly in two regions: (1) the southeastern United States (except for most of peninsular Florida); and (2) the southwestern United States (i.e., extreme southwestern Colorado, central and southeastern Arizona, southwestern New Mexico, and Trans-Pecos Texas), Mexico, Guatemala, and El Salvador. These large, widely disconnected subranges are themselves highly discontinuous: *A. cellus* is always montane in the southwestern United States, Mexico, and Central America, occurring from elevations of 825 to 2745 m (2700 to 9000 ft)—usually from 1525 to 2440 m (5000 to 8000 ft); and it is partial to low mountain and hill country in the southeastern United States, occurring from near sea level to perhaps 730 m (2400 ft)—usually below 610 m (2000 ft). Predictably, its Mexican distribution looks ragged—see Figure 90, in which total presumptive range is a composite of pine-oak forest, boreal forest, and cloud forest, as mapped by Leopold (1959, fig. 6). Extraordinarily local in the southeastern United States, where it seems to favor damp woods, *A. cellus* is more generally distributed (and more common) within suitable habitat elsewhere.

So far as is known, *A. cellus* has persisted only at Kerrville in the no-man's-land between subranges; and it may now be extinct there. Kerrville lies in the very hilly, much dissected southeastern sector of the Edwards Plateau in central Texas. Kerrville material (which turns out to be crucial to my interpretation of this skipper) was all collected by an English naturalist, H.G. Lacey, probably on his ranch about 12 km (7 mi) southwest of Kerrville, at an elevation of about 550 m (1800 ft). Except for occasional trips to England, Lacey lived there from 1882 to 1919, seriously sampling local lepidopterans from 1898 on and specifically recording captures or sightings of *A. cellus* on 17 April 1899, 13 and 15 April 1900, 1 September 1900, 4 and 16 and 19 April 1901, and 7 April 1902, at which times it was apparently common (Kendall and Kendall, 1971). Because Lacey stopped taking notes on *A. cellus*, because the Kendalls have not found it around Kerrville (or elsewhere on the Edwards Plateau), because this area has been extensively over-



FIGURE 1.—Spatial distribution of *Autochton cellus*. Dots are spots from which I have seen specimens; circles, other known localities.

grazed by sheep and goats that were introduced before the turn of the century (and because the skipper's larval foodplants here must be herbaceous, low-growing, patchily distributed, and acceptable—as well as accessible—to these rumi-

nants), the Kendalls (1971:36) think that *A. cellus* is "probably no longer in the area." I would not yet write it off: the southern Edwards Plateau is laced with rough canyons some of which may continue to harbor this local, secretive species.

Kendall's (1974) statement that it "has not been found in this region since 1902" (based as much on holes in the Lacey notes as on the notes themselves) is incorrect. Clark (1936) gave no year other than 1901 for Kerrville specimens of *A. cellus* (USNM), which supports Kendall. But I have examined Lacey material dated April and August 1907 (LACM), April 1910 (AMNH), and June 1917 (LACM), which indicates that *A. cellus* lasted at Kerrville at least as long as Lacey.

Among American skippers (especially those of the eastern United States) *A. cellus* is so distinctive that I accept many distribution records without insisting on seeing voucher specimens. Nevertheless, I think it advisable to distinguish such records (they are the circles rather than dots in Figure 1) and to give their sources: southwestern New Jersey and northern Delaware (Shapiro, 1966); northeastern Maryland (B. Mather, letter dated 3 October 1975 referring to a specimen from Tolchester, Kent County, 10 August 1936, collected by "Department of Entomology," specimen and record L547 of the Natural History Society of Maryland, noted by Mather on 14 January 1956 [I cite full particulars here because the locality is on the Eastern Shore and Fales (1974), in his regional checklist of Maryland skippers and butterflies, fails to list *A. cellus* for that region]); southwestern Virginia (1979 Season Summary, *News of the Lepidopterists' Society*, No. 2, p. 22, 1980); eastern North Carolina (Brimley, 1938) and southwestern North Carolina (Season's Summary, 1961, *News Lepid. Soc.*, No. 3, p. 10, 1962); western South Carolina (data in the files of R.B. Dominick transcribed by me on 23 August 1975), northcentral South Carolina (1980 Season Summary, *News Lepid. Soc.*, No. 2, p. 24, 1981), and southeastern South Carolina (Gatrelle, 1975); northern, eastern, and southern Georgia (Harris, 1972); northern Florida (1979 Season Summary, *News Lepid. Soc.*, No. 2, p. 22, 1980); central Alabama (Mather and Mather, 1958; B. Mather, letter dated 18 September 1975); Tennessee (Osburn, 1895; Season's Summary, 1960, *News Lepid. Soc.*, No. 4, p. 11, 1961; Season Summary for 1977, *News Lepid. Soc.*, No.

2, p. 9, 1978); southern Ohio—Hocking and Jackson counties (Clark, 1936), Lawrence County (1971 Field Season Summary, *News Lepid. Soc.*, No. 2, p. 17, 1972), and Vinton County (1972 Field Season Summary, *News Lepid. Soc.*, No. 2, p. 11, 1973); central Indiana (Shull and Badger, 1972) and southern Indiana (1980 Season Summary, *News Lepid. Soc.*, No. 2, p. 21, 1981); southern Illinois (Irwin and Downey, 1973); eastern and southern Missouri (Clark, 1936; Remington, 1955; J.R. Heitzman, letter dated 17 September 1975); northern Arkansas (Freeman, 1945; Annual Summary for 1967, *News Lepid. Soc.*, No. 3, p. 16, 1968; J.R. Heitzman, letter dated 17 September 1975); southwestern New Mexico (1972 Field Season Summary, *News Lepid. Soc.*, No. 2, p. 8, 1973; Ferris, 1976); southwestern Durango (C.D. MacNeill, letter dated Halloween 1975); Guerrero (Xucumanatlan and Omilteme) and Puebla (Pinal) (Godman and Salvin, 1894). This compilation of sources is not exhaustive, chiefly because I am not cramming every possible circle into Figure 1.

Nor am I citing published records that often exist for localities from which I have examined material (the dots in Figure 1). With these dots, as with the circles, I am avoiding the sort of saturation plot that obscures information by providing too much.

Although in this paper a list of specimens examined is superfluous, I offer the following (from a fairly worn individual I found among miscellaneous undetermined skippers) because it constitutes a new and disjunct state record:

Colorado, Montezuma County, Stoner, 3 July 1971, 1 ♂, H. Flaschka (AMNH).

Autochthon cellus is not mentioned in *Butterflies of the Rocky Mountain States* (Ferris and Brown, 1981), not even as a species that is presently unknown but likely to surface in time.

In the eastern United States, *A. cellus* occurs primarily in hilly regions (i.e., various uplands and plateaus, from Ozark to Appalachian; mountain valleys; Piedmont; and rolling

coastal plain, as in central Mississippi, southern Georgia, and northern Florida; see Figure 1); but it occasionally turns up in coastal flatlands, as in Dorchester County, South Carolina, Grimesland, North Carolina, and the Delmarva Peninsula. The absence of records for southeastern Virginia, central North Carolina, and northeastern South Carolina (Figure 1) is probably an accident of (very limited) sampling. Of this skipper, Holland (1931:338) said carelessly, "It is common in the Carolinas," which bothered Clark (1936:10) and bothers me.

QUESTIONABLE RECORDS.—The wide range of *A. cellus* would be much wider (and much harder to understand) if all published distribution records were valid.

Late in the last century, *A. cellus* was reported from two adjacent localities in the northeastern United States: the vicinity of Newark, New Jersey (Smith, 1890), and Brooklyn, Long Island (White, 1894). These records, variously repeated and ignored in subsequent literature, have not been verified. In light of the known geographic and ecologic distribution of *A. cellus*, they are not outlandish; but any populations that might have existed probably vanished long ago.

Though neither original report is fully satisfactory, Smith's seems the more reliable. It stemmed from lists of local captures furnished to him for a catalog of New Jersey insects by a number of Newark collectors who had formed an entomological society, which met regularly. Besides *A. cellus*, the 18 pyrgines in the pooled New Jersey list (Smith, 1890) included what we now call *Epargyreus clarus* (Cramer) and *Achalarus lyciades* (Geyer), the only eastern North American skippers that could possibly be confused with *Autochton cellus*. (*Achalarus lyciades* is more like *Autochton cellus* than is *E. clarus*, but neither resembles *A. cellus* closely. *Achalarus lyciades* is much more common than *Autochton cellus* but less abundant than *E. clarus*.) It is significant that Smith credited all three species to the Newark area and specified that *A. cellus* was "taken rarely by the Newark

collectors." Of course, at that time, the illustrated syntheses and books that so facilitate identification were lacking. But, if the Newark collectors were communicating among themselves effectively, they all should have been able to separate and correctly name these three pyrgines with ease. Yet the possibility remains that one or more of them could not and listed *A. cellus* by mistake. In later reports, Smith (1900, 1910) merely reiterated what he had said in 1890 and added an erroneous foodplant record gleaned from early literature. White's (1894) list of the Lepidoptera taken by him in Prospect Park, Brooklyn, in 1893 contained only six skippers, only three of which were pyrgines. Because these included *A. cellus* and *E. clarus* but not *Achalarus lyciades*, the possibility of confusion seems greater.

There are a few reports of *A. cellus* from Pennsylvania; and this skipper does occur in at least the southeastern part of that state; but, of the three specimens labelled Pennsylvania that I have seen, two actually come from Arizona or Mexico. Among localities for *A. cellus*, Lindsey (1921)—followed by Lindsey, Bell, and Williams (1931)—listed "Pennsylvania, July," whereas Clark (1936:7) specified "Pennsylvania: . . . Lititz, near Lancaster, June 25, July 14, 16, 1892; J. J. Heiserman (3, U.S.N.M.)." These (male) specimens, which I have given genitalia dissection numbers X-46, X-47, and X-48, bear older labels as shown below. (Roman type denotes machine-printed data; italic type, data handwritten in ink. Ink is red on the "Barnes/Collection" label and black on all others. Bracketed numbers indicate separate labels.)

Specimen	Label
Male X-46: [1]	Lititz
	<i>VII.14. Pa.</i>
	[2] Col. J. J. Heiserman Lititz, Pa.
	[3] Barnes Collection
Male X-47: [1]	Lititz
	<i>VII.16 Pa.</i>
	[2] Col. J. J. Heiserman

- [3] Barnes
Collection
Male X-48: [1] *Lititz Pa.,*
Jun. 25, 1892
J.J. Heiserman

The two distinct patterns of labelling indicate that the history of males X-46 and X-47 differs from that of male X-48. Clark's citation of these label data distorts them a bit: year of capture really appears only on male X-48; and even though Heiserman's name is on all three specimens, he does not appear to be the collector of males X-46 and X-47. Clark's added information "near Lancaster" is correct: Lititz is 13 km (8 mi) due north of that city. Lindsey undoubtedly got "Pennsylvania, July" from males X-46 and X-47 when they still belonged to Barnes; for Lindsey (1921:3) acknowledged that Barnes "very generously allowed me the freedom of his fine collection and library, and also supplied me with many specimens for study." After the Barnes collection passed into the USNM collections in 1931, these two males misled Clark far more seriously. In the midst of his short section on "Variation" in *A. cellus*—which begins, "This butterfly appears to be unusually uniform in its characters, both locally and throughout its range," and ends, "So far as we have been able to determine there are no variations of geographical significance in this butterfly . . ."—Clark (1936:13) makes a point of the fact that specimens "from Pennsylvania (pl. 3, figs. 13, 14) are as large as those from Arizona (pl. 3, figs. 11, 12), with which they agree in their ground color as well as in all other details." His figures 13 and 14 are black-and-white photographs of the upper and under sides of male X-47. I know that both this male and male X-46 come from Arizona (or possibly New Mexico or northern Mexico) because they are (1) large, (2) extensively yellow at the apex and along the costa of the hindwing dorsally, and (3) blessed with genitalia that clearly differ (in valval and uncus morphology) from any occurring in the eastern United States (see sections on Size, Facies, and Male Genitalia below). Because the handwrit-

ten dates on these males (14 and 16 July) could be correct, it is worth adding that the middle of July coincides, on the one hand, with the peak of the single flight period in Arizona and, on the other, with the gap between spring and summer flight periods in the Middle Atlantic States (see section on Temporal Distribution and Figure 2). Clark did perceive some variation in size and color in *A. cellus*, but—thanks especially to two Arizona specimens mislabelled Pennsylvania—he saw no geographic pattern to such variation and pronounced it individual and therefore trivial.

Male X-48, which Clark apparently dismissed, is in all respects (size, facies, genitalia) typical of males from the Middle Atlantic States. Its date of capture (25 June) puts it within the spring flight period for that region (see Figure 2). And its label looks proper in every way. The only thing against it is a sort of "guilt by association" with the two grossly mislabelled Arizona males in the USNM collections. In its favor are three published Pennsylvania records attributed to Heiserman (sic) and drawn from Lancaster County (where Lititz is): locality unspecified, June; Mt. Hope, June; and Hopeland, July. Unfortunately, these corroborative data come from Tietz (1952), an uncritical compilation that is riddled with errors. Tietz also offers a record, attributed to Haimbach, from Perkaspie, June (in Bucks County about 40 km [25 mi] NNW of Philadelphia). Williams (1941) includes *A. cellus* in his "list of butterflies which may be found within 50 miles of Philadelphia" but marks it "rare or doubtful." Shapiro (1966), calling *A. cellus* a "questionable Pennsylvania resident," repeats the Perkaspie record and adds "doubtful." There are recent Pennsylvania records, however: Ehle took seven examples of *A. cellus* at blackberry blossoms along a wooded road in Lancaster County on 12–14 June 1979 (1979 Season Summary, *News Lepid. Soc.*, No. 2, p. 24, 1980).

In a four-line note, Girault (1900) claimed to have found *Achalaorus* (sic) *cellus* "abundant" in Anne Arundel County, Maryland

(which is south of Baltimore and east of Washington, D.C.). Clark (1936:9) expressed "a certain amount of doubt" about this record because it placed the skipper beyond its usual habitat range. Although we now realize, mainly from sound records from the Delmarva Peninsula and the Carolina coastal plain (see above), that *Autochton cellus* could occur in Anne Arundel County, I continue to doubt Girault's identification because his skipper was "abundant." Fales (1974) uncritically saved this record from the oblivion it deserves.

Grossbeck (1917) reported *A. cellus* from opposite ends of Florida. The northern record, Tallahassee, 17 April, C.J. Maynard (first published by Scudder [1889:1856]), has been confirmed in modern times. The southern one, Biscayne Bay (i.e., the Miami region), A.T. Slosson, has not. Clark (1936:9) questioned this record along with that for Anne Arundel County, Maryland, and for the same reason. Kimball (1965) repeated it without reservations, even though the linearly and ecologically large gap between Tallahassee and Miami had not been narrowed significantly: Kimball's nearest record to Miami—and the southmost locality from which I have seen material in the eastern United States—is Gainesville, which is still northern Florida. To me, *A. cellus* in southern Florida is biologically unreasonable.

Clark (1936:9) dispatched a phony California example of *A. cellus* before it saw the black of print:

Capt. N. D. Riley wrote us that there is in the British Museum a specimen from Lord Walsingham's collection labeled "California." Lord Walsingham himself collected only in northern California, mainly in Colusa, Shasta, and Siskiyou Counties in July and August, 1871. He was always exceedingly careful regarding the labeling of his material. The specimen was presumably acquired by purchase or otherwise, and was mislabeled before coming into his possession. Dr. John A. Comstock . . . writes us that this species does not occur in California, and Commander Charles M. Dammers . . . is equally positive on this point.

This effort notwithstanding, Evans (1952:121) blithely included "1 ♂ California"

in his list of *A. cellus* material in the British Museum, without questioning the label's precision. Emmel and Emmel (1973:95) picked up this record and challenged it:

Evans (1965) [sic] lists California as a locality for this species in his catalogue. Since we have seen no specimens from the state, the specimen on which he based this was probably mislabeled.

The merry-go-round goes round.

Evans (1952:121) put the last two localities in his list of British Museum *A. cellus* material in quotation marks, which was his way of questioning their validity: "1 ♂ 'Venezuela'. 1 ♂ 'Cuba'." I would have let these far-out sleeping records die. But Riley (1975) resurrected the Cuban male with a flourish—a life-size color painting (plate 22, figure 3) and full text treatment (pages 166–167) in *A Field Guide to the Butterflies of the West Indies*. Riley is too indulgent when he writes (page 167), "The only specimen known from Cuba, the male figured on Plate 22, may be no more than a vagrant from the mainland. Confirmation of its occurrence is needed before it can be accepted as an indigenous species," and, again, in a distribution table (page 205), when he grants *A. cellus* "visitor" rather than "very doubtful" status. What on earth would even a transient *A. cellus* be doing in Holguín?

TEMPORAL DISTRIBUTION

Autochton cellus appears to be univoltine in the southwestern United States and adjacent northwestern Mexico but multivoltine elsewhere (Figure 2). The widespread multivoltine condition is probably primitive and the univoltine condition, derived—in this case, in response to a Recent drying trend in the Southwest where precipitation has usually become limited to winter and summer, and vigorous growth of the skipper's larval foodplants has, in turn, become linked with the summer rains.

Except for southeastern Arizona, dated specimens examined are too few to yield temporal histograms approximating normal curves (Figure

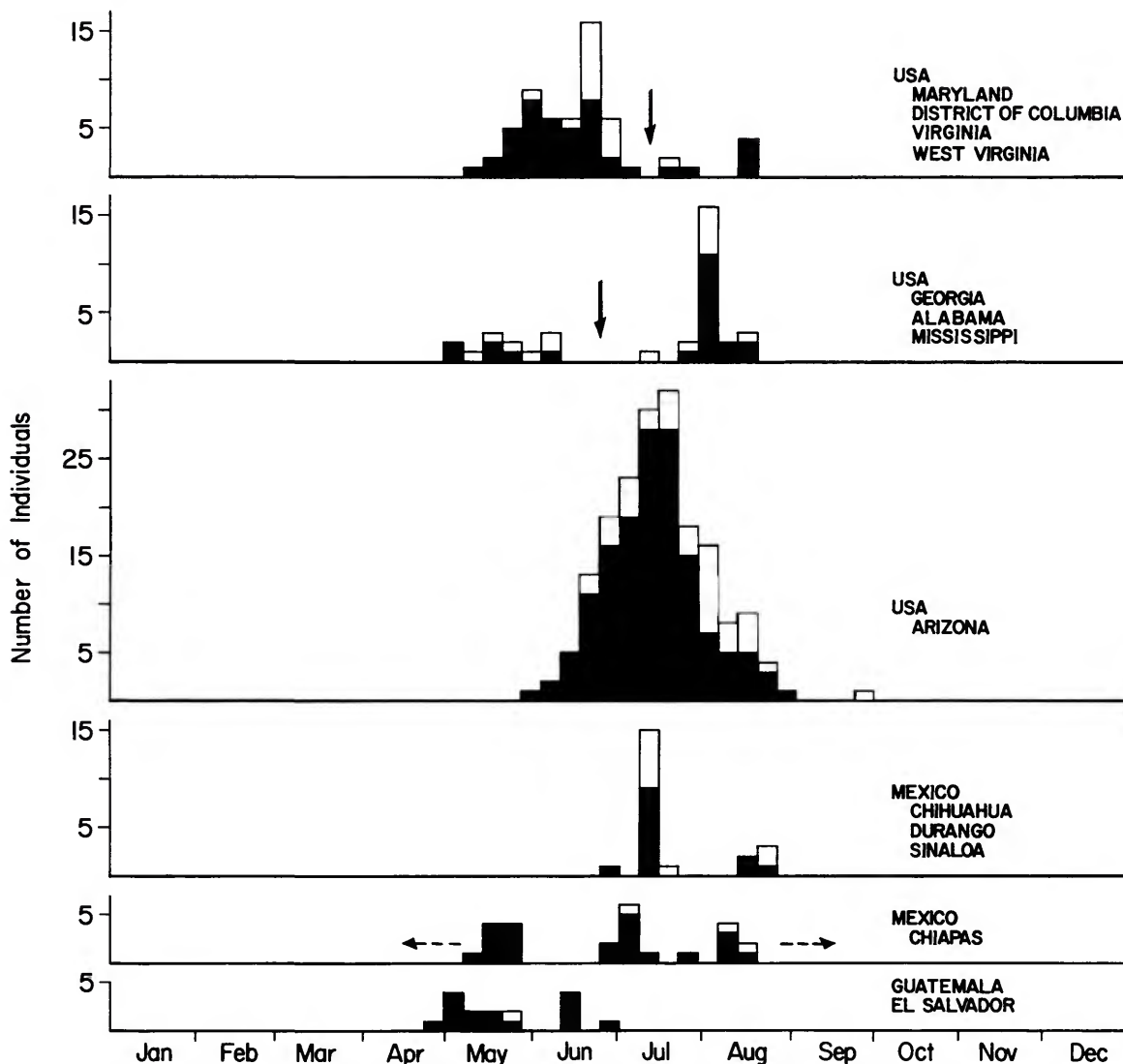


FIGURE 2.—Temporal distribution of wild-caught adults of *Autochton cellus* (based on material examined). Bars for males are black; bars for females (stacked on males) are white; solid arrows show known intergenerational gaps; dashed arrows indicate unspecified collection dates in April and September (see text); the temporal class interval is one week.

2); but the deficient data do indicate general flight patterns. Throughout its range in the eastern United States, *A. cellus* is bivoltine, flying first in May/June and then again in July/August. All of the eastern dates at hand (including those

not used in Figure 2) point to this pattern; and J.R. Heitzman (letter dated 17 September 1975) notes that, in Missouri and Arkansas, *A. cellus* "has two distinct broods from mid-May to mid-June and late July through August." The only

deviants worth mentioning appear earlier (in mid- and late April); as expected, they come from the southern edge of the range (extreme southern Georgia [Harris, 1972] and northern Florida), save one from Menifee County, Kentucky, taken 24 April 1976 in what was an unusually early spring (C.V. Covell, Jr., letter dated 6 May 1976).

In Texas, *A. cellus* is multivoltine; and there, as in southern Georgia and northern Florida, it is far enough south that the first generation starts to emerge in April (at least at Kerrville and in the Chisos Mountains). Lindsey, Bell, and Williams (1931) wrote, "Texas and Arizona, April, July to September"; April is correct for Texas but not for Arizona, where the single flight period centers around July (Figure 2).

Fragmentary data show that *A. cellus* must be multivoltine in most of Mexico. Fully dated specimens from the extreme south (Chiapas) reflect an extensive flight season (Figure 2) which is actually even longer, as evidenced by partially dated (therefore unplotable) Chiapas material from April 1962, April 1975, September 1962, and September 1976. More than two generations are likely involved. Though dates are similarly incomplete on all but two of the specimens I have examined from the state of México and the Distrito Federal in central Mexico, every month from May through October occurs, which indicates a long flight season comparable to that in Chiapas. Dates on the three specimens I have seen from Nuevo León in northeastern Mexico (21 June 1940, 17 September 1976, and 24 September 1975) indicate at least two broods. Only the modest material from Chihuahua, Durango, and Sinaloa in northwestern Mexico, all of which is fully dated, gives a temporal pattern (Figure 2) that could agree with the unimodal distribution from southeastern Arizona (though the possibility of error due to limited sampling cannot be ruled out).

That the flight season of *A. cellus* looks so much shorter in Guatemala and El Salvador (Figure 2) than it does in central and southern Mexico may be nothing more than an artifact of

limited collecting in relatively remote areas: one collector took all the plotted Guatemala specimens at one locality, from late May to late June, in a single year; and a pair of collectors took all the plotted El Salvador specimens at one locality, from late April to latter May, in two consecutive years.

Females of *A. cellus* emerge later than males (Figure 2).

SIZE

METHODS.—Using a vernier caliper that reads to tenths of millimeters and purposely changing its reading after every measurement, I took the winglength of each specimen on each of two different days and averaged nonidentical results before calculating the statistics in Table 1. Most dual measurements differed, if at all, by only 0.1 or 0.2 mm; none differed by more than 0.4 mm.

RESULTS.—Males of *A. cellus* average smaller than females and greatly outnumber them in collections (Table 1). (The same may be said of many other pyrgines—see, for example, data on *Erynnis* and *Celotes* in Burns, 1964, 1974.) The male really is the smaller sex. But the sex ratio in nature is probably even and the preponderance of males in samples, artificial: males do several things—most notably, patrol limited areas in connection with meeting mates—that make them more conspicuous to collectors and easier to catch.

There is a large measure of geographic variation in size (Table 1): *A. cellus* is smallest in the eastern United States (where male forewing length averages about 21 mm), medium-sized in Texas (male forewing nearly 22 mm) and central Mexico (22–22½ mm), large in Chihuahua and Arizona (23 mm), and progressively larger still in southern Mexico and northern Central America (Chiapas, 24 mm; Guatemala, 25¾ mm; El Salvador, about 26 mm). In other words, mean size decreases to the northeast, increases to the northwest, and increases strikingly to the southeast of a region extending from central Texas to central Mexico. Modest local deviations do not

TABLE 1.—Length (mm) of right forewing of *Autochton cellus*.

Sample	Sex	N	Range	Mean with standard error	Standard deviation	Coefficient of variation
Washington, D.C., and vicinity	♂	18	19.4–23.0	21.49±0.18	0.78	3.64
	♀	9	20.2–24.3	23.06±0.42	1.26	5.47
Alabama: DeKalb County	♂	10	19.6–21.9	20.81±0.21	0.66	3.16
	♀	5	21.4–22.6	22.18±0.25	0.55	2.48
Mississippi: Hinds County	♂	5	19.6–21.2	20.46±0.29	0.65	3.16
	♀	5	21.7–23.6	22.66±0.34	0.76	3.35
Texas: Kerr County	♂	5	21.0–23.1	21.86±0.37	0.82	3.74
	♀	8	20.1–23.8	22.09±0.39	1.10	4.96
Arizona: Chiricahua Mountains	♂	29	20.3–24.9	22.62±0.18	0.96	4.24
	♀	5	22.5–24.0	23.30±0.29	0.64	2.75
Arizona: Huachuca Mountains	♂	24	21.7–25.4	23.90±0.19	0.93	3.88
	♀	1	24.6			
Arizona: Santa Rita Mountains	♂	20	21.2–25.6	23.10±0.25	1.10	4.78
	♀	5	22.6–25.1	23.72±0.48	1.06	4.48
Chihuahua: Hidalgo del Parral	♂	9	21.4–24.8	23.13±0.38	1.13	4.87
	♀	5	24.2–26.2	25.20±0.35	0.79	3.14
Michoacán	♂	16	20.2–23.2	22.08±0.22	0.89	4.04
	♀	1	23.6			
D.F., México, Morelos	♂	17	21.0–24.6	22.72±0.26	1.08	4.74
	♀	6	21.6–25.0	23.15±0.49	1.20	5.18
Veracruz	♂	12	21.6–23.4	22.54±0.19	0.64	2.86
	♀	3	22.2–23.8	23.13		
Chiapas	♂	19	23.0–25.7	24.32±0.18	0.76	3.14
	♀	4	24.0–27.5	25.50±0.89	1.78	6.98
Guatemala	♂	7	24.8–26.4	25.71±0.19	0.52	2.00
El Salvador: Cerro Miramundo	♂	9	24.6–26.7	25.92±0.24	0.73	2.83
	♀	1	27.8			

mask these general trends.

Bits of literature jibe with Table 1. Evans (1952:121) gave male forewing length as 24 mm, which is not surprising because most of the specimens he studied came from regions where the skipper runs large (by his count, the British Museum had 39 ♂ 11 ♀ from Arizona and 28 ♂ 14 ♀ from Mexico but only 7 ♂ [no ♀] from the eastern United States). Clark (1936:18) mentioned that *A. cellus* is very perceptibly smaller in West Virginia than in Arizona. Holland (1931:338) observed that "Mexican specimens are larger" (than, I presume, those from the eastern United States).

CAUTIONS.—The measured samples are unavoidably heterogeneous. Some represent points in space and time; others, points in space only;

still others encompass—unevenly—appreciable to large areas and span—irregularly—appreciable to long periods of time. Which samples are truly comparable? They vary undesirably in size (from 1 to 29) and are rarely as big as they should be.

Pooled samples may be biased in subtle ways that can seldom be detected. For example, forewings appear shorter in the Chiricahua Mountains of Arizona than in neighboring ranges (Table 1); but this may stem in part from the fact that adults that grew up in a year of record drought (1973–1974)—when larval food was likely scarce—dominate the Chiricahua sample: these (starved and stunted?) specimens average smaller than the others. The Chiricahua sample of 29 males comprises three from July 1908, 10

from June 1958, and 16 from July 1974. I am aware of a threat of bias here simply because my wife and I collected the 1958 and 1974 specimens ourselves and saw how drastically conditions differed in the same area between the two years. (Because I spread all but the three specimens from 1908, another possible source of within-sample heterogeneity is essentially circumvented.)

One potential source of irrelevant size variation deserves special comment. Owing to a dearth of dated, measurable specimens (i.e., spread specimens with intact right forewing tips) from the multivoltine populations of the eastern United States, and an inability to assign many Mexican specimens for certain to the first as opposed to a subsequent generation, I could not rigorously analyze (and segregate) possible temporal variation in size as I did in *Erynnis*. There

I showed that, in any given area, first generation ("spring") individuals of a multivoltine species average significantly smaller than second and third generation ("summer") individuals of that same species (Burns, 1964). Such a pattern of smaller spring and larger summer individuals is common among cold-blooded, short-lived, multivoltine animals in temperate climates.

However, if environmental variation of this kind occurs in *A. cellus*, it does not distort the picture of strong geographic size variation in Table 1 to any important degree. Both where the skipper is largest (Chiapas, Guatemala, El Salvador) and where it is smallest (eastern United States), it is apparently multivoltine. All measured individuals in the Washington, D.C., sample are strictly first generation; and those in the El Salvador sample (dating from April and May) and in the Guatemala sample (dating from May

TABLE 2.—Temporal composition (by month) of samples of *Autochton cellus* measured for Table 1.

Sample	Sex	N	Apr	May	Jun	Jul	Aug	Sep	Oct	No date
Washington, D.C., and vicinity	♂	18		1	17					
	♀	9			9					
Alabama: DeKalb County	♂	10					10			
	♀	5					5			
Mississippi: Hinds County	♂	5		1	1	1	2			
	♀	5		2	1	1	1			
Texas: Kerr County	♂	5			1		1			3
	♀	8	3	1						4
Arizona: Chiricahua Mountains	♂	29			10	19				
	♀	5			2	3				
Arizona: Huachuca Mountains	♂	24			1	6	5			12
	♀	1				1				
Arizona: Santa Rita Mountains	♂	20				20				
	♀	5				3	2			
Chihuahua: Hidalgo del Parral	♂	9				9				
	♀	5				5				
Michoacán	♂	16				5	11			
	♀	1					1			
D.F., México, Morelos	♂	17		1	3	6	5	2		
	♀	6				3	1		1	1
Veracruz	♂	12			1	7				4
	♀	3				3				
Chiapas	♂	19		5	1	8	4	1		
	♀	4	1			1	2			
Guatemala	♂	7		1	6					
El Salvador: Cerro Miramundo	♂	9	4	5						
	♀	1		1						

and June) are presumably also first generation. Since these samples are temporally comparable, one can assume that their widely divergent winglengths primarily reflect genetic differences. Even though the Chiapas sample is temporally mixed, it is clearly intermediate between both mixed and unmixed central Mexican and unmixed Central American samples with respect to winglength (as well as geography). Within the eastern United States, all measured individuals in the Washington sample are first generation, as noted; but all those in the DeKalb County, Alabama, sample are strictly second generation. Yet these temporally displaced samples are similar in winglength (Alabama means are actually smaller than Washington means), and both are also similar to a mixed Hinds County, Mississippi, sample comprising as many first as second generation individuals. (I deliberately excluded from consideration one abnormally small specimen—a first generation male from the vicinity of Washington with a winglength of 16.8 mm—because of the excessive and meaningless contribution it would make to the sample variance. Underfed lepidopteran larvae succeed on occasion in metamorphosing into dwarves; larvae with plenty of food do not correspondingly overeat and produce giants.) The four samples from southeastern Arizona and northern Mexico all come from univoltine populations flying at about the same time. (See Table 2 for a complete breakdown on the dates of measured specimens.)

FACIES

Individuals of *A. cellus* from the eastern United States and Texas have little (or rarely no) yellow at the apex and along the costa of the hindwing dorsally: what yellow there is clings narrowly to the wing edge. By contrast, individuals from Arizona and New Mexico, Mexico, Guatemala, and El Salvador are almost always conspicuously yellow at the apex and along the costa of the dorsal hindwing: yellow invades the wing appreciably (see Figures 3–18). Among all specimens examined, the only noteworthy exceptions are ten from central Mexico (chiefly Michoacán) that

are nearly as narrowly yellow as specimens from the eastern United States and Texas. Even in central Mexico, however, most specimens show extensive yellow.

MALE GENITALIA

The male genitalia of *A. cellus* (Figures 19–36, 85–89) more or less resemble those of various other species not just of *Autochton* but also of such related genera as *Achalarus*, *Thorybes*, *Urbanus*, and *Astrartes*: the uncus divides into a pair of long, posteriorly-directed prongs while the underlying gnathos remains undivided (looking, in *A. cellus*, like a scoop). Evans (1952) repeatedly mentioned this genitalic conservatism among the genera comprising the tail end of his C or *Urbanus* Group of pyrgines. Although the valvae of these skippers vary more than the uncus and gnathos, certain shapes tend to recur. Against this general background of genitalic restraint, the degree of geographic variation in the genitalia of *A. cellus* seems the more remarkable.

Figure 20 shows male genitalia of the kind that has always been figured for *A. cellus* in the past (see Introduction). The juxta, which has not been shown before, looks very like a brassiere—especially in isolation (Figure 21). Because it has the flexibility of a brassiere, its cups assume various curves, largely as a function of the relative positions of the paired valvae, to which the juxta is laterally attached (Figures 32–36, 87). Variation is not geographic. Geographic variation involves the uncus, the valvae themselves, and the cornutus within the aedeagus.

The paired uncus prongs are either together (Figure 22) or slightly apart (Figure 23) in the eastern United States but well separated and usually divergent (Figures 20, 25, 26, and 85) in the Southwest (Arizona, New Mexico, and Colorado), Mexico, and Central America. Texas specimens show at least some space between the uncus prongs but are notably variable—particularly at Kerrville, where they run a gamut from what occurs in the eastern United States, through peculiarly intermediate individuals (Figure 24), to what occurs in the Southwest and Mexico. In

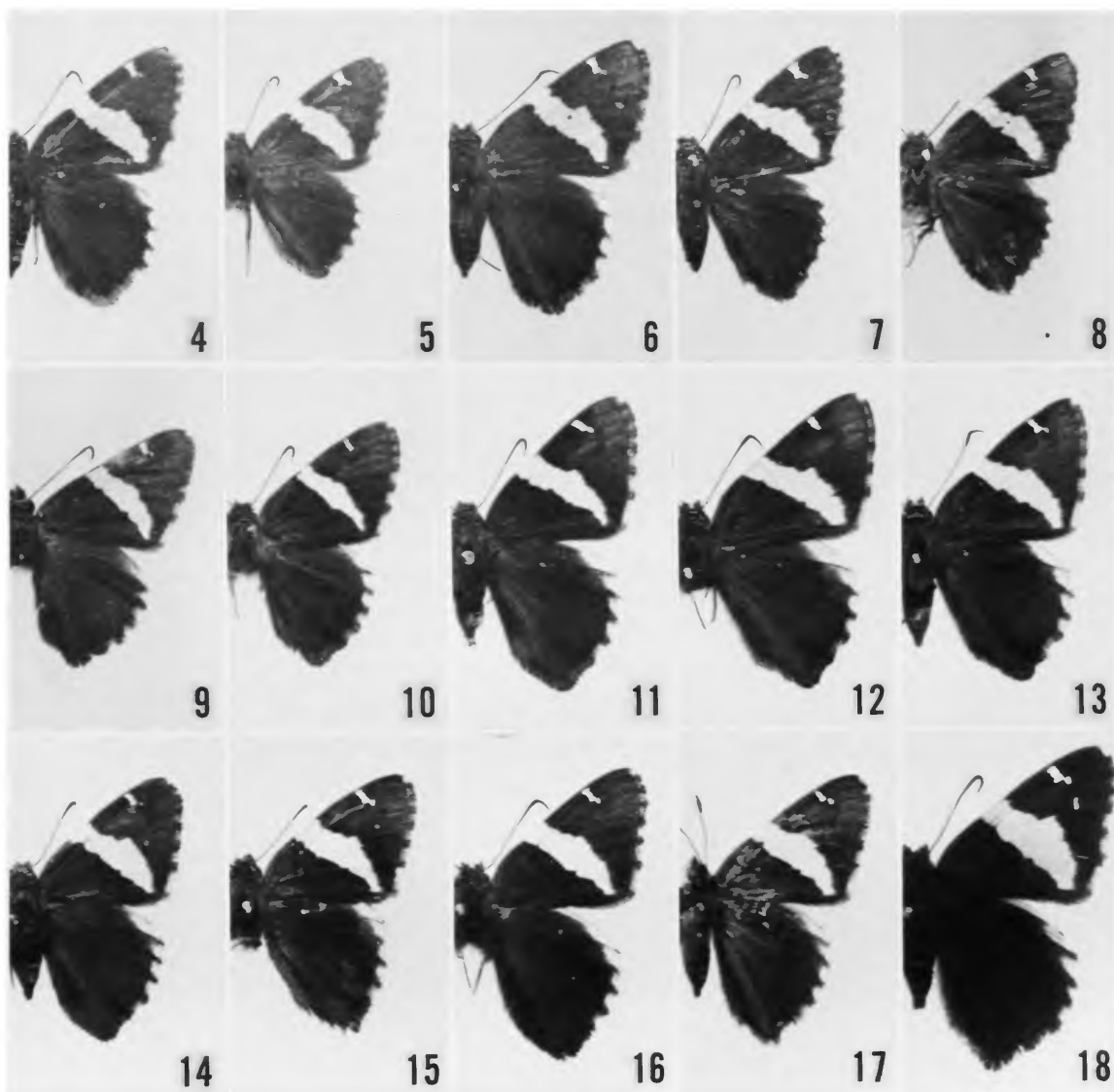


FIGURE 3.—Sources of the *Autochthon cellus* males in Figures 4–18.

the East, uncus prongs are together in one-quarter to one-third of the males and variably (but never widely) parted in the others; variation looks individual, not geographic. Again, in the Southwest and most of Mexico, where uncus prongs are far apart, they are parallel rather than divergent in scattered individuals. In Central

America, where uncus prongs are widely divergent, they are more robust (Figure 26) than elsewhere.

The valvae are low (Figures 27, 28) in the eastern United States but high (Figures 20, 30, 31, and 88) in the Southwest, Mexico, and Central America. In the high valva, the two dorsal



FIGURES 4–18.—Right wings of males of *Autochton cellus* in dorsal view: 4, Widewater, Maryland, 3 Jun 1934, A.H. Clark (USNM); 5, Charleston, West Virginia, 22 May 1900 (USNM); 6, Montgomery Co., Virginia, 31 May 1900, E.A. Smyth (USNM); 7, Canyon Land Park, DeKalb Co., Alabama, 4 Aug 1973, C. Bryson; 8, Jackson, Hinds Co., Mississippi, 25 Jul 1959, B. and K. Mather; 9, Kerrville, Texas, Aug 1907, H. Lacey (LACM); 10, Green Gulch, Big Bend National Park, Brewster Co., Texas, ex larva 15 Apr 1968, R.O. and C.A. Kendall; 11, South Fork Cave Creek, 1620 m (5300 ft), Chiricahua Mountains, Cochise Co., Arizona, 26 Jul 1974, J.M. and S.N. Burns (USNM); 12, Miller Canyon, 1830 m (6000 ft), Huachuca Mountains, Cochise Co., Arizona, 3 Jul 1958, J.M. and S.N. Burns (USNM); 13, Madera Canyon, 1830 m (6000 ft), Santa Rita Mountains, Santa Cruz Co., Arizona, 1 Jul 1958, J.M. and S.N. Burns (USNM); 14, 40 km (25 mi) W Hidalgo del Parral, 2075 m (6800 ft), Chihuahua, Mexico, 15 Jul 1964, J. Powell (UCB); 15, Zacualpan, Mexico, Aug 1915 (AMNH); 16, 19 km (12 mi) NW Ciudad Mendoza, Veracruz, Mexico, 11 Jul 1974, J. Powell (UCB); 17, Oaxaca, Mexico, no date (USNM); 18, Hda. Montecristo, 2300 m (7550 ft), Cerro Miramundo, Metapán, El Salvador, 30 Apr 1972, S. and L. Steinhauser (AME).



FIGURE 19.—Sources of the *Autochton cellus* male genitalia in Figures 20–36 and 85–89.

projections are usually so elevated and the ventral caudally pointing projection so narrowed that most of the posterior edge of the valva looks nearly vertical in lateral view. Again, in lateral view, the two dorsal projections tend to be slanted caudally in the low valva (Figures 27, 28) but upright in the high valva (Figures 20, 30, and 31). The valvae of Texas specimens are

intermediate between low and high (Figure 29) or, more often, essentially high; but the dorsal projections are as often slanted caudally as they are upright. In specimens from Nuevo León, Mexico, immediately to the south, dorsal projections still slant caudally although the valvae are quite high (Figure 88).

Throughout the range of *A. cellus*, the valvae

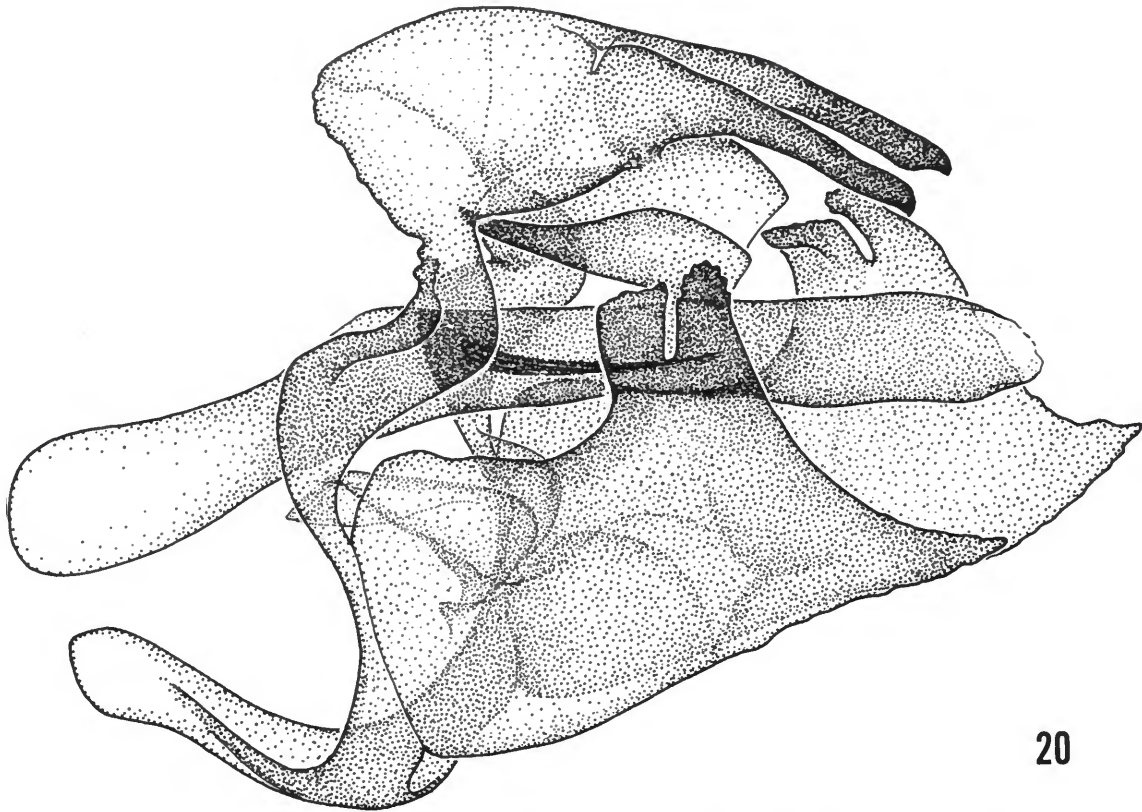


FIGURE 20.—Complete male genitalia of *Autochton cellus* in left posterolateral view. Specimen from 19 km (12 mi) NW Ciudad Mendoza, Veracruz, Mexico, 11 Jul 1974, J. Powell (JMB 1348) (UCB).

are mildly asymmetric. The midsection of the valva, which is lower than either end, is a little higher in the left valva than it is in the right valva (see Figures 20, 27–31, and 88—or, if you cannot see the difference, measure them). The ventrocaudal end of the left valva is generally longer and, in lateral view, often narrower than the ventrocaudal end of the right valva (Figures 20, 27–36, 87, and 88).

The cornutus comprises a bundle of spines of differing lengths all basally united. In the eastern United States, at least the longest spine—and often the second and sometimes the third longest—swells appreciably at the tip (Figures 32, 33); but in the Southwest, Mexico (excluding Nuevo León), and Central America, all spines taper to points (Figures 35, 36). (Since living

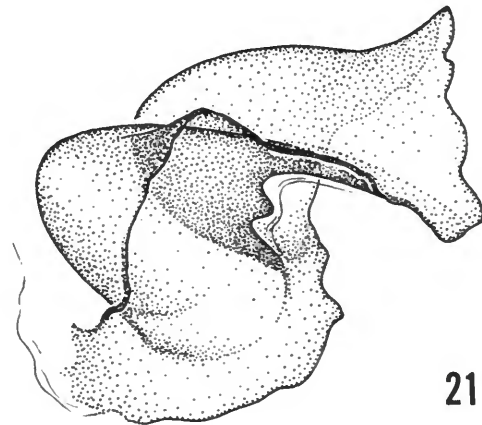
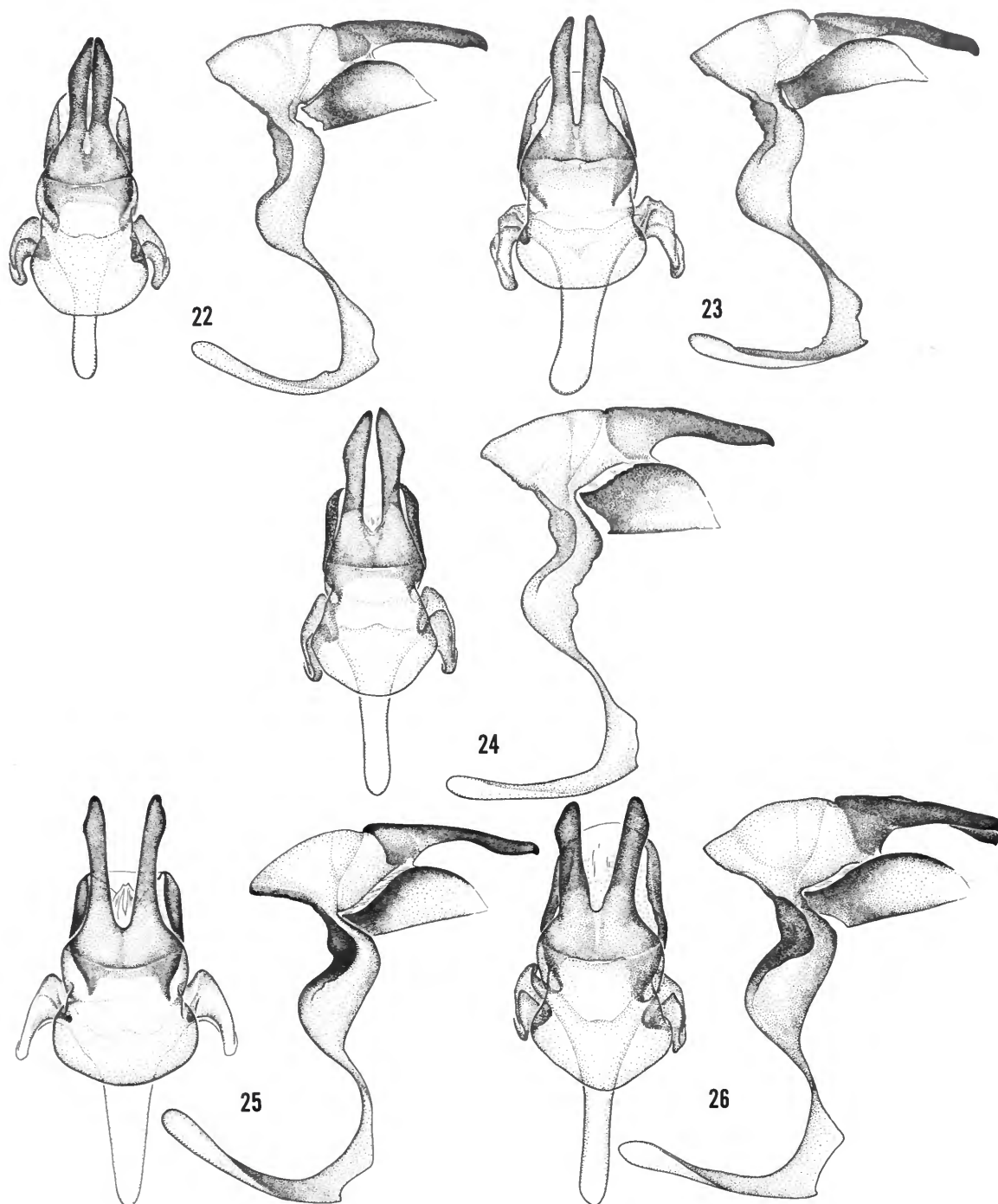
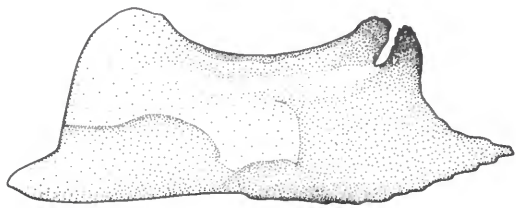


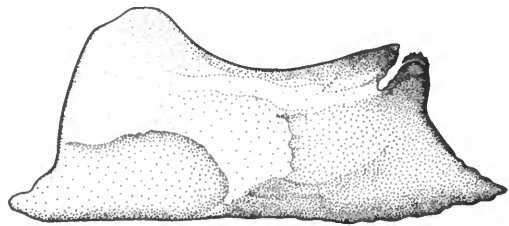
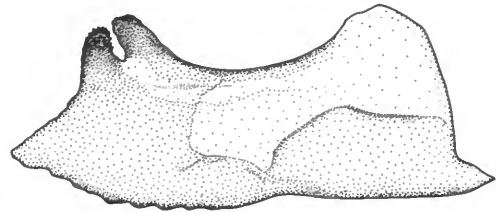
FIGURE 21.—Juxta of *Autochton cellus* in right anterodorsolateral view. Specimen from Canyon Land Park, DeKalb Co., Alabama, 4 Aug 1973, C. Bryson (JMB 1362).



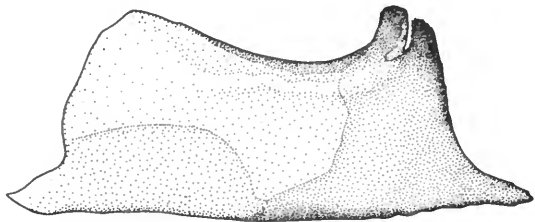
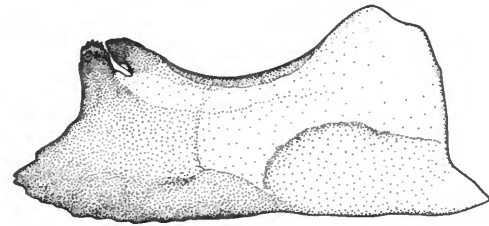
FIGURES 22–26.—Geographic variation in male genitalia of *Autochthon cellus* (uncus, tegumen, gnathos, vinculum, and saccus in dorsal and left lateral views): 22, Widewater, Maryland, 3 Jun 1934, A.H. Clark (X-52) (USNM); 23, Canyon Land Park, DeKalb Co., Alabama, 4 Aug 1973, C. Bryson (JMB 1362); 24, Kerrville, Texas, Jun 1917 (X-5) (LACM); 25, South Fork Cave Creek, 1620 m (5300 ft), Chiricahua Mountains, Cochise Co., Arizona, 16 Jun 1958, J.M. and S.N. Burns (JMB 1335) (USNM); 26, Volcán Santa María, Guatemala, Jun (X-58) (USNM); see Figures 20 and 85–89 for males from Mexico.



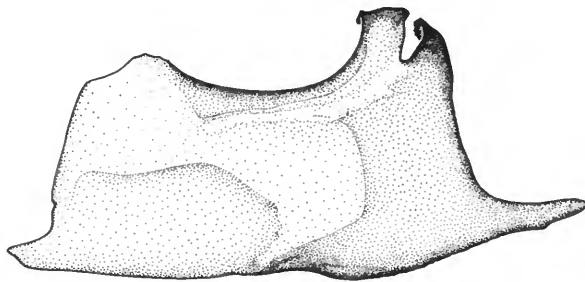
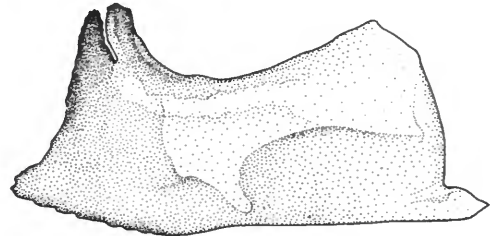
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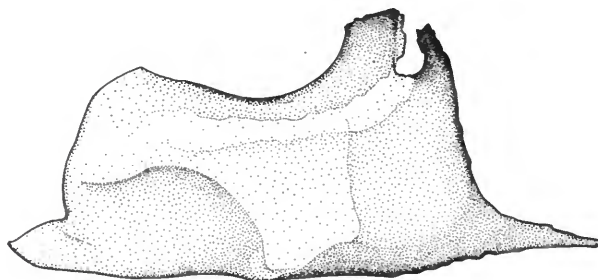
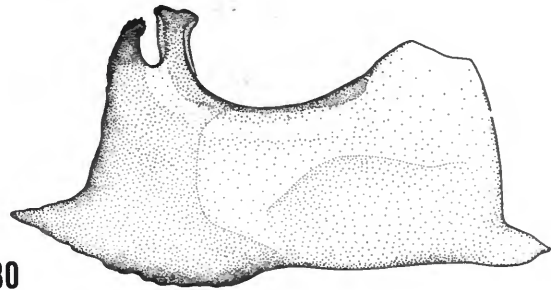
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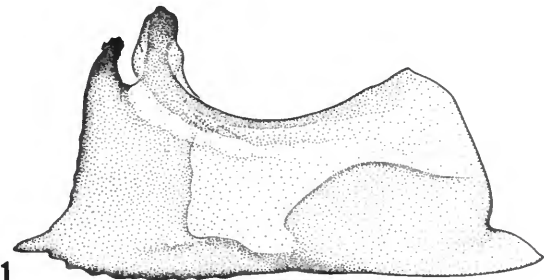
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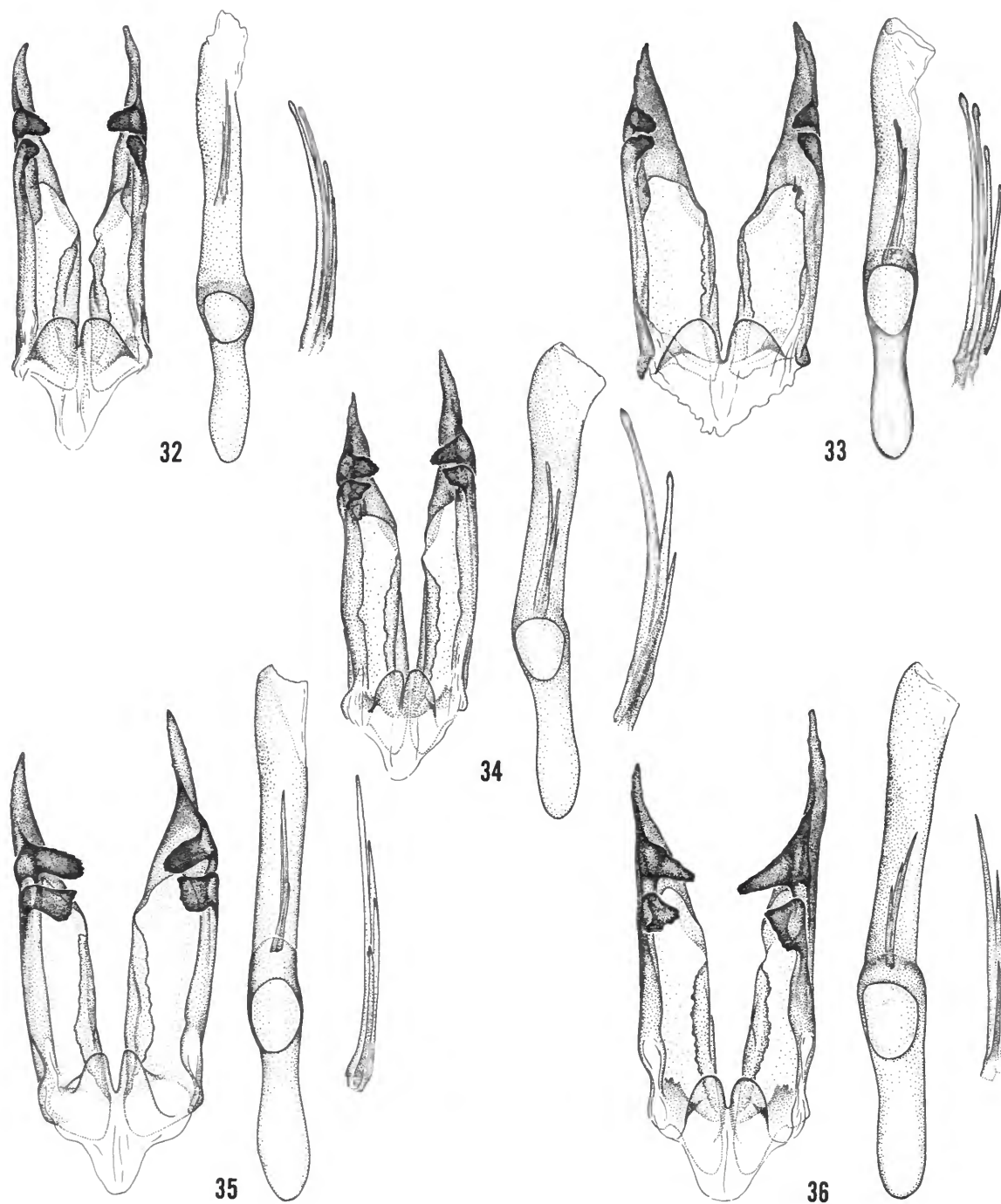
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FIGURES 27-31.—Geographic variation in male genitalia of *Autochton cellus* (left and right valvae in lateral view): 27, Maryland; 28, Alabama; 29, Texas; 30, Arizona; 31, Guatemala (for full specimen data, see Figures 22-26; see Figures 20 and 85-89 for males from Mexico).



FIGURES 32-36.—Geographic variation in male genitalia of *Autochton cellus* (valvae and aedeagus in dorsal view, plus blowup of cornutus from various angles): 32, Maryland; 33, Alabama; 34, Texas; 35, Arizona; 36, Guatemala (for full specimen data, see Figures 22-26; see Figures 20 and 85-89 for males from Mexico).

organisms are as variable and contrary as they are, looking at enough of them may weaken characters of this sort: I have seen one male from West Virginia none of whose cornutus spines swells and one from Guatemala whose longest cornutus spine hints at an apical swelling.) Like the uncus and the valvae, the cornutus is more variable in the (geographically intermediate) Texas populations. At Kerrville, the cornutus ranges from no swollen spines, through slight to definite swelling of the longest spine, to conspicuous swellings of both the longest and second longest spines (Figure 34). Specimens from adjacent Nuevo León show slight suggestions of apical swelling of the longest spine (Figure 89).

FEMALE GENITALIA

The female genitalia of *A. cellus* (Figures 37–57) have not previously been figured or described. They are in some respects more similar to those of certain other related Group C pyrgines than to those of other species of *Autochton*. (As in all of these skippers, there are large, paired, KOH-resistant, crinkled sacs immediately dorsad and laterad of the ductus bursae but not connected to it; these sacs, as well as the ductus seminalis, are omitted from all figures.) The bursa copulatrix is membranous except for the antrum—a short, variably sclerotized zone of the ductus bursae just cephalad of the ostium bursae. A short, membranous, anteriorly directed cul-de-sac arises ventrally and slightly to the right about halfway along the ductus bursae, at which point the ductus bursae generally bends a bit to the left (Figures 38, 39). The lamella antevaginalis is sclerotized laterally but not midventrally and is variably distinct from, or fused with, the lamella postvaginalis. The lamella postvaginalis is well sclerotized, deeply and broadly notched in the middle of its posterior edge, and densely clothed with fine spines, chiefly along its posterior margin and on its dorsal surface.

Geographic variation is most evident in the lamella postvaginalis and the antrum. In the eastern United States, the broad midventral notch

in the posterior edge of the lamella postvaginalis is more or less U-shaped in ventral view, the spines around it are heavier, and the antrum is smaller and more delicately sclerotized, whereas, in Arizona, Mexico, and Central America, the notch is strongly W-shaped, the spines a little lighter, and the antrum larger and better sclerotized (contrast Figures 38 and 39 and then compare Figures 40–56). In addition, the lamella antevaginalis tends to be more united with the lamella postvaginalis in the Southwest, Mexico, and Central America than in the eastern United States.

The notch in the lamella postvaginalis changes from a W to a U when the sclerotized material that is folded deeply and rather sharply inward and upward at the bottom of the W flattens out. In the eastern United States, a little over half of the females examined show traces of a fold (e.g., Figures 42, 44), but the infolding is so slight that the shape is basically a U. Variation from no fold to a small one appears to be individual rather than geographic. In Texas, however, truly intermediate notches occur in half of the females from Kerrville (e.g., Figure 45) and in the only female from the Davis Mountains (Figure 46); other Kerrville females and the dissected female from the Big Bend (Figure 47) are about like those from Arizona, Mexico, and Central America.

Texas females are like those from Arizona, Mexico, and Central America with respect to spines and antrum except that the females with an intermediate notch in the lamella postvaginalis also appear to have an intermediate antrum (Figures 45, 46).

Because they combine the deep fold in the W-shaped notch of the lamella postvaginalis with the more extensively sclerotized antrum, females from Arizona, Mexico, and Central America would seem to offer better guidance to the aedeagus (Figure 57).

LARVAL FOODPLANTS AND RELATED BEHAVIOR

The known larval foodplants of *A. cellus* are low-growing, twining or trailing species in several

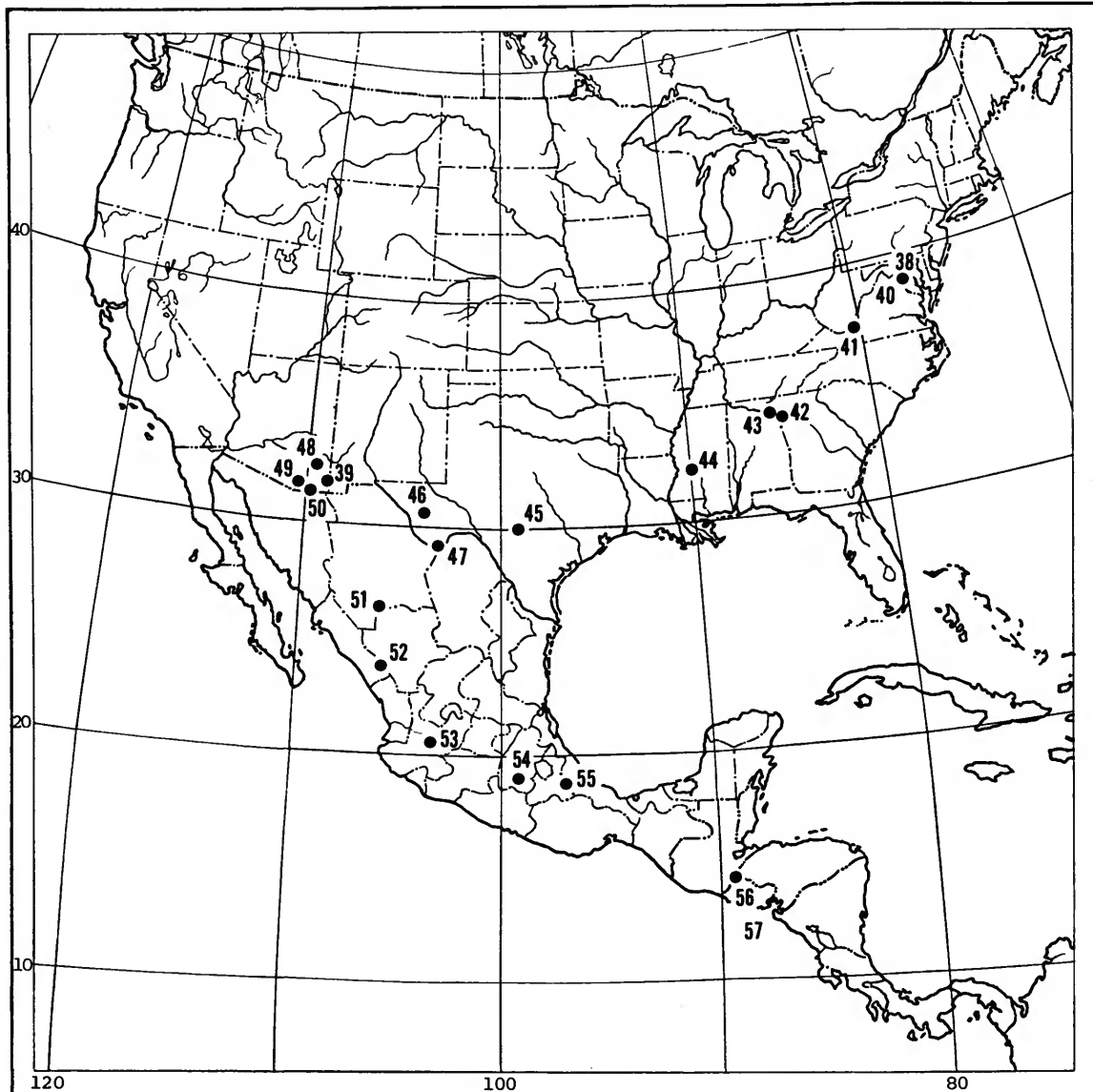
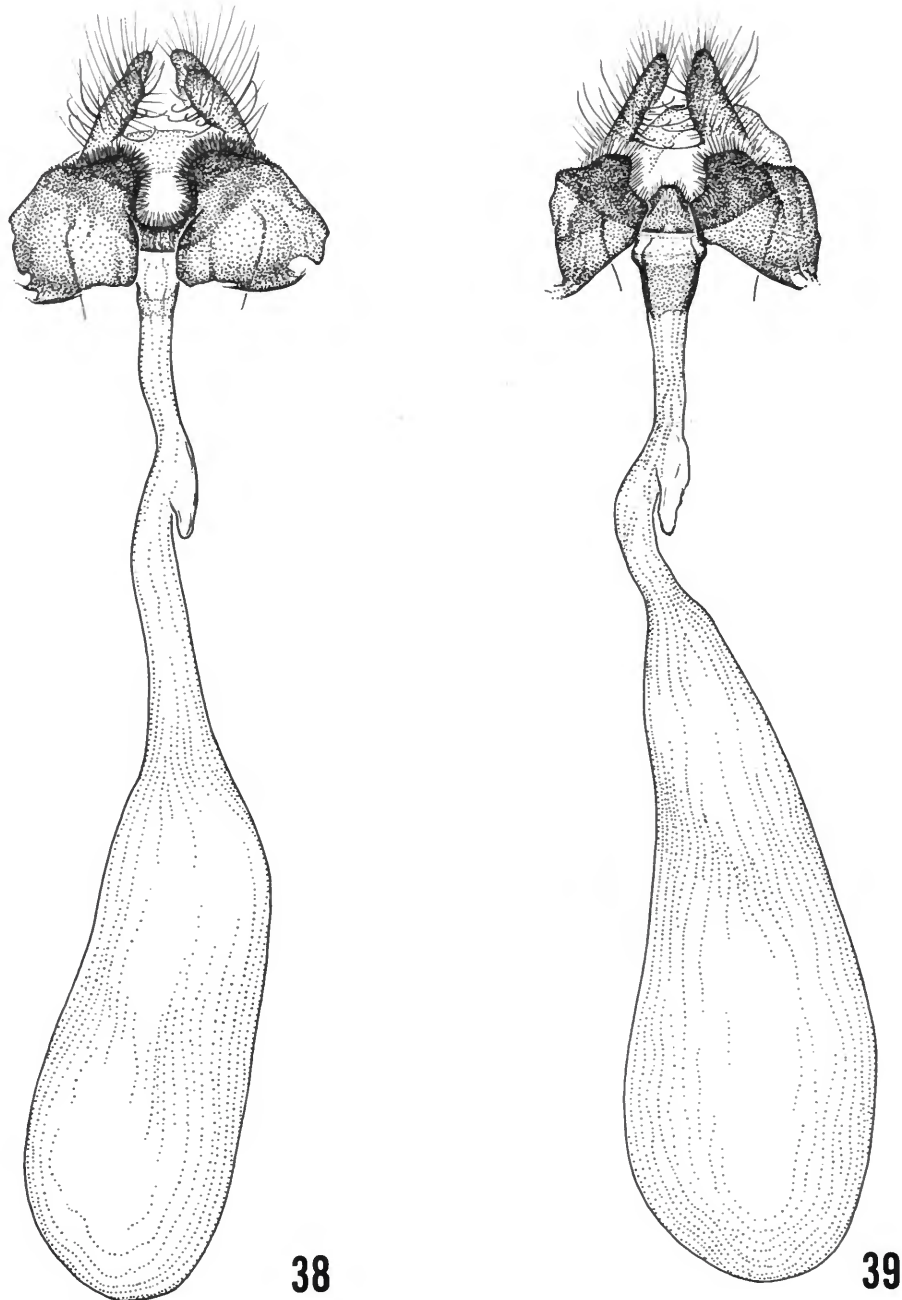


FIGURE 37.—Sources of the *Autochton cellus* female genitalia in Figures 38–57.

more or less closely related genera of Leguminosae: *Amphicarpaea*, *Clitoria*, *Phaseolus*, and *Vigna* (chiefly the first and third of these). Since all foodplant records come from the United States (and only from Maryland, Georgia, Texas, and Arizona), *A. cellus* probably eats legumes in some other genera, as well.

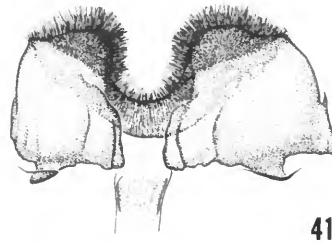
Upriver from Washington, D.C., in Maryland woods 1.8 km (1.1 mi) southeast of the Great Falls of the Potomac, A.H. and L.F. Clark (and friends) found a total of almost 600 eggs and larvae of *A. cellus* (in all five larval instars) on *Amphicarpaea bracteata* (Linnaeus) Fernald during the summer of 1934 and reared a few adults



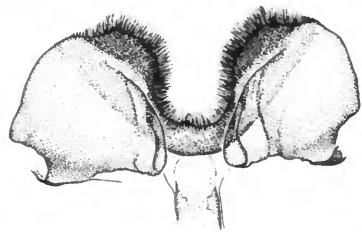
FIGURES 38, 39.—Geographic modes in female genitalic form in *Autochton cellus* (complete female genitalia plus papillae anales in ventral view): 38, Potomac River, Widewater, Maryland, 24 Jun 1934, G.W. Rawson (X-61) (USNM); 39, upper Pinery Canyon, 1830–2130 m (6000–7000 ft), Chiricahua Mountains, Cochise Co., Arizona, 19 Jul 1974, J.M. and S.N. Burns (JMB 1337) (USNM).



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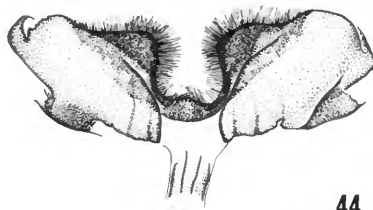
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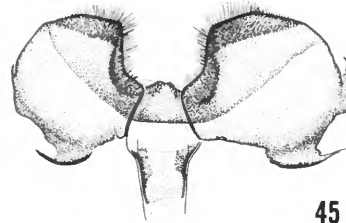
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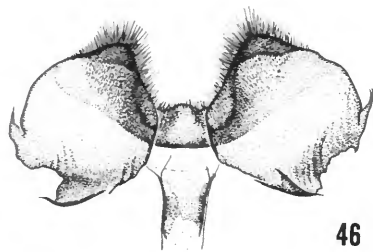
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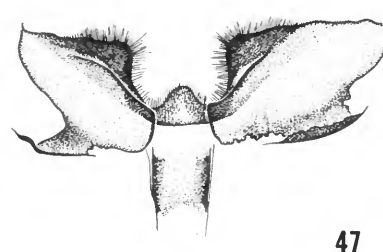
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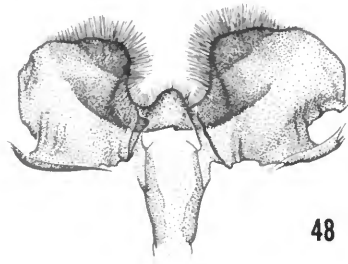


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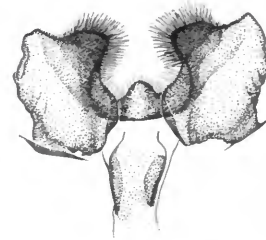


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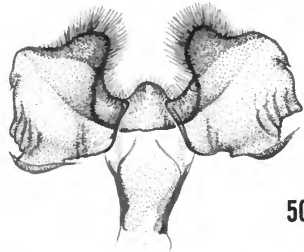
FIGURES 40-47.—Geographic variation in female genitalia of *Autochton cellus* (sterigma and posterior end of ductus bursae in ventral view): 40, Fairfax Co., Virginia, 21 Jun 1913 (X-62) (USNM); 41, Montgomery Co., Virginia, 26 Jun 1900, E.A. Smyth (X-63) (USNM); 42, Rockmart, Georgia, 14 Jul 1946, P.W. Fattig (X-64) (USNM); 43, Canyon Land Park, DeKalb Co., Alabama, 4 Aug 1973, C. Bryson (X-82); 44, Clinton, Hinds Co., Mississippi, 28 May 1961, M. and E. Roshore (JMB 1338); 45, Kerrville, Texas, Apr 1910, H. Lacey (JMB 1344) (AMNH); 46, near Sawtooth Mountain, Jeff Davis Co., Texas, 4 Jul 1969, W.P. Hord (JMB 1346); 47, Green Gulch, Big Bend National Park, Brewster Co., Texas, ex larva 21 Nov 1966, R.O. and C.A. Kendall (X-85).



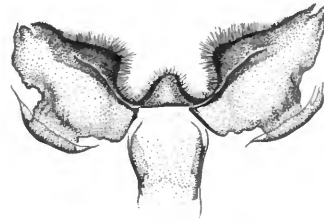
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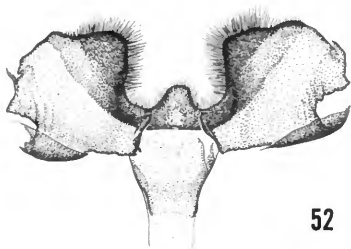
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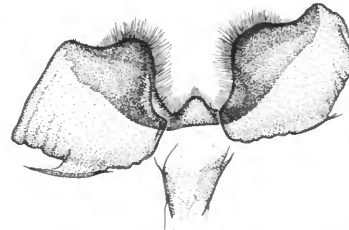
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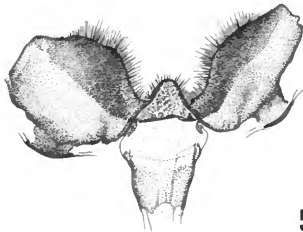
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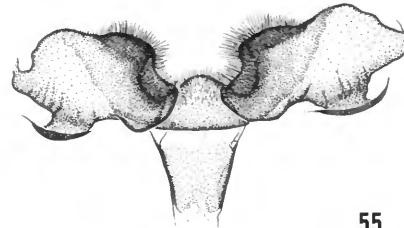
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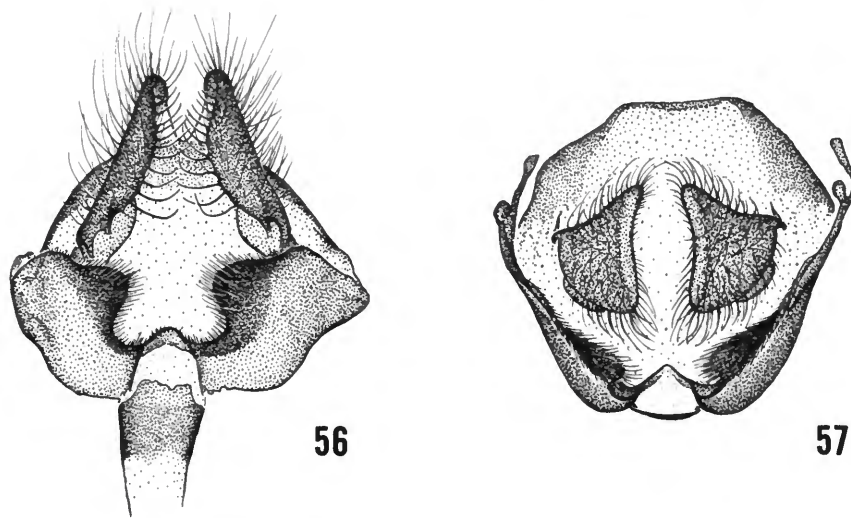


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FIGURES 48-55.—Geographic variation in female genitalia of *Autochton cellus* (sterigma and posterior end of ductus bursae in ventral view): 48, Swift Trail twixt Ladybug Saddle and Shannon Park, 2620-2740 m (8600-9000 ft), Graham Mountains, Graham Co., Arizona, 7 Jul 1958, J.M. and S.N. Burns (JMB 1341) (USNM); 49, Madera Canyon, Santa Rita Mountains, Arizona, 15 Jul 1947, J.A. Comstock and L.M. Martin (X-68) (LACM); 50, Huachuca Mountains, Arizona, 16-23 Jul (X-70) (USNM); 51, 40 km (25 mi) W Hidalgo del Parral, 2075 m (6800 ft), Chihuahua, Mexico, 15 Jul 1964, J. Powell (X-72) (UCB); 52, 39 km (24 mi) W La Ciudad, 2290 m (7500 ft), Durango, Mexico, 19 Jul 1964, J.A. Chemsak (X-74) (UCB); 53, Jalisco, Mexico, 15 Jul (X-75) (AMNH); 54, Cuernavaca, Morelos, Mexico, Jul 1965, N.L.H. Krauss (X-78) (AMNH); 55, 19 km (12 mi) NW Ciudad Mendoza, Veracruz, Mexico, 11 Jul 1974, J. Powell (JMB 1347) (UCB).



FIGURES 56, 57.—Female genitalia of *Autochton cellus*; sterigma and posterior end of ductus bursae, plus papillae anales, in specimen from Hda. Montecristo, 2300 m (7550 ft), Cerro Miramundo, Metapán, El Salvador, 21 May 1972, S. and L. Steinhauser (JMB 1378) (AME): 56, ventral view; 57, aedeagal-eye view.

(Clark, 1936). Years later, near Riverside Drive in the Atlanta area of Georgia, J.C. Symmes found females of *Autochton cellus* ovipositing on this legume (Harris, 1972).

In Green Gulch and Pine Canyon and along the Lost Mine Trail, in the Chisos Mountains, Big Bend National Park, Texas, R.O. and C.A. Kendall (assisted once by W.W. McGuire) repeatedly found larvae, or eggs and larvae, of *A. cellus* on *Phaseolus wrightii* Gray—first on 5 October 1966 and then on 13 October 1967, 15 and 21 September 1971, 27 September 1972, and 17 May 1973—and reared a total of 11 adults from four different collections (R.O. Kendall, field notes with letter dated 10 October 1974; Kendall, 1974).

In Cave Creek Canyon and the South Fork of Cave Creek Canyon, at elevations of 1615 to 1830 m (5300 to 6000 ft) in the Chiricahua Mountains, Cochise County, Arizona, from 25 July to 9 August 1974 (with help one July afternoon from C.D. MacNeill and a novel observation from J.A. Powell early in August), I found a few hundred eggs and larvae of *A. cellus*, mostly

on *Phaseolus grayanus* Wooton and Standley but also on *Vigna* sp. and on what is probably *Clitoria mariana* Linnaeus. (Determinations of the last two foodplants, by B.G. Schubert in December 1974 and January 1975, and R.S. Cowan in January 1984, cannot be more precise because specimens perforce lacked flowers and fruit.)

On 10 August 1974 I started driving eastward with a dozen half-grown larvae of *A. cellus* and a bag of fresh-picked *P. grayanus*. A week later, at Galivants Ferry, South Carolina, with the foodplant long spoiled and the larvae dead or dying, I desperately offered leaves of cultivated soybean, *Glycine max* (Linnaeus) Merrill, which two last- (fifth-) instar larvae accepted. Both had been in the second larval instar on 3 August. They quit eating in Baltimore, Maryland, on 29 and 31 August and pupated three days later on 1 and 3 September; overwintered (September to June) in Lexington, Massachusetts; and emerged in Annandale, Virginia, on 18 July 1975 (male) and 21 to 25 July 1975 (female). The (later-emerging) female had pupated first.

Some comments on the foodplants are in or-

der. *Phaseolus wrightii* and *P. grayanus* are so close that the latter has been treated as a variety of the former, and both are questionably distinct from species in adjacent Mexico (Kearney and Peebles, 1951:483–484; Rickett, 1970:360). *Phaseolus* and *Vigna* are so close that authorities cannot separate them cleanly (R.S. Cowan, personal communication, 1984). *Glycine max* is “rather closely related to . . . *Amphicarpaea*” (Correll and Johnston, 1970:879). *Amphicarpaea bracteata* occurs not only in the eastern United States and adjacent southern Canada but also, rarely, near Orizaba, Veracruz (Correll and Johnston, 1970:879), which is within the Mexican range of *Autochton cellus*. *Clitoria mariana*, too, is disjunct in somewhat the manner of *A. cellus*, occurring in the eastern United States from about 40°N latitude south to Florida and Texas and again in southern Arizona—specifically (Kearney and Peebles, 1951:479),

Sierra Ancha (Gila County), and mountains of Cochise, Santa Cruz, and Pima counties, . . . 4,000 to 6,000 feet [1220 to 1830 m]. . . . This . . . plant is . . . remarkable as an example of interrupted distribution, being apparently absent in the area between central Texas and southeastern Arizona. It is infrequent in Arizona except in the Chiricahua Mountains and in Santa Cruz County, where it is reported to be locally abundant.

I watched preoviposition behavior of a female *A. cellus* late in the afternoon of 25 July 1974 at 1615 m in the Chiricahua Mountains on the shaded canyon bottom beside the South Fork of Cave Creek, which was flowing. The female flew just above the forest floor, frequently lighting on low leaves—including those of three species of oak (*Quercus*), as well as some other plants—before rejecting them. When she finally lit on the plant of her choice, *Phaseolus grayanus*, she crawled beneath one of its tripartite leaves, 8–10 cm above ground, where she stayed for what seemed an eternity. After she flew, I found she had laid three eggs in a cluster in the middle of the ventral surface of one of the leaflets. These eggs hatched slightly before the end of July.

Once I saw that *P. grayanus* was a foodplant, it stood out as a distinctive and common ele-

ment in the local herbaceous flora; and early stages of *A. cellus* came easily because eggs were usually in clusters (though always on the ventral sides of leaves) and because every first- and second- (and often also third-) instar larva was in a conspicuous shelter, a flap cut from the edge of a leaflet and folded dorsally (with silk). In the South Fork of Cave Creek Canyon, besides the innumerable egg clusters and larval shelters from *P. grayanus*, four clumps of one, two, three, and three eggs, plus three shelters with third-instar larvae, turned up on *Clitoria mariana*, on which J.A. Powell witnessed oviposition by *A. cellus* on 5 August 1974; and three clumps of three, five, and nine eggs, plus five shelters with first-instar larvae and seven shelters with second-instar larvae, turned up on a species of *Vigna* on 9 August 1974. Again, all eggs were laid on ventral surfaces of leaflets and all flap-shelters were turned dorsad. In these respects, at least, *A. cellus* behaves in southeastern Arizona the way it does near Washington, D.C. (Clark, 1936).

Altogether, I scored 33 of the egg clusters I collected, with the following result:

Number of eggs in cluster	1	2	3	4	5	6	7	8	9
Frequency	4	6	8	5	3	2	2	2	1

This, too, corresponds with observations near Washington by Clark (1936:26): “Though single eggs are commonly found, most of the eggs are deposited in groups of two or three. Strings of four are frequent and strings of five . . . occasional. One string of six was found.” Moreover, R.O. Kendall (field notes of 17 May 1973) wrote regarding *A. cellus* in Big Bend National Park, Texas: “Eggs were deposited on undersurface of leaves of *Phaseolus wrightii*, singly or in clusters up to eight.” Very few skippers are known to batch their eggs.

Autochton sierradror, new species

FIGURES 58–84, 90

HOLOTYPE.—Male; Mexico, Hidalgo, near Jalcála, 2–3 July 1965, O.S. Flint, Jr., and M.A.

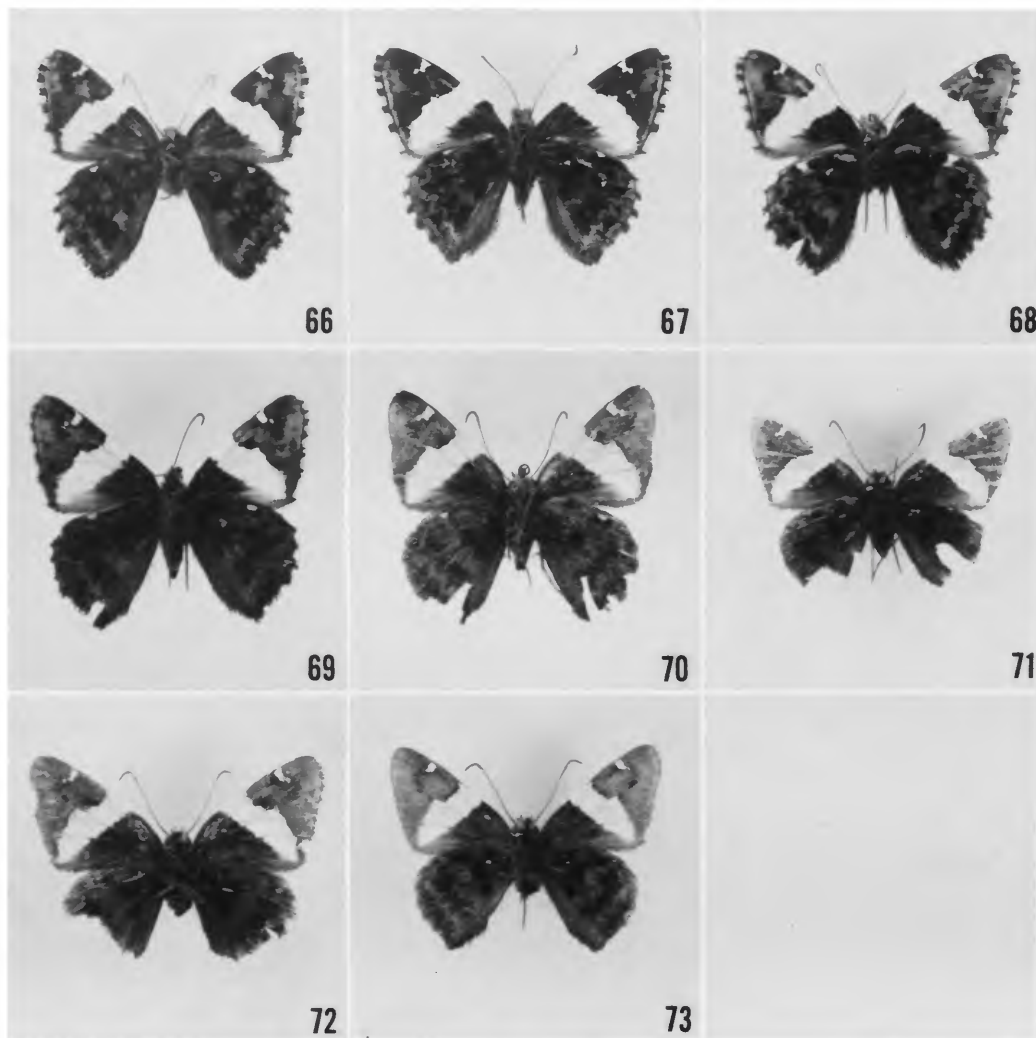


FIGURES 58–65.—Type-series of *Autochton sierradror* (comprising males from Mexico) in dorsal view (all approx. $\times 1$): 58, holotype, near Jacala, Hidalgo, 2–3 Jul 1965, O.S. Flint, Jr., and M.A. Ortiz (USNM); 59, vicinity Encarnacion, 2400–2450 m (7900–8000 ft), Hidalgo, 16 Feb 1969, L.D. and J.Y. Miller (AME); 60, 61, 62, vicinity Encarnacion, 2300–2400 m (7550–7900 ft), Hidalgo, 3 Aug 1973, L.D. and J.Y. Miller (AME); 63, Chipinque Mesa, 1310 m (4300 ft), Nuevo León, 20 Sep 1975, J. Chemsak (UCB); 64, 6 km (4 mi) W Iturbide, 1680 m (5500 ft), Nuevo León, 24 Sep 1975, J. Powell and J. Chemsak (UCB); 65, as for Figure 64 except 13 Sep 1976, J. Powell (USNM).

Ortiz, USNM Type 101312.

DESCRIPTION.—A multivoltine skipper (adults from February, July, August, and September; see complete dates in legend of Figures 58–65)

occurring at middle elevations in the Sierra Madre Oriental (see localities and altitudes in legend of Figures 58–65 and see Figure 90). Nudum segments usually 19 or 20, but ranging



FIGURES 66-73.—Type-series of *Autochton siernadror* in ventral view (all approx. $\times 1$): specimens arrayed as in Figures 58-65.

from 17 to 21 (Table 3). Size (mean male forewing length 22 mm; Table 3) and facies (Figures 58-73) as in populations of *A. cellus* inhabiting the same general region, but genitalia (Figures 74-84) distinct (at least in males): tegumen relatively long, sometimes nearly as long as uncus (much longer than in *cellus*); uncus prongs parallel and together (rather than divergent) except at tips, which turn slightly outward; uncus prongs

in characteristic contact at a point just cephalad of their turned out tips; in dorsal view, uncus prongs not notably tapered toward tip (as they are in *cellus*); saccus no longer than tegumen (very much shorter than in *cellus*); valvae lower distally than proximally, with the posterior dorsal process (which is finely dentate) broader than the anterior dorsal process; valvae less asymmetric than in *cellus*; aedeagus shorter than in *cellus*.

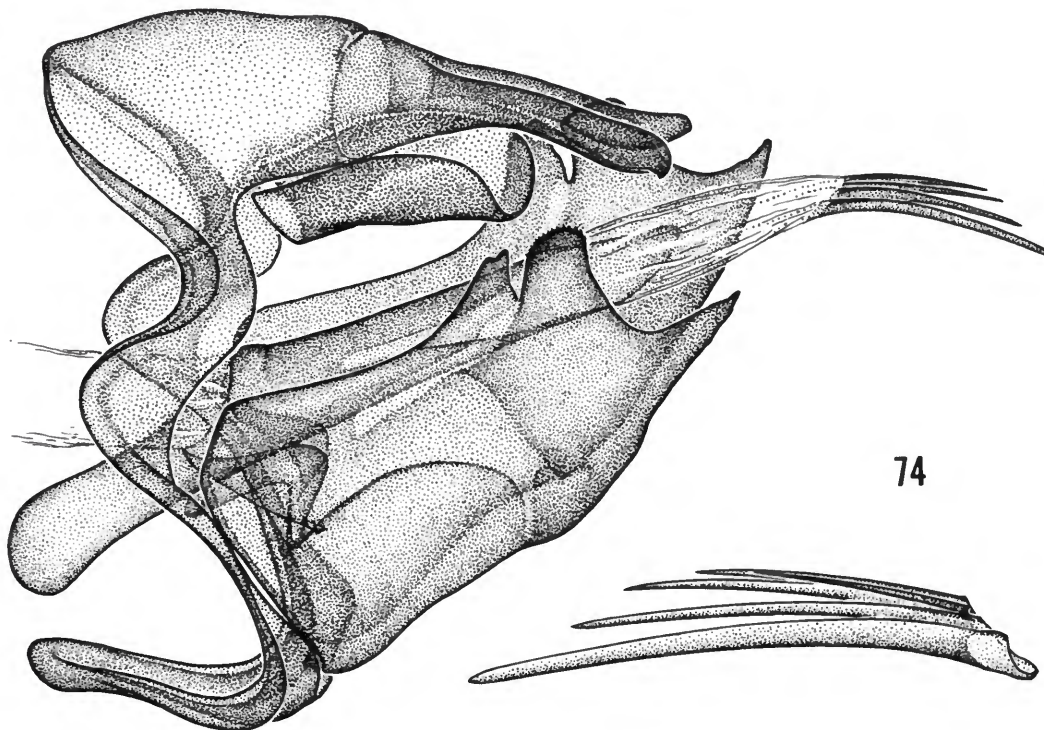


FIGURE 74.—Complete male genitalia of holotype of *Autochton siermadror* in left posterolateral view, with cornutus exerted, plus blowup of cornutus. Specimen from near Jacala, Hidalgo, Mexico, 2–3 Jul 1965, O.S. Flint, Jr., and M.A. Ortiz (X-1641) (USNM).

TABLE 3.—Length (mm) of right forewing and number of nudum segments in the type-series of *Autochton siermadror*.

Mexican state	Male in figures	Winglength (mm)	Number of nudum segments
Hidalgo	58, 66	21.3	20
	59, 67	22.9	19
	60, 68	21.7	20
	61, 69	22.5	19
	62, 70	22.6	17
Nuevo León	63, 71	20.5	21
	64, 72	23.4	20
	65, 73	21.6	18
		$\bar{x} = 22.06$	

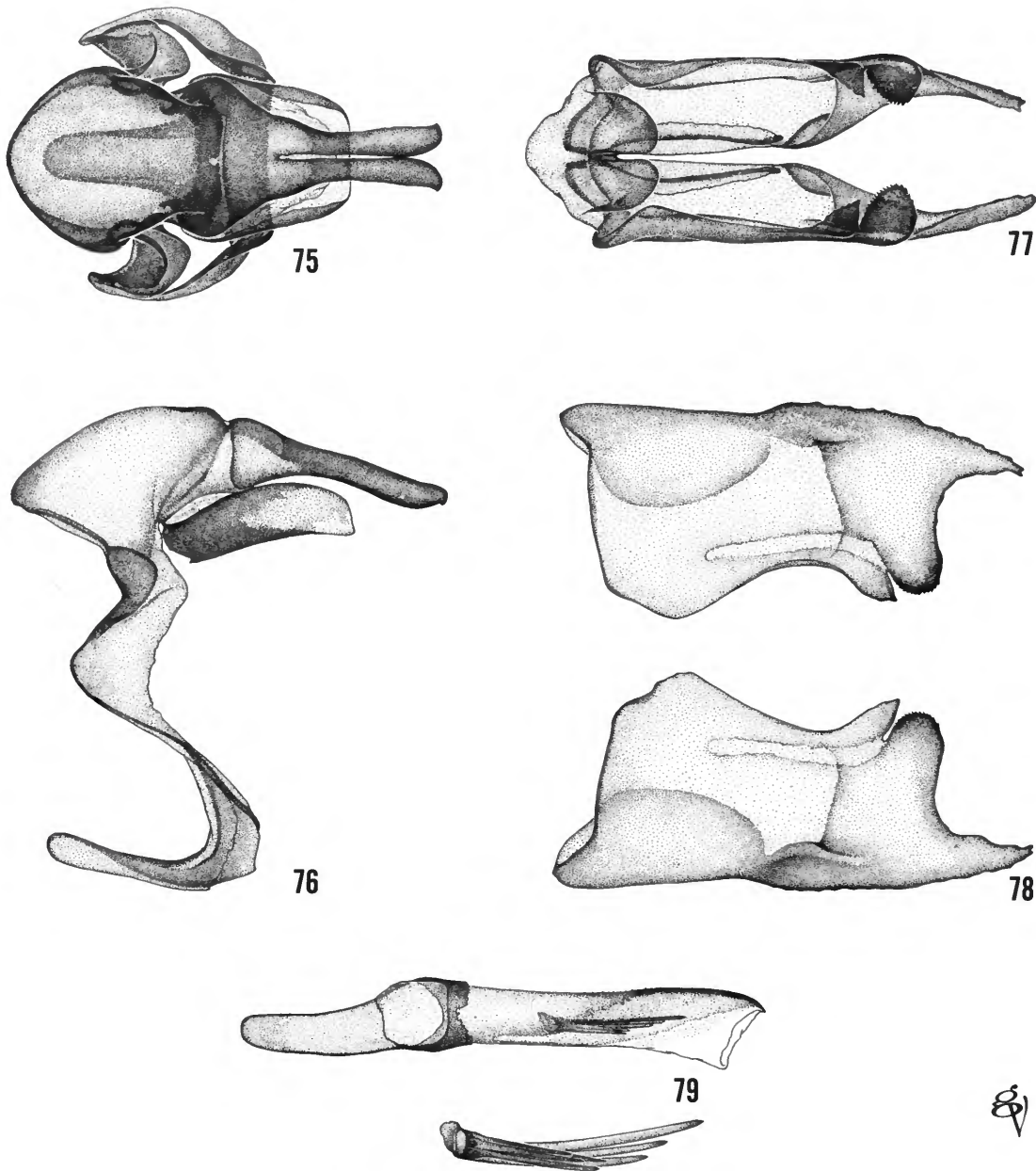
(Compare male genitalia of *siermadror* in Figures 74–84 with those of *cellus* in Figures 20–36 and, especially, Figures 85–89, which show directly comparable views of a *cellus* male that is almost

sympatric with the *siermadror* male in Figures 80–84.)

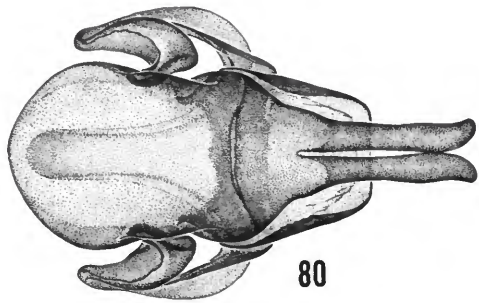
HABITAT.—The known specimens of *A. siermadror* (eight males) all come from pine-oak forest varying in aspect from mesic and open to dry and scrubby. It is likely, then, that *A. siermadror* coexists with *A. cellus*. Though sympatry has yet to be established, the two species have always been found close to one another (see Figure 90).

Discussion

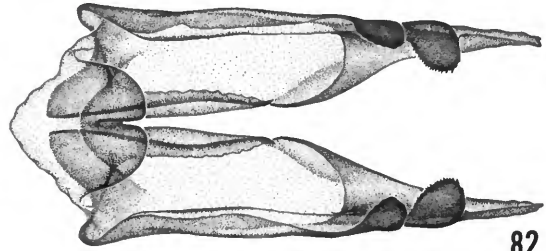
Most of my systematic research over the past quarter-century has involved detailed studies at and around the species level, especially in skipper butterflies. In this connection, I have become ever more deeply enamored of male and female genitalia. Without understanding exactly why



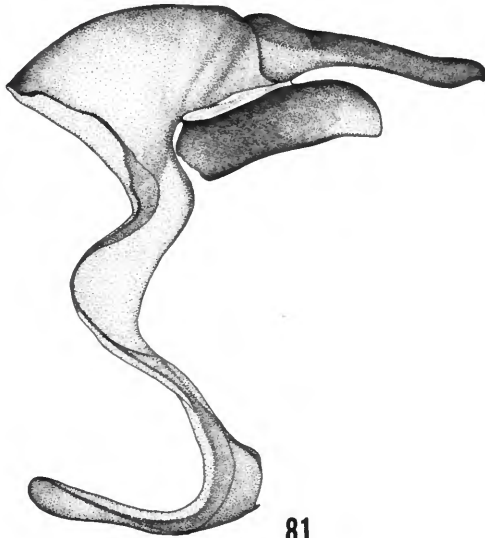
FIGURES 75-79.—Male genitalia of paratype of *Autochthon sierradror* from vicinity Encarnacion, 2300-2400 m (7550-7900 ft), Hidalgo, Mexico, 3 Aug 1973, L.D. and J.Y. Miller (JMB 1379) (AME): 75, uncus, tegumen, gnathos, vinculum, and saccus in dorsal view; 76, uncus, tegumen, gnathos, vinculum, and saccus in left lateral view; 77, valvae in dorsal view; 78, valvae in lateral view; 79, aedeagus in dorsal view, plus blowup of cornutus.



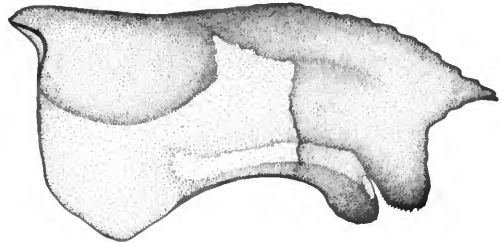
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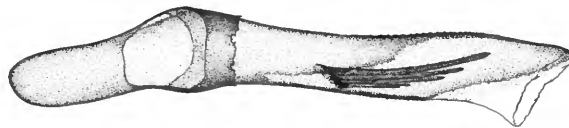
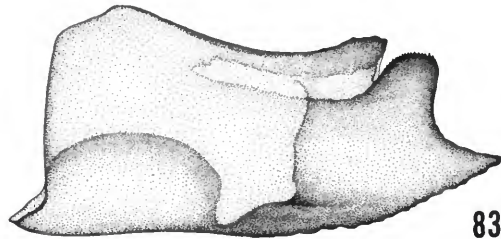
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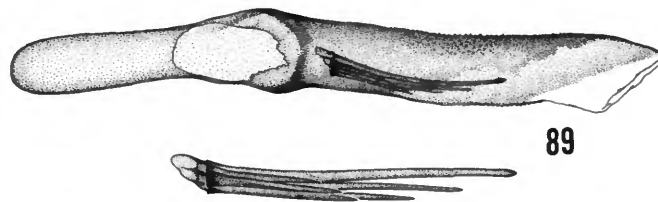
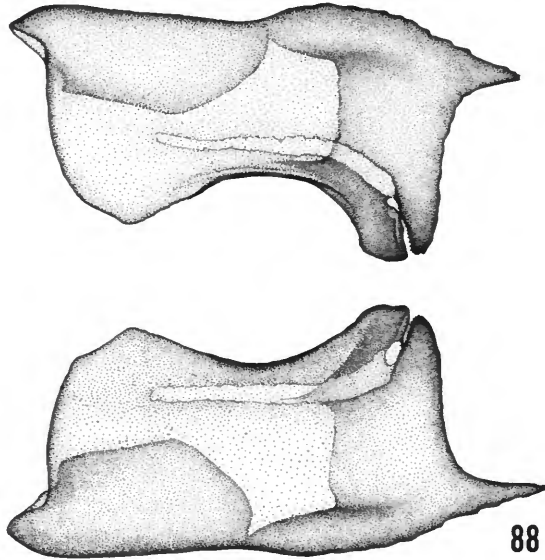
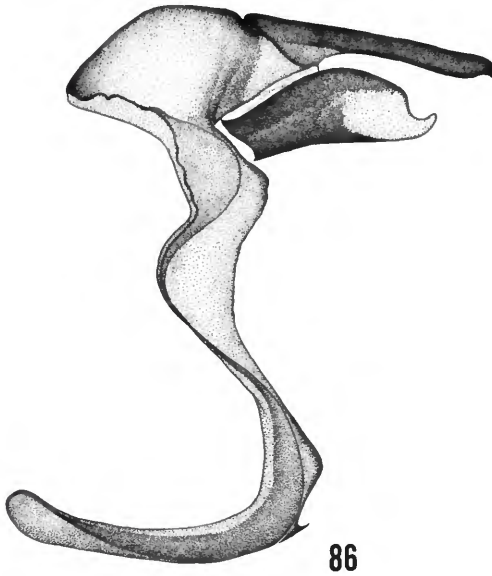
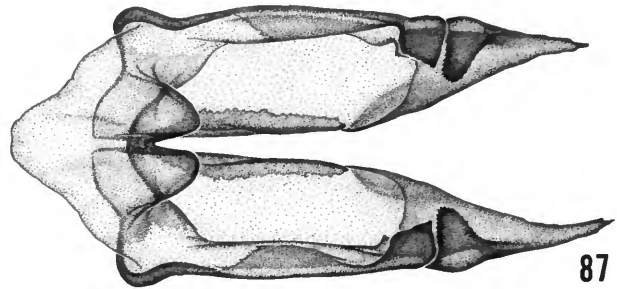
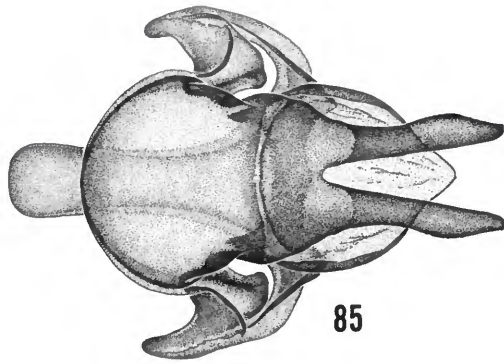


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FIGURES 80-84.—Male genitalia of paratype of *Autochthon sierradror* from 6 km (4 mi) W Iturbide, 1680 m (5500 ft), Nuevo León, Mexico, 13 Sep 1976, J. Powell (JMB 1403) (USNM): parts and views as in Figures 75-79.



Figures 85-89.—Male genitalia of *Autochthon cellus* from 29 km (18 mi) W Linares, 820 m (2700 ft), Nuevo León, Mexico, 24 Sep 1975, J. Chemsak and J. Powell (JMB 1405) (USNM); parts and views as in Figures 75-79.

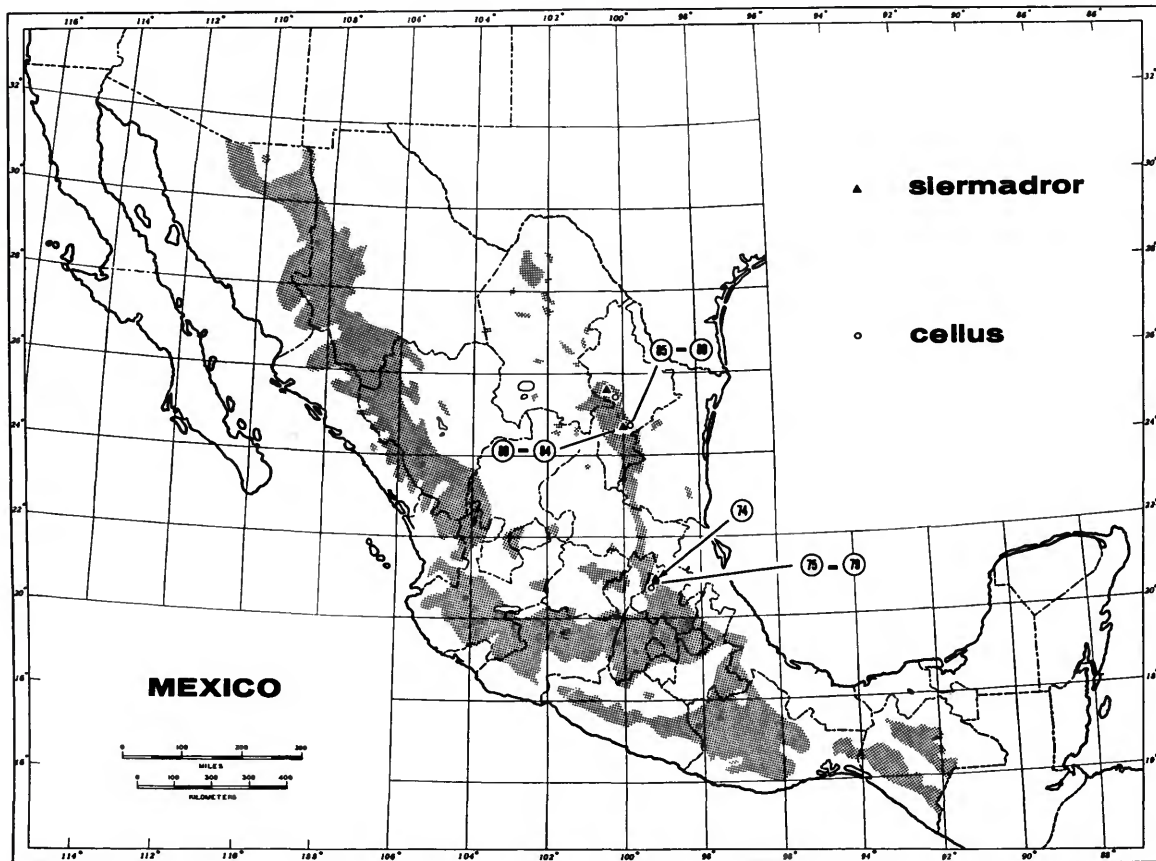


FIGURE 90.—Spatial distribution of sibling species of *Autochton* in Mexico. Localities for *A. sierrador* are marked by triangles and its type-locality also by an arrow; proximal records of *A. cellus* are marked by circles; total presumptive distribution of *A. cellus* is stippled; sources of the *A. sierrador* and *A. cellus* male genitalia in Figures 74–89 are indicated.

they are so good, I enjoy using them and thinking about them.

I argued early on and again recently (Burns, 1964, 1983) that genitalic differences between well-differentiated subspecies or sister species may be nonadaptive. Such differences, which are clearly genetic, often strike me as spin-offs of something like Mayr's (1954) "genetic revolution" (rapid genetic change leading quickly, in turn, to more extensive genetic reorganization in small, isolated, and therefore inbred, founder populations). Though complete mechanisms for genetically but harmoniously shaking up a mini-

isolate remain elusive (awaiting, say, far better comprehension of the behavior of DNAs and some of their molecular contacts), they probably involve rather more than selection (Burns, 1983:355). Gould and Lewontin (1979) and Gould (1980) vigorously doubt that selection is the supreme perpetrator. To say that genitalic differentiation may be nonadaptive is not to deny that male and female adjust to one another morphologically when accidental shifts in either's genitalic form so demand (Burns, 1983:341), but such coevolution is secondary.

Although individual variation in genitalia is

ubiquitous and often generous, if one learns to recognize it and allow for it, the genitalia will usually look remarkably constant over the geographic range of a differentiate. Between sister differentiates one may then detect “constant” genitalic differences, sometimes so wonderfully gross as not to be missed by anyone, but sometimes exceedingly small. Because I have seen even the most trivial genitalic differences hold, even when the sister differentiates are allopatric and the range of each is discontinuous as well as extensive (Burns, 1964, 1983), I infer that these differences arise by chance in a tiny population, where they become fixed, and thereafter get carried wherever the differentiate goes, which may be “down/The lubricated gullet of extinction” (Burns, 1975b) but may be far and wide. I have trouble imagining a modest genitalic difference being selectively favored in a large population, gradually replacing what has come before, and finally spreading uniformly through the entire species population in all its far-flung and fragmented glory.

I do not see genitalia varying geographically as though in direct response to geographically varying selection. Whenever I have encountered geographic variation in genitalia and analyzed it in detail, I have had to conclude that genitalic differences originated in geographic isolation and variation resulted from secondary contact and hybridization between differentiates (Burns, 1964 and unpublished). *Autochton cellus* is no exception. By contrast, what I do find varying geographically and, at times, in parallel ways that must be ascribed to selection (e.g., Burns, 1964:204–205) are color-pattern, size, and voltinism. Differentiation in these kinds of “external” characters can be superimposed on a differentiate whose genitalia (among other things) tend to remain constant and true—till spun in the roulette of “genetic revolution” once more under special circumstances. For years I have felt, intuitively, that most differentiation happens in the speciation process, which is allopatric, promoted by founders, rapid, random, and, on occasion, highly productive (Burns, 1975b). I write much

of this with a nod to what I like to call “punct-rockers,” those paleontologists who have shaken phyletic gradualism and evolutionary theory generally with notions of punctuated equilibria and hierarchy (Eldredge, 1971; Eldredge and Gould, 1972; Stanley, 1975, 1979; Gould and Eldredge, 1977; Gould, 1980; Eldredge, 1982 [1983]).

Geographic variation in the genitalia of *A. cellus* supports the pattern noted above. In each sex, despite considerable variation, there is essentially one kind of genitalia in the eastern United States and another from the Southwest (Arizona, New Mexico, Colorado) through Mexico to northern Central America. Variably intermediate genitalia occur together with the Southwestern/Mexican kind in Texas, which is geographically intermediate; and faintly intermediate genitalia (in males, at least) occur in adjacent Nuevo León. (For details, see sections on Male and Female Genitalia and Figures 19–57 and 85–89.) Readers with a gradualist bent may tend to see clinal variation in the genitalia from about the city of Washington to Arizona. I thought I did, myself, before analyzing numerous genitalia and properly appreciating and segregating individual variation.

Geographic variation in what seems a trifling color character (the extent of yellow dorsally at the apex and along the costa of the hindwing) corresponds with geographic variation in genitalia, except that the shift from one mode of expression to the other is abrupt, Texas populations resembling those in the eastern United States (see section on Facies and Figures 3–18).

None of the critical geographically varying characters (male genitalia, female genitalia, and facies) breaks in exactly the same way, though all change across the same area where populations are few and far between. This entire region is one of enormous biotic stress and transition. Two of the plants that *A. cellus* eats presently occur on opposite sides of it but not in it (see section on Larval Foodplants).

From all this I infer that *A. cellus* gave rise to a miniisolate that underwent a genetic minirevolution resulting in a mini- (but genitalic) differ-

entiate that expanded its range. When these mother and daughter (so-called sister) differentiates made contact, they were compatible and hybridized. Their contact later weakened, apparently dissolving in very recent time; but evidence of extensive interbreeding between them remains. Because the distribution of *A. cellus* is much more extended, complex, and discontinuous from the southwestern United States to El Salvador than it is in the eastern United States, because the sister species of *A. cellus* (*A. siermad-*

ror) is Mexican (Nuevo León to Hidalgo), and because all other species currently placed in *Autochton* variously occur between extreme southern Arizona and southern Brazil and Argentina (Evans, 1952), the mother differentiate within *A. cellus* is almost certainly the one now ranging from the Southwest through Mexico to Central America. Somewhere off its northeastern frontier, I presume, it founded a miniisolate that became the daughter differentiate now inhabiting the eastern United States.

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