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PYRGUS COMMUNIS AND *PYRGUS ALBESCENS* (HESPERIIDAE: PYRGINAE) ARE SEPARATE TRANSCONTINENTAL SPECIES WITH VARIABLE BUT DIAGNOSTIC VALVES

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ABSTRACT. Since 1906, the question of whether *Pyrgus albescens* Plötz is a species distinct from *Pyrgus communis* (Grote) or only a subspecies (or mere form) of it, has arisen repeatedly with no real resolution. Although these differentiates are superficially inseparable, highly variable features of the valves (claspers) of the male genitalia distinguish them—provided the valval variation is properly analyzed. Most workers erroneously have seen this excessive variation as more or less continuous, taken the supposed intergrades as evidence of interbreeding, and so considered the differentiates subspecies.

Since 1963, I have critically compared the genitalia of 3060 males (1910 *P. communis* and 1150 *P. albescens*) to determine not only their taxonomic rank but also their geographic distribution: *P. communis* ranges from southern Canada through most of the United States to southern Mexico; *P. albescens*, from the southern United States to southern Mexico. Long considered a southwestern differentiate (in the USA) ranging no farther east than the Corpus Christi area of Texas, *P. albescens* actually extends eastward along the Gulf Coast to the Atlantic Coast of Florida and currently is expanding its eastern range. Narrowly sympatric in the eastern and far western USA, these species are broadly sympatric in the southwestern USA and montane Mexico. Though more austral than *P. communis*, *P. albescens* flouts conventional wisdom by occurring high in various southwestern mountains. In Mexico, it extends from coast to coast and through the entire Baja California peninsula.

The rampant, ostensibly continuous genitalic variation in mixed samples of these species is clearly bimodal. Comparison of genitalia throughout each species' range shows fully as much intraspecific genitalic variation in areas removed from interspecific contact as in areas of overlap. The variation is inherent in each species, not a result of hybridization. I develop these points with comparative figures of the genitalia of 484 males (253 *P. communis* and 231 *P. albescens*) from diverse situations.

Pyrgus communis is slightly larger than *P. albescens* in average size.

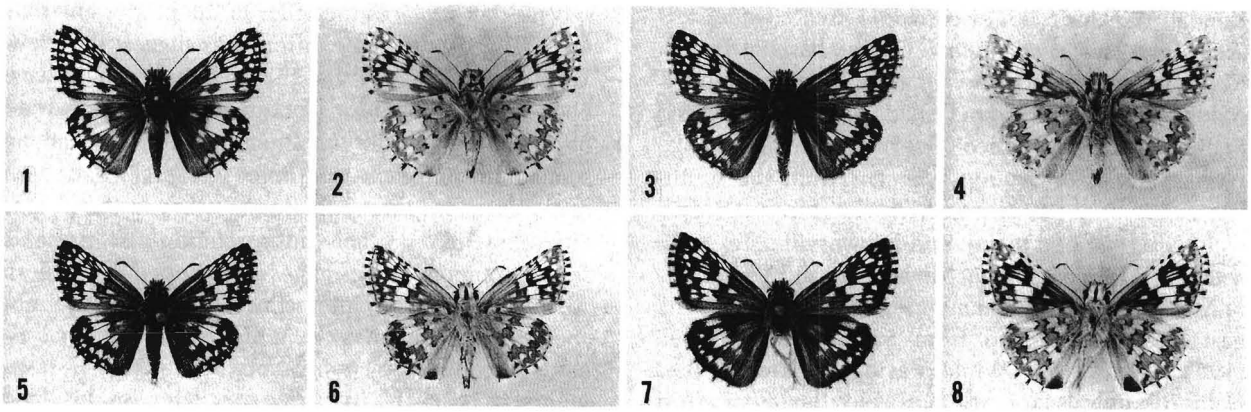
Additional key words: genitalia, geographic distribution, speciation, systematics, variation.

Pyrgus communis (Grote 1872) and *P. albescens* Plötz (1884) have a checkered history. These black-and-white skipper species (Figs. 1–8) were originally described more than once; they were variously referred to different genera (*Hesperia*, *Pyrgus*, *Syrichtus*, *Urbanus*); and names applied to related, similar-appearing species were misapplied to them. Nevertheless, by the time Lindsey et al. (1931) was published, most nomenclatural problems—which involved homonymy as well as synonymy, specific identity, and proper generic usage—had been solved; and these skippers were designated by the names we continue to use today. Current synonymy may be found in Evans (1953), dos Passos (1964), and Miller and Brown (1981, 1983).

On the other hand, biological problems involving the mutual status of *Pyrgus communis* and *albescens*—i.e., whether they are completely separate species, variably hybridizing species, freely interbreeding subspecies, or one and the same taxon—surfaced early in this century and persist to its end. Knowledge of the geographic distributions of these skippers—which, early on, was unavoidably sketchy and partly erroneous—is still notably deficient.

Just seven months after Skinner (1906a:96) briefly described what he called "*Pyrgus occidentalis* n. sp." (=*P. albescens*) from "the Northwest territory [an invalid source for this skipper] and . . . the southwest generally" (specifically "San Bernardino Ranch, Cochise Co., Arizona, . . . and Brownsville, Texas"), he (Skinner 1906b:278) backtracked by declaring, "This is not a species, but only a form or geographical race of *tessellata*" (Scudder) (=*P. communis*). But eleven years later, on 27 September 1917, "Williams made some interesting remarks on the genus [*Pyrgus*], especially regarding characters possessed by the genitalia and illustrated them by drawings. He stated that, based on the genitalic characters, *occidentalis* seems to be distinct from *tessellata*" (Cresson 1918:38). Lindsey (1921:41) treated *occidentalis* as a race of *tessellata* with the comments "California, Arizona and Texas. This form is scarcely worthy of a name, but may be regarded as a pale southwestern geographical race. I have not looked for differences in the genitalia." However, the observation by "Williams . . . regarding the apparent specific distinctness of *H. occidentalis* Skin. and *tessellata* Scud. on the basis of genital structure led [Barnes & Lindsey 1921:79] to examine a long series of these races. . . . The genitalia do undoubtedly show two very easily separable forms of valves, but these are connected by a great variety of intermediate forms. . . . It is impossible to draw a definite line between the extreme forms, so we prefer to retain the old conception of *occidentalis* as a pale western race of *tessellata*."

Independently investigating the relationship of these two entities from a greater distance, Swiss lepidopterist Reverdin (1921) took what, for that time, was the remarkable step of comparing 90 dissections of their male genitalia. He recognized, thoroughly de-



FIGS. 1–8. *Pyrgus* males in dorsal (odd-numbered) and ventral (even-numbered) views; collected by J. M. Burns (and deposited in USNM). **1, 2, 5, 6,** *P. albescens*. **3, 4, 7, 8,** *P. communis*. **1–4,** Southwestern Research Station of the American Museum of Natural History, Cave Creek Canyon, Chiricahua Mountains, 5400 ft [1645 m], Cochise County, Arizona, USA, 7 September 1959. **5, 6,** Cantonment, Escambia County, Florida, USA, 7 September 1984. **7, 8,** Skippers, Greensville County, Virginia, USA, 25 September 1980.

scribed, and carefully illustrated two divergent genitalic extremes (which he even found coexisting in Chihuahua City, Mexico); and, at first, he thought that they characterized the two differentiates in question. But he encountered so much genitalic variation and so many transitional forms between the extremes—as well as specimens from the American specialists Williams and Lindsey that had *occidentalis* labels but the "wrong" kind of genitalia—that he rejected this idea, concluding (while admitting that the evidence was still imperfect) that *tessellata* (=*communis*) is a distinct and well-defined species whose male genitalia display a wide range of variation and that *occidentalis* (=*albescens*) is only a variety of it, occurring in a southwestern portion of its range and far to the south of that. (For far southern *occidentalis*, Reverdin listed Panama and even Surinam—areas which, in reality, greatly exceed the southern limits of both *P. albescens* and *P. communis*. Reverdin's [1921:pl. 7, figs. 1, 2, and 6] excellent photographs of male genitalic extremes—all of which he ascribed to *tessellata*—depict, respectively, a typical example of *P. communis*, a typical example of *P. albescens*, and a mildly atypical *P. communis*.)

Given the studies of Barnes and Lindsey (1921) and particularly Reverdin (1921), it is not surprising that Skinner and Williams (1923:289)—while clearly illustrating the basic valval difference between *tessellata* (fig. 7) and *occidentalis* (fig. 8)—called the latter nothing but a variety of the former. They noted that "The [varietal] name should be restricted to apply only to the smaller, paler form of the species inhabiting the low arid regions along the Rio Grande to the north and south, and thence to and up the Californian coast." Using revised nomenclature that is still current, Lindsey et al. (1931:pl. 10, figs. 7, 8) reprinted the diagnostic Skinner and Williams (1923) genitalic figures but reiterated the Lindsey (1921) view of *albescens* as a weak race of *P. communis* ranging from California to Texas and Mexico.

Later, with no intention of probing the *communis*/*albescens* relationship but, rather, in an effort to gain some appreciation of levels of individual variation in the male genitalia of skippers, Lindsey (1939:174) turned to *P. communis* (in the strictest sense) "solely because of the availability of a long series of reared specimens, most of them closely related. The genitalia of 100 males were mounted on microscope slides, projected at the same magnification, and measured from the magnified image in millimeters to provide data for statistical study." Four of the five measurements taken (Lindsey 1939:fig. 1) involved the distal end of the valve (which happens to be that part of the valve where *P. communis* and *P. albescens* differ most); and the individual variation there (in what had to be pure *communis*) was enormous: coefficients of variation for the four valval measurements were 10.48, 25.44, 29.14, and 59.42.

In his field guide, Klots (1951:216) wrote, "Opinions differ as to whether *albescens* should be considered a color variety or subspecies of *communis*, or a separate species. Despite its name it varies through the same range from dark to light forms as *communis*. But it appears to be constantly genitalically distinct from *communis*, with which its range overlaps. So I treat it as a distinct species." At about the same time, Evans (1953)—with his post-Mayr (1942) proclivity for lumping related species that seemed at least partly allopatric into a single polytypic species (see Burns &

Kendall 1969 for fuller discussion)—treated *albescens* as a subspecies of *communis*. On the basis of British Museum (Natural History) material, he recorded *P. communis communis* from Canada through the United States to southern Mexico (Guerrero, Puebla, and Veracruz) and *P. communis albescens* from the southwestern United States (southern California, Arizona, Colorado [just one male], and Brownsville, Texas) to southern Mexico (Colima, Michoacán, and Veracruz).

After recording *P. communis albescens* from 20 mi. east of Descanso and from San Quintin, Powell (1958:31) observed, "While previously known in Baja California only as far north as Angeles Bay, *albescens* is a typical arid-country form and is to be expected throughout the peninsula. The Descanso specimen, a male, is intermediate between *albescens* and *communis communis* in genitalic structure, as is characteristic of populations in the San Diego [California] area."

Tilden (1965:91) opened his questioning note with "The status of *Pyrgus communis* Grote and *Pyrgus albescens* Ploetz is one of the unsettled problems in the study of American Hesperiidae. *P. albescens* has been considered a form or a subspecies of *P. communis*, or a distinct species"; and he (Tilden 1965:93) closed it with "*P. communis* and *P. albescens*, while perceptibly different, do not seem to exhibit the degree of differences usually associated with either specific or subspecific status. Since each occupies a range, with intergradation along the lines of meeting and in some instances over considerable areas as well, they do not seem to be forms of one another in the usual sense of the term. There seems to be no taxonomic category that expresses their relationship precisely." In the body of his short paper, Tilden provided some new distributional and ecological information, some of which he used to justify his taxonomic equivocation. For example, "In Arizona, specimens from north of the Mogollon Rim were *P. communis*, as were those from higher elevations in the isolated ranges to the south. The higher elevations of such ranges as the Santa Catalina Mountains and the Santa Rita Mountains yield *P. communis*, while the open desert usually is inhabited by *P. albescens*. At Sycamore Canyon, Santa Cruz County, Arizona, specimens with genitalia of both types were taken. This is a locality of intermediate elevation. . . . On the basis of available data, it appears that *P. communis* occupies cool and temperate regions, even when such areas occur as islands surrounded by deserts. *P. albescens* seems to be adapted to low-elevational warm areas, which may be either dry (Arizona, southern California) or humid (Gulf Region of Texas) [this was a novel and, as it turns out, significant observation]. . . . [Some workers] regard each as a valid species that replaces the other in the proper environment. . . . The genitalic differences suggest this view. Yet it seems unlikely that this treatment would have been proposed by these workers had they been aware of the degree of intergradation that takes place along some of the interfaces. . . . [Some workers] regard each as a subspecies that replaces the other in the proper environment. . . . This interpretation also presents some problems. If the ranges are mapped in southern Arizona, we find the interesting condition of one subspecies (*P. communis communis*) existing as small islands surrounded by populations of the other (*P. communis albescens*)." Two decades later, in his field guide, Tilden treated *albescens* as a subspecies but remarked, "Status remains unsettled; some experts consider it a separate species" (Tilden & Smith 1986:256).

At that point in time, Austin (1986:55) introduced his analysis of the situation in Nevada with "The status of *Pyrgus communis* (Grote) and *Pyrgus albescens* Plötz . . . has been in question up to the present. They have been treated as separate species, as subspecies, or neither (Tilden 1965). Even the most recent regional and taxonomic treatments vary"; and he (Austin 1986:57) concluded with "Intermediacy, at least in southern Nevada, is greater than previously reported. This indicates that the two phenotypes are closely related, and are probably no more than allopatric subspecies of *Pyrgus communis*." He examined the left valves of more than 500 Nevadan males; classified them as *communis*, *albescens*, or intermediate; and mapped their distribution, with the following results: "Individuals of the *P. communis* phenotype occur throughout Nevada (Fig. 2); those of the *P. albescens* and intermediate phenotypes occur in southern Nevada except for one *P. albescens* from Carson City (Fig. 2). At most stations where *P. albescens* were taken, intermediates and *P. communis* were taken also. Individuals with intermediate valvae occur only within the range of *P. albescens*. There is no strict ecological or elevational segregation in southern Nevada, but phenotype proportions do vary. The *P. albescens* phenotype dominates at lower elevations and latitudes. Intermediates and *P. communis* become more prominent with increase in elevation and latitude. . . . The Nevada distribution is compatible with that previously noted (Tilden 1965) for *Pyrgus communis*; the latter is a more northern and higher elevation phenotype, *P. albescens*, a lower-elevation and more southerly phenotype."

For southeastern Arizona, Bailowitz and Brock (1991:59) treated these skippers as sibling species and repeated the Tilden (1965) view of the more cool-adapted *communis* occupying mountain islands in a

sea of the more warm-adapted *albescens* but conceded that "the situation is not quite so clear cut as genitalic intergrades occur regularly in areas of overlap." Specifically they noted that, in contrast to the widespread *albescens*, "*communis* is restricted to the higher mountain ranges. Tilden (1965) cited the taxon from the Sta Catalinas, Sta Ritas, and even Sycamore Cyn but all specimens examined genitalically from these areas have proved to be *albescens*. To date, confirmed records exist only for the Pinaleños, Chiricahuas, and the Dragoons with several intermediate specimens from around Safford."

Differences of opinion endure. They are reflected most recently in *Systematics of Western North American Butterflies* where the checklist of California butterflies (Emmel et al. 1998:836) calls *communis* and *albescens* separate species while, on the facing page, the checklist of Nevada butterflies (Austin 1998:837) calls them subspecies.

The subspecific interpretation hinges on the perception of genitalic intergrades between *communis* and *albescens* (presumably stemming from interbreeding between the differentiates). As indicated above, such intermediacy has repeatedly been seen and cited over the years. I started looking into the *communis*/*albescens* relationship in 1963; and, for far more than a decade, I, too, saw continuous valval intergradation. But I finally realized that it does not exist—that, instead, males of each species (Figs. 1–8) vary greatly in valval expression around readily separable modes (Figs. 9–20) and that even the seemingly continuous variation actually forms two discrete clusters. There are no intergrades. There are two reproductively isolated species.

MATERIALS AND METHODS AND RELEVANT BACKGROUND

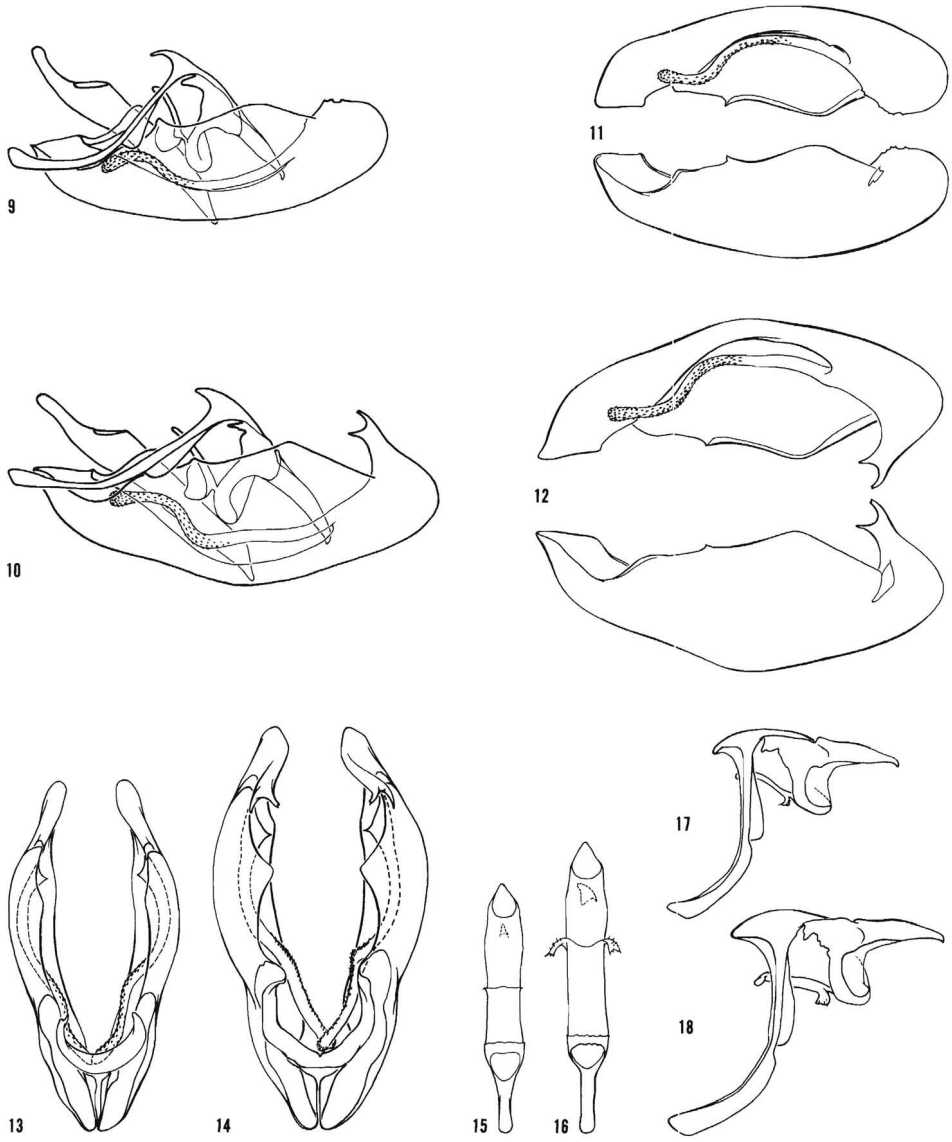
Over the course of this prolonged project I critically compared the genitalia of 3060 males (I still cannot distinguish females of *P. communis* from those of *P. albescens*) and pinned my sex-and-determination label on each. Genitalia were fully dissected (after brief boiling of detached abdomens in 10% KOH) and stored free in one-dram vials of glycerol (Burns 1997) or, more often, were partly dissected—or simply dusted—dry, *in situ*, to expose the valves. From 1978 to 1981 a detached observer prepared a 4″ × 6″ file card for each male that he dissected (his dry-dissected males were individually coded P-1 to P-975) as well as for each previously KOH-dissected male, with a drawing of the distal end of its left valve on one side and all other information, including field data, on the reverse. I gradually came to recognize two discrete clusters within ostensibly continuous valval variation by repeatedly playing a sort of genitalic solitaire—i.e., by thoroughly mixing and shuffling the cards and trying to sort the genitalia to kind without knowing their geographic origin in advance.

Material accumulated from many sources (see Acknowledgments) was augmented both by my own opportunistic collecting in various situations and, more importantly, by field trips expressly for *P. communis* and *P. albescens* with my wife, Sarah: to southeastern Arizona in 1974, to southcentral California in 1987, to northern New Mexico in 1989, to eastern Arizona in 1991, and to southeastern Arizona in 1999. Where these skippers fly together, we sampled them randomly because they are superficially inseparable.

While collecting material for my evolutionary study of *Erynnis* (Burns 1964), Sarah and I incidentally had taken males of *albescens* (but not of *communis*) at high elevations in mountains of southeastern Arizona, as follows:

Chiricahua Mountains: Rustler Park, 8500 ft [2590 m], 21 June 1958, 1 ♂.
Pinaleño Mountains: Treasure Park, 8900 ft [2715 m], 19 June 1958, 1 ♂;
Soldier Creek Campground, 9400 ft [2865 m], 26 June 1958, 1 ♂;
Swift Trail, twixt Ladybug Saddle & Shannon Park, 8600–9000 ft [2620–2745 m], 27 June 1958, 1 ♂.
Blue Range of White Mountains: twixt Grey Peak & Rose Peak, 6000–7000 ft [1830-2135 m], 6 June 1959, 4 ♂.
White Mountains: K.P. Cienega, 5 mi [8 km] S Hannagan Meadows, 9000 ft [2745 m], 6 June 1959, 1 ♂.

Somewhat conversely, on 25 April 1959, we—and on 3 and 6 September 1959, I—had taken males of both *communis* and *albescens* together at relatively low elevations of 4600 to 4100 ft (1400 to 1250 m) on the bahada at the foot of the Chiricahua Mountains and much farther out in the desert, a little north of Rodeo, New Mexico. Because these data did not support Tilden's (1965) Arizonan pattern of highland *communis* and lowland *albescens*, we made the Southwestern Research Station (in the Chiricahua Mountains) of the American Museum of Natural History our base of operations during the summer of 1974, with the intention of sampling *Pyrgus* in numbers from the desert floor to the tops of several of the mountain islands to see whether *communis* and *albescens* really do show average differences in their elevational preference and remain partially segregated for that reason. Unfortunately, Arizona had just been through a long, record-



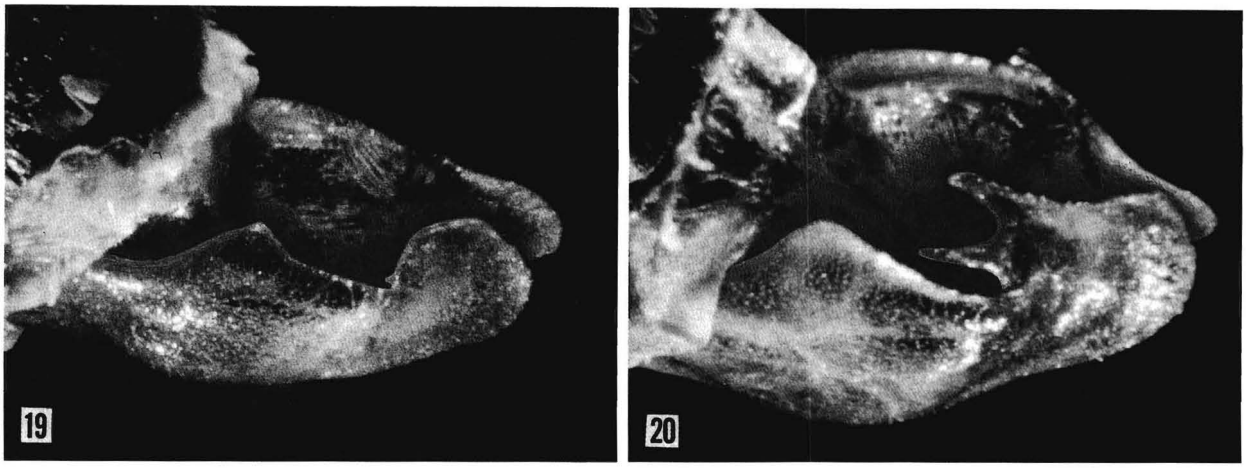
FIGS. 9–18. Genitalia of 2 ♂ *Pyrgus* from Portal, Chiricahua Mountains, 4800 ft [1465 m], Cochise County, Arizona, USA, 21 & 30 July 1974, J. M. & S. N. Burns (USNM). **9, 11, 13, 15, 17,** *P. albescens* (odd-numbered) (genitalia dissection no. X-1016). **10, 12, 14, 16, 18,** *P. communis* (even-numbered) (X-1013). **9, 10,** complete genitalia (minus right valva) in left lateral view. **11, 12,** left valva in medial (upper) and lateral (lower) views. **13, 14,** both valvae in dorsal view. **15, 16,** aedeagus in dorsal view. **17, 18,** tegumen, uncus, gnathos, vinculum, and saccus in left lateral view.

breaking drought so severe that most rhopaloceran populations were extremely depressed. The only place we could find these normally common and widespread skippers in any numbers was at Portal, at the base of the Chiricahuas, in an irrigated alfalfa field (complete with weedy, malvaceous larval foodplants, including the introduced *Malva parviflora* L.), whose owners graciously allowed us to work its perimeter again and again. During the early seventies, I had been preparing to publish on a complex, transcontinental hybrid zone between *communis* and *albescens*. Our hard-won 1974 Portal sample of 119 *Pyrgus* males, plus a lot of subsequent genitalic solitaire, changed all that.

In the end I examined the genitalia of 1910 males of *P. communis* (Canada 100, USA 1700, Mexico 110) and 1150 males of *P. albescens* (USA 930, Mexico 220).

GENITALIC DIFFERENCES

Differences between *P. communis* (Figs. 10, 12, 14, 16, 18, 20) and *P. albescens* (Figs. 9, 11, 13, 15, 17, 19)



FIGS. 19, 20. Genitalia *in situ* of 2 ♂ *Pyrgus*; left dorsolateral view. **19,** *P. albescens*, Cantonment, Escambia County, Florida, USA, 7 September 1984, J. M. Burns (USNM). **20,** *P. communis*, Skippers, Greensville County, Virginia, USA, 9 October 1982, J. M. Burns (USNM).

appear in the valves (or claspers) of the male genitalia—primarily at the distal end. Here, in *communis*, a major process sweeps anterodorsally, typically terminating in a pair of prominent prongs (Figs. 10, 12, 20). By contrast, in *albescens*, the distal end of the valve presents a relatively low profile, either with or without (Figs. 9, 11, 19) one or two incipient prongs which are usually so undeveloped as to look more like teeth. Secondarily, the body of the valve is higher and more massive in *communis* (Figs. 10, 12, 20) than it is in *albescens* (Figs. 9, 11, 19), where it is typically lower and leaner (a difference not previously reported).

Because some arguments in my analysis of genitalic variation depend on knowing how these skippers are geographically distributed with respect to each other, I consider that next.

GEOGRAPHIC DISTRIBUTION

Pyrgus communis ranges from southern Canada through most of the United States to southern Mexico. In Canada (see Layberry et al. 1998:45 [map]) it occurs primarily in southern portions of the Prairie Provinces (Manitoba, Saskatchewan, and Alberta) plus southeastern British Columbia; eastward, it edges into far southern Ontario. Although in the USA (Fig. 21) it extends from coast to coast and from sea level to over 10,000 ft (3050 m), in the East it shuns northern New England (Maine, New Hampshire, and Vermont) and adjacent eastern New York—and, at the other extreme, the southern tip of Florida—while in the West it essentially avoids southern California and adjacent southwestern Arizona. In Mexico (Fig. 22) it extends south at least to Oaxaca, apparently through interior, more or less montane, country (however, the spotty data [Fig. 22] may be somewhat misleading, especially in view of this skipper's low-level, coastal-plain occurrence in Cameron County at the southmost tip of Texas just across the Mexican border [Fig. 21]).

Pyrgus albescens ranges from the southern United States to southern Mexico. In the western USA (Fig. 21) it extends from southern California through southern Nevada, the southwestern corner of Utah, all or almost all of Arizona, and southern and central New Mexico (with one male straying northward in California [Calaveras County], Nevada [Carson City according to Austin 1986], Utah [Tooele County], and Colorado [Alamosa County]), and on through western Texas to southern Texas (as far east as the Corpus Christi area of the Gulf Coast according to Tilden 1965). This has long been considered its eastern limit. But, in reality, *P. albescens* continues eastward along the Gulf coastal plain through eastern Texas, southern Louisiana, southern Mississippi, southern Alabama, southern Georgia, and the Florida panhandle to a point on the Atlantic Coast nearly halfway down the Florida peninsula (Fig. 21). Repeatedly characterized as an arid-country differentiate, *albescens* clearly thrives in very humid climates, too (as noted before by Tilden [1965]). In mainland Mexico (Fig. 22) it occurs from coast to coast and extends south at least as far as Veracruz and Guerrero; moreover, it extends the entire length of the Baja California peninsula (Fig. 22 and Brown et al. 1992:35 [map]).

Despite their similar southern limit in mainland Mexico—which may be attributable, at least in part, to replacement by a near relative, *P. adepta* (Plötz)—*P. communis* and *P. albescens* differ sharply in total distribution, with *albescens* much the more austral of the

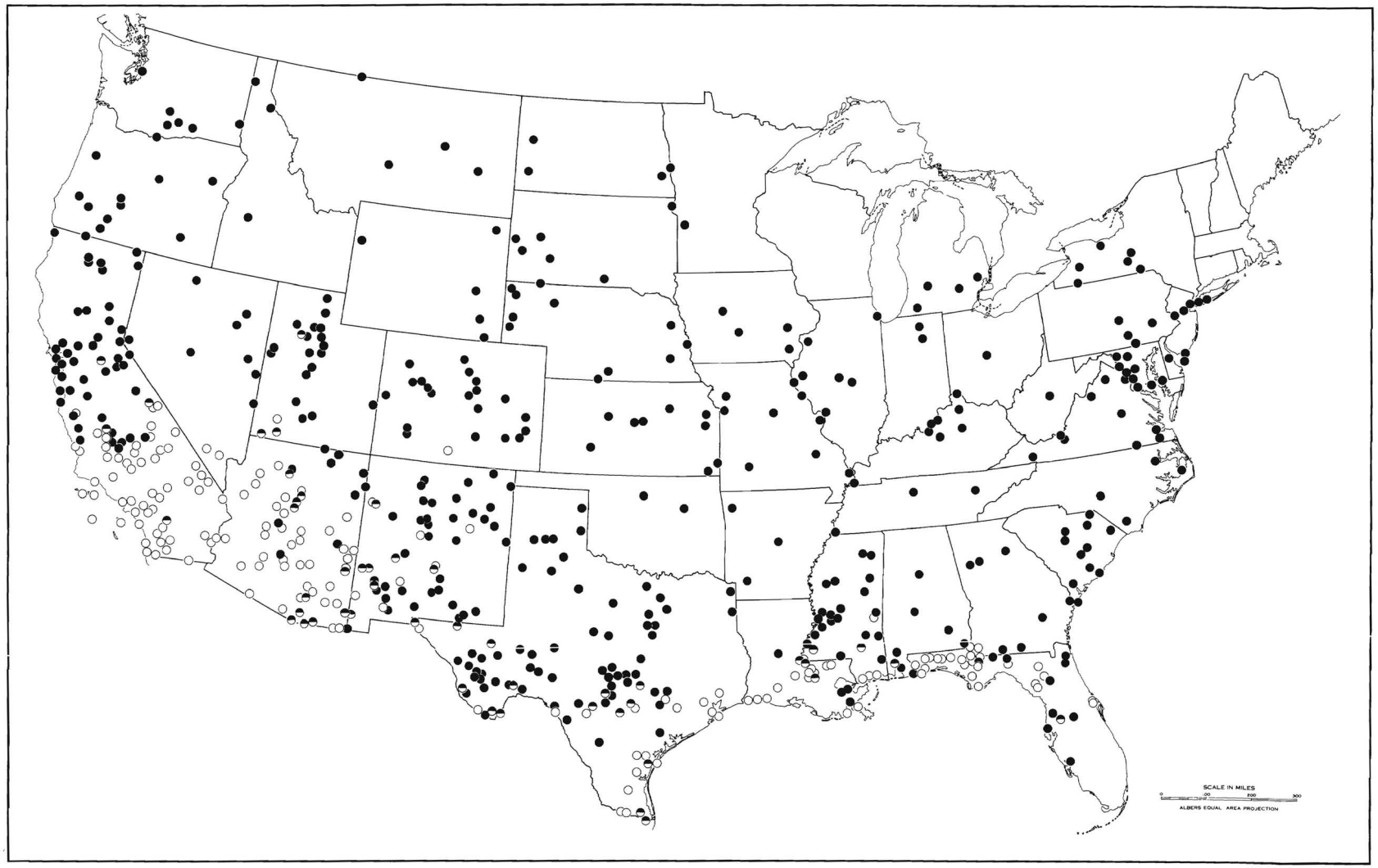


FIG. 21. Geographic distribution of *Pyrgus communis* and *P. albescens* in the United States of America (based on males whose genitalia I have examined). Dots, *P. communis*; circles, *P. albescens*; half-dots, both species at the same spot.

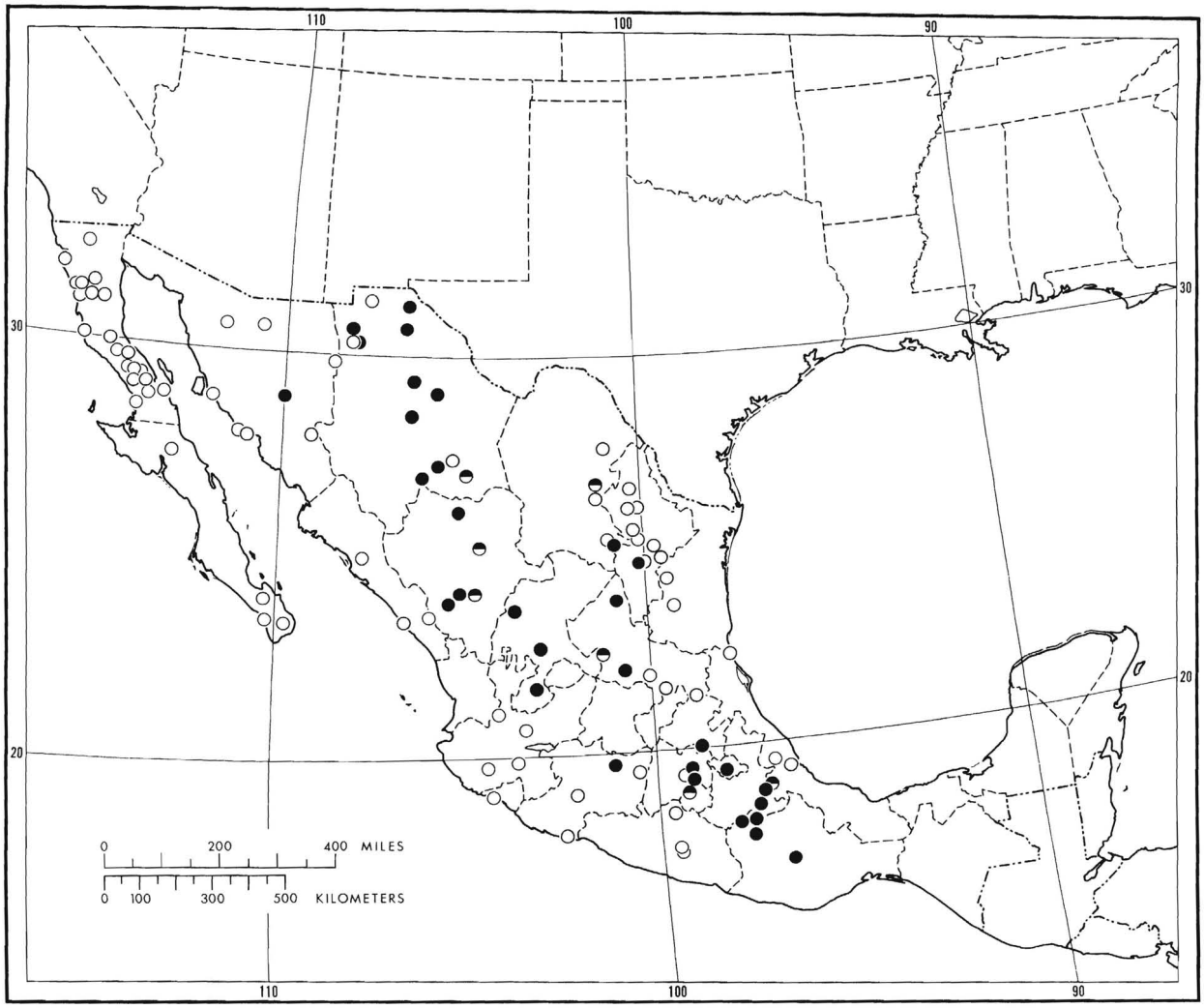
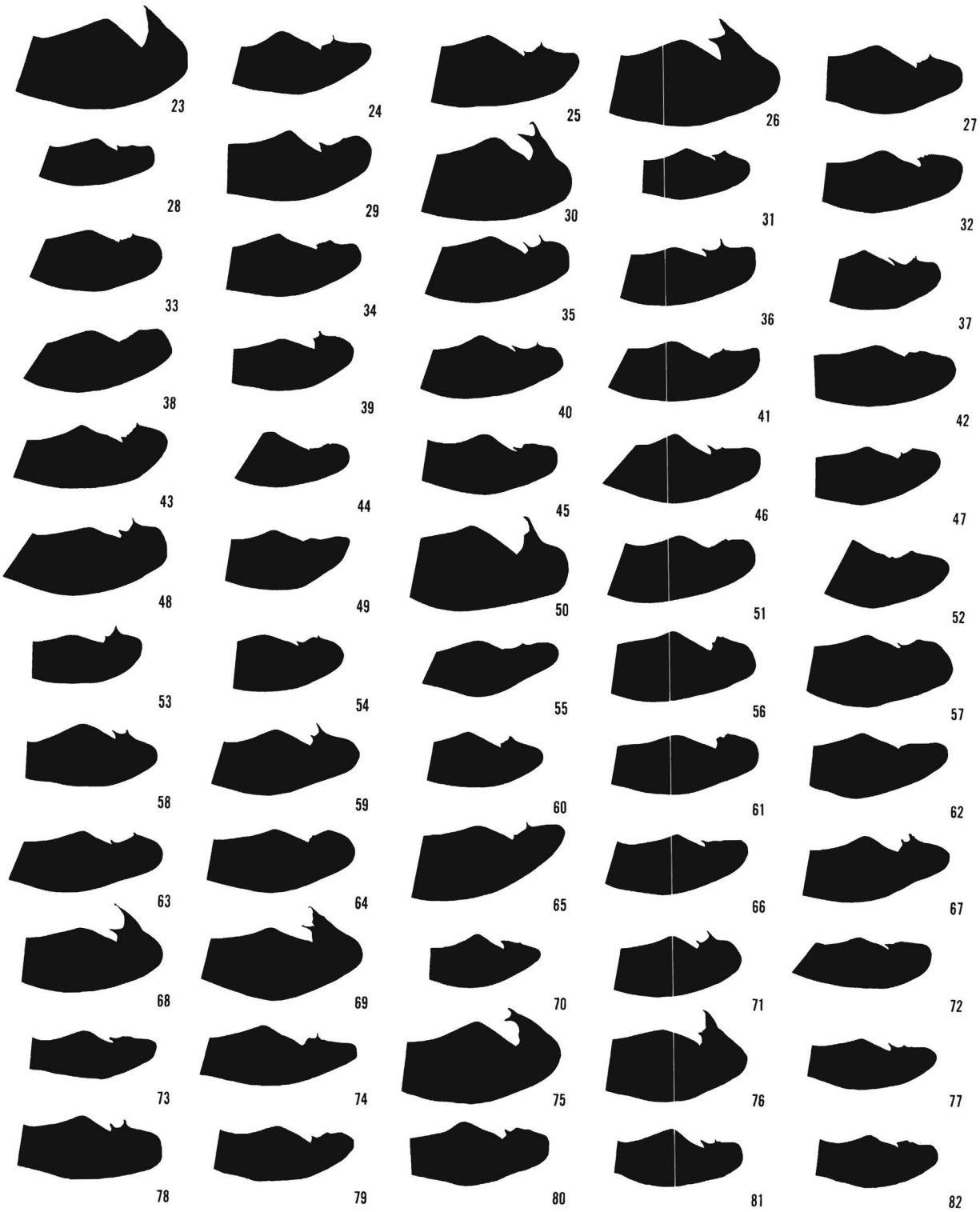


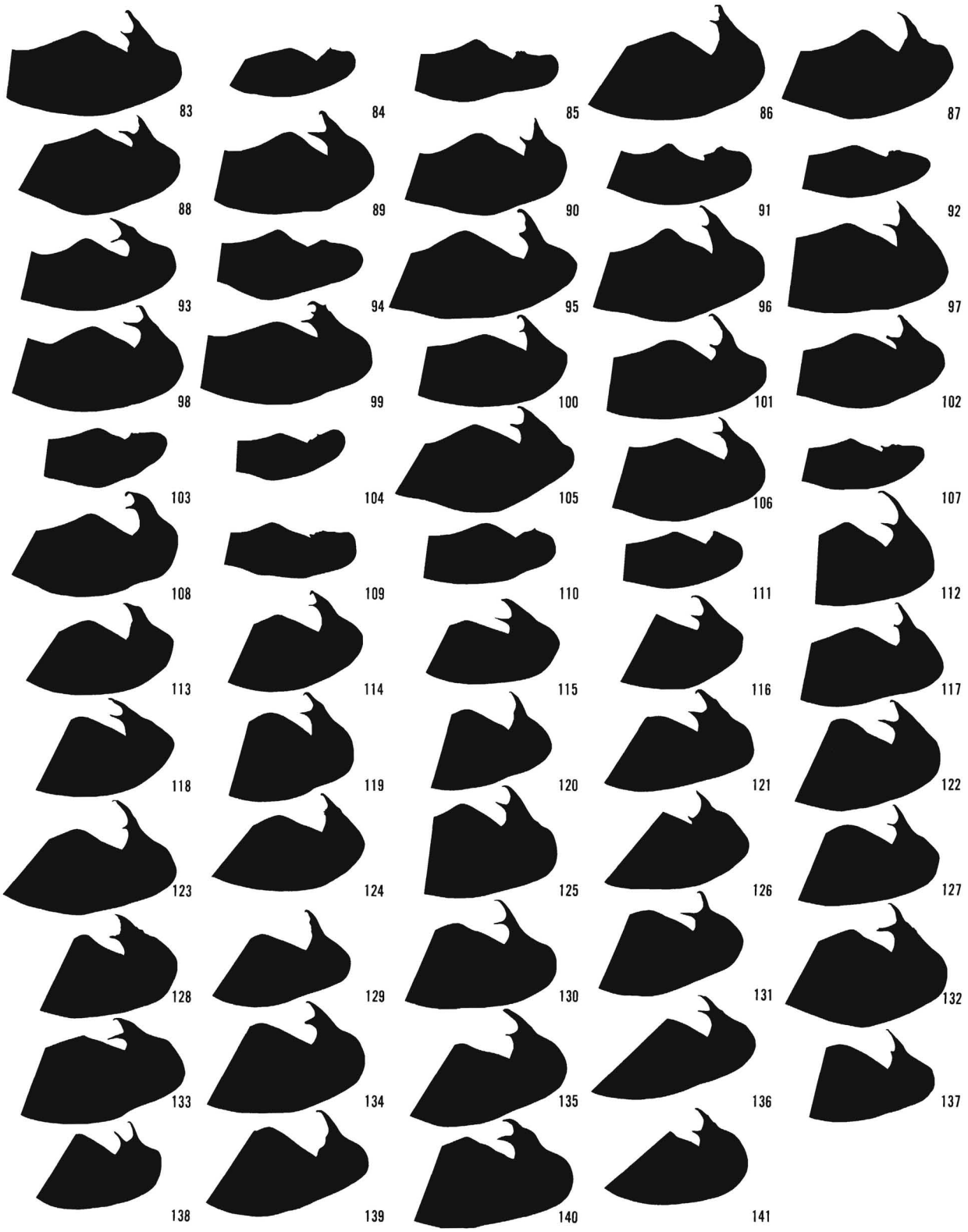
FIG. 22. Geographic distribution of *Pyrgus communis* and *P. albescens* in Mexico (based on males whose genitalia I have examined). Dots, *P. communis*; circles, *P. albescens*; half-dots, both species at the same spot.

two. But their spatial interaction is not simple. Except for one male *albescens* from western Calaveras County (Mokelumne Hill, F. E. Blaisdell [CAS]) and one male *communis* from the San Jacinto Mountains (Tahquitz Canyon, Riverside County, 21 October 1939, F. H. Rindge [AMNH]), *communis* and *albescens* closely replace each other across southcentral California with little or no regard for elevation (Fig. 21). Each species seems to inhibit the other's expansion. Again, they appear to be only narrowly sympatric along the Gulf Coast from eastern Texas to Florida (Fig. 21). On the other hand, these species are broadly sympatric through the southwestern USA and montane Mexico (Figs. 21, 22)—areas in which they may have been in contact for the longest time.

How recent is the range of *P. albescens* in the eastern USA? My earliest record is 1 ♂ from 3 mi (4.8 km) east of Liberty, Liberty County, Texas (this is northeast of Houston), which was reared out on 24 July 1923 from a larva on *Sida rhombifolia* L. (Malvaceae) (USNM). The next *albescens* come from Houston itself on 4 July 1949 (1 ♂, J. J. Winston [LACM]) and 11 & 12 August 1957 (3 ♂, J. M. & S. N. Burns [USNM]). Specimens from Louisiana (49 ♂, G. Strickland [USNM]) and Mississippi (18 ♂, B. Mather, M. & E. Roshore, R. Kergosien, C. Bryson [MEM, USNM]) date from the sixties and early seventies—one from 1960, the rest from 1967–72 (for an exact plot of most localities in these two states, see Fig. 375). Specimens from the western tip of Florida (Escambia County)



FIGS. 23–141. Genitalia of 119 ♂ *Pyrgus*—in order of capture—from a single field at Portal, Chiricahua Mountains, 4800 ft [1465 m], Cochise County, Arizona, USA, summer of 1974, J. M. & S. N. Burns (USNM); distal end of left valva in lateral view. **23–27,** 11 July; **28, 29,** 13 July; **30–43,** 17 July; **44–46,** 18 July; **47–49,** 20 July; **50–52,** 21 July; **53–67,** 23 July; **68–87,** 27 July; **88–111,** 30 July; **112–141,** 5 August. **23, 26, 30, 50, 68, 69, 75, 76, 83, 86–90, 93, 95–102, 105, 106, 108, 112–141,** *P. communis* (N = 56). **24, 25, 27–29, 31–49, 51–67, 70–74, 77–82, 84, 85, 91, 92, 94, 103, 104, 107, 109–111,** *P. albescens* (N = 63).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date from 22 May 1976 (Pensacola Beach, 1 ♂ [USNM]) and 7 September 1984 (Cantonment, 12 ♂, J. M. Burns [USNM]). Those from farther east in Florida as well as directly to the north in Alabama and Georgia (34 ♂, J. V. Calhoun) date from 1989–95. An eastward progression of *albescens* suggested by these dates could be an artifact because the dates largely reflect times when I begged sympathetic, suitably situated, local collectors to sample *Pyrgus*. (Most collectors find these ubiquitous skippers trashy and do not stoop to collecting them, especially not in series). If the presence of *albescens* along the Gulf Coast is none too recent, then consider this: Grote (1872:69) described *P. communis* from "central Alabama"—presumably the vicinity of Demopolis, which was his home—so he may have come within a hundred miles (160 km) of catching its look-alike, *P. albescens*, instead (or besides).

However, it is clear that *P. albescens* is currently increasing in numbers and spreading eastward and southward in Florida at a rapid rate. In September and October 1999, J. V. Calhoun caught a total of 70 male *albescens* not only in most counties of the panhandle but also at the top of the peninsula—in Alachua, Gilchrist, and Levy counties—and nearly halfway down the peninsula in Pasco County on the Gulf side and in Volusia and Brevard counties on the Atlantic side (Fig. 21). At the same time, he caught no *P. communis* whatsoever. In Pasco County, he took 12 male *albescens* in the very area (southeast of Dade City) in which, 9 and 10 years earlier, at similar times of year, he got only *communis*. In examining the *Pyrgus* material of the Florida State Collection of Arthropods, I found 33 male *P. communis*—taken between 1942 and 1977 in Alachua, Clay, Duval, and Liberty counties—but no Florida examples of *P. albescens*. At least at this evolutionary moment, *albescens* seems to be expanding at the expense of *communis* and even displacing it—a potentially instructive situation that should be closely followed.

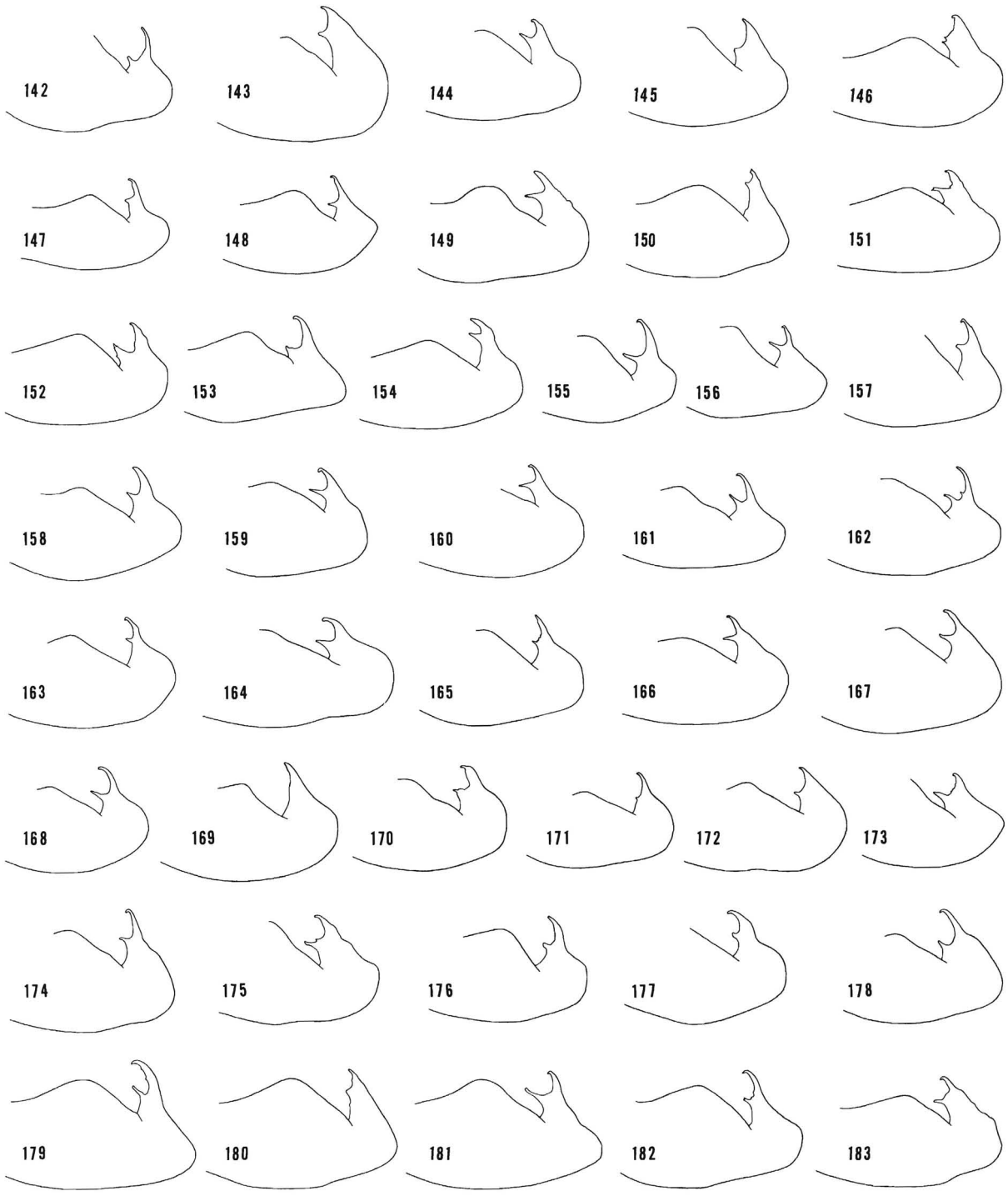
In the southwestern USA, where overlap is so extensive, some northern records of sympatry go further back in time. For example, at Ft. Wingate, McKinley County, New Mexico, *P. albescens* was taken on 18 June 1906 and *P. communis* on 19 July 1906 (AMNH); and at St. George, 2800 ft (855 m), Washington County, Utah, both species were taken on 10 June 1919 by T. Spalding (AMNH). Defying a strictly lowland pattern, *albescens* (1 ♂) flew with *communis* (11 ♂ in all) at Loop Camp, 7400 ft (2255 m), 13 mi (21 km) southwest of Grantsville, Tooele County, in northern Utah between 16 & 20 July 1958, F., P., & J. Rindge (AMNH). In a large majority of cases, the sympatry of *P. communis* and *P. albescens* indicated by half-dots in Figs. 21 and 22 has also involved synchrony.

Where *P. communis* and *P. albescens* coexist, their mutual spatial relations are no doubt dynamic and, therefore, rather unpredictable. *Pyrgus communis* has long been known as a mobile species whose northern distributional limit fluctuates considerably. Both species regularly invade weedy, disturbed habitats. Though predominantly austral, *albescens* shows up high on the tops of various mountain islands (see Materials and Methods and Relevant Background for some specific examples). Even the Portal, Arizona, sample of *Pyrgus* (Figs. 23–141) shifts, over 26 days, from mostly *albescens* to mostly *communis*.

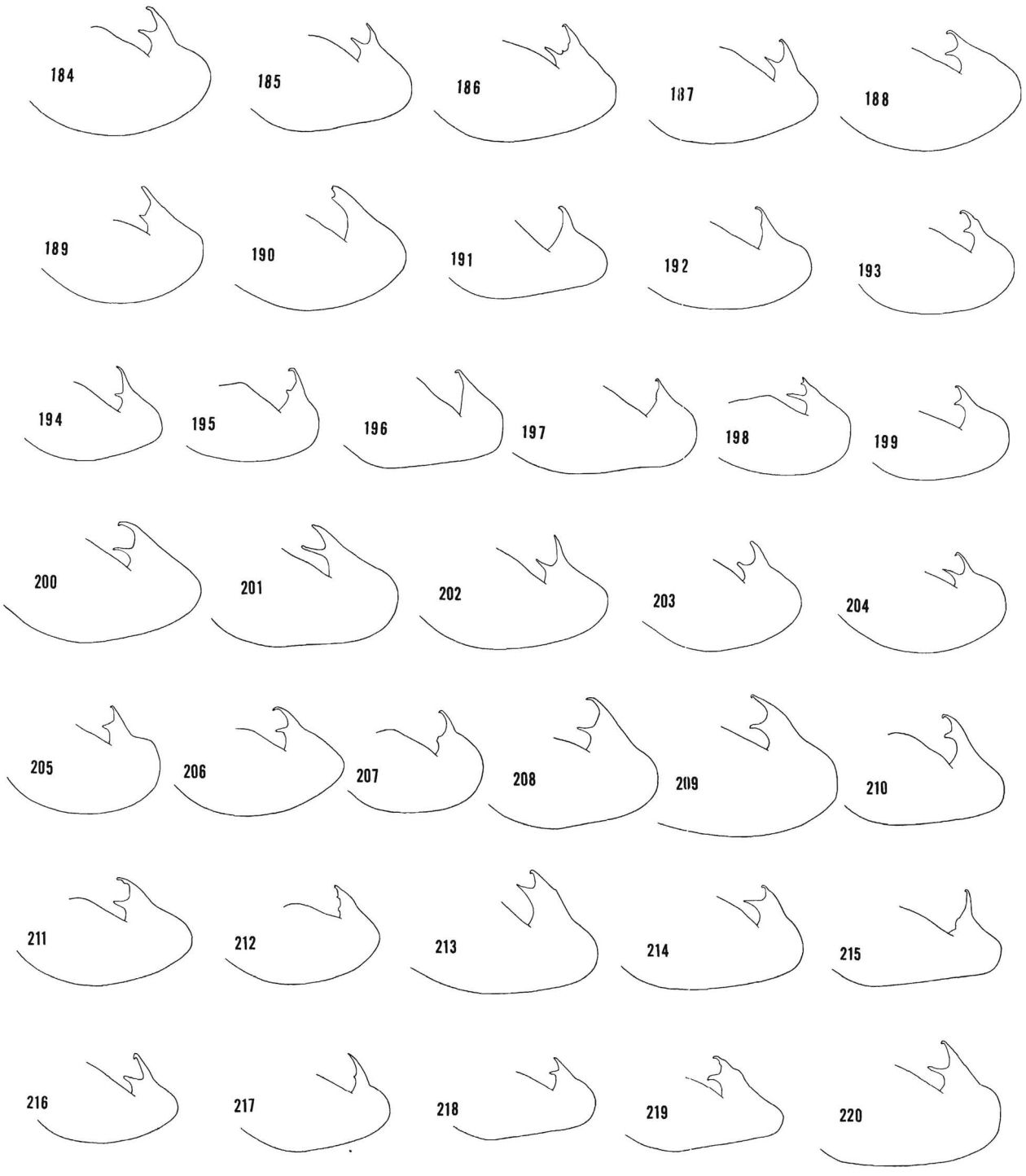
GENITALIC VARIATION

Although the rampant variation in the male genitalia of the Portal, Arizona, sample of *Pyrgus* (Figs. 23–141) may look continuous at first, it clusters about two distinct modes. The variation around each of these modes is extraordinary. In *P. communis*, with the higher, more massive valve, the diagnostic valval process varies so much in its length and width, and in the relative development of its paired, terminal prongs, that no two individuals are exactly alike. In some of the more extreme individuals, the lower terminal prong is weakly developed (Figs. 76, 100, 123, 137) or vestigial (Figs. 50, 120, 124) or completely missing (Figs. 23, 87, 113, 129, 139)—yet even then the resulting, simpler, one-prong process varies from narrow (Figs. 87, 129, 139) to intermediate (Fig. 113) to wide (Fig. 23). Occasionally, an extra terminal prong appears (Fig. 99). Most individuals express the typical two-prong process (Figs. 26, 30, 68, 69, 75, 83, 86, 88–90, 93, 95–98, 100–102, 105, 106, 108, 112, 114–119, 121, 122, 125–128, 130–136, 140, 141), but each in his own way; and in one, this process is uncommonly short (Fig. 138). It is no wonder that Lindsey (1939), in measuring four aspects of the valval process and its prongs in 100 males of *P. communis*, obtained such enormous coefficients of variation.

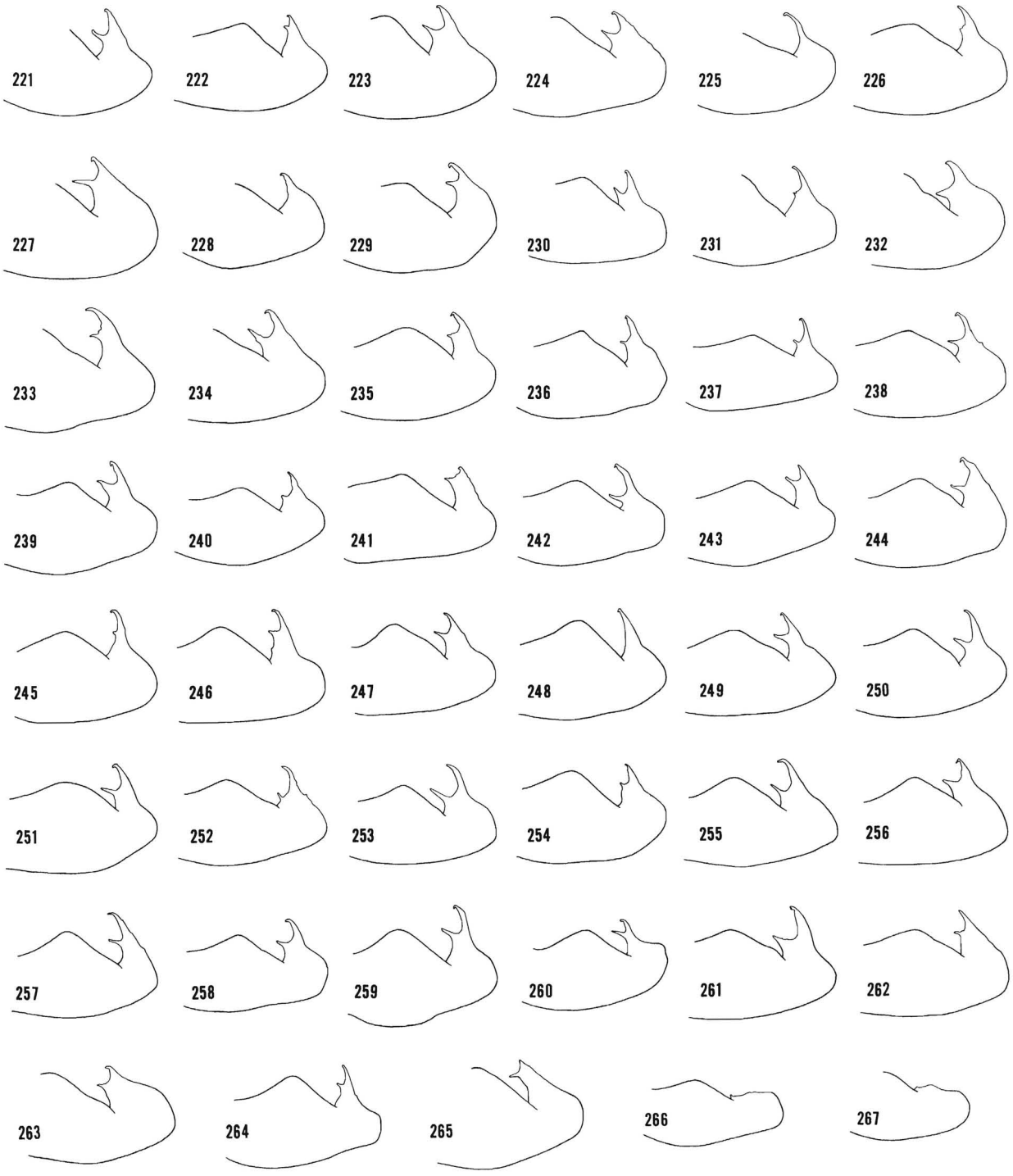
Again, in *P. albescens*, with its lower, leaner look, the variation in the valve is so great that every individual is visibly unique—but none occupies the gap between *albescens* and *communis*. The dorsodistal end of the valve, which rarely is fairly even (Figs. 49, 62), usually shows traces (Figs. 28, 32, 33, 38, 41, 42, 44, 47, 51, 52, 55, 61, 64, 70, 72, 73, 82, 84, 92, 94, 103, 104, 109–111) or real beginnings (Figs. 24, 27, 29, 31, 34, 45, 54, 56, 57, 60, 66, 74, 77, 79, 80, 85, 91, 107) or clear expressions (Figs. 25, 36, 37, 39, 40, 43, 46, 48, 53, 58, 59, 63, 65, 67, 78, 81) of one or two teeth, which rarely develop further into incipient but modest



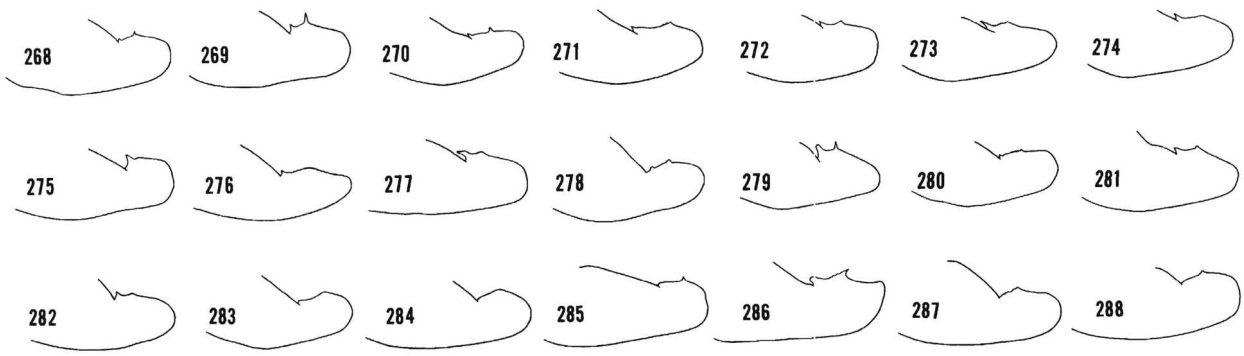
FIGS. 142–183. Genitalia of 42 ♂ *Pyrgus communis* from Galivants Ferry, Horry County, South Carolina, USA, 16 August 1957 to 27 September 1981, J. M. Burns (USNM); distal end of left valva in lateral view.



FIGS. 184–220. Genitalia of 37 ♂ *Pyrgus communis* from Meade County, South Dakota, USA, 27 to 30 July 1975 (USNM); distal end of left valva in lateral view.



FIGS. 221–267. Genitalia of 45 ♂ *Pyrgus communis* (3 March to 30 May 1966 and 30 April to 3 June 1967) plus 2 ♂ *P. albescens* (16 May and 3 June 1967) from Austin, Travis County, Texas, USA, J. M. Burns (USNM); distal end of left valva in lateral view.

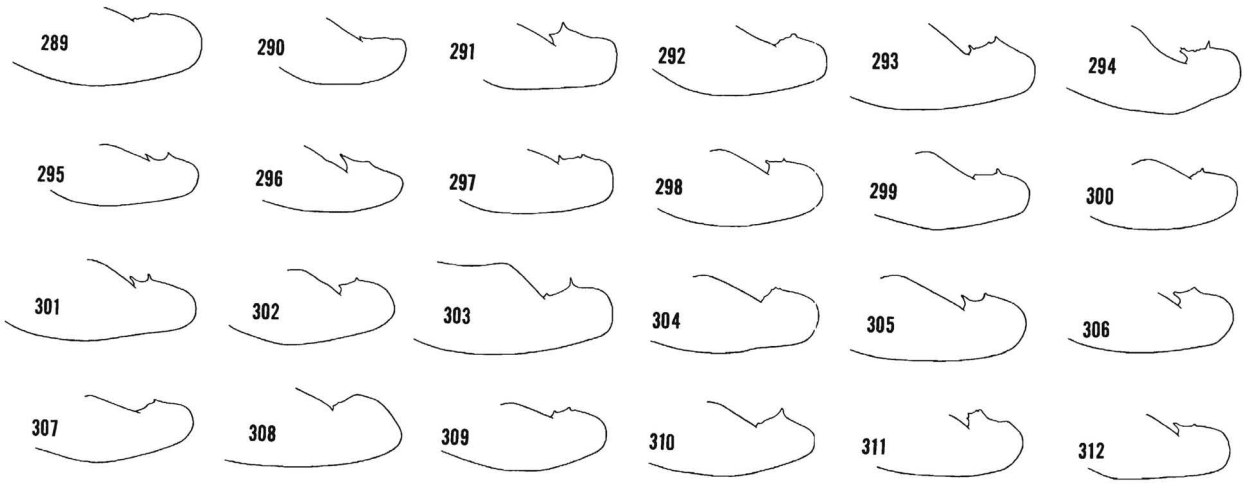


FIGS. 268–288. Genitalia of 21 ♂ *Pyrgus albescens* from Harlingen, Cameron County, Texas, USA, 8 December 1957 to 21 June 1958, J. Hunt (UCB); distal end of left valva in lateral view.

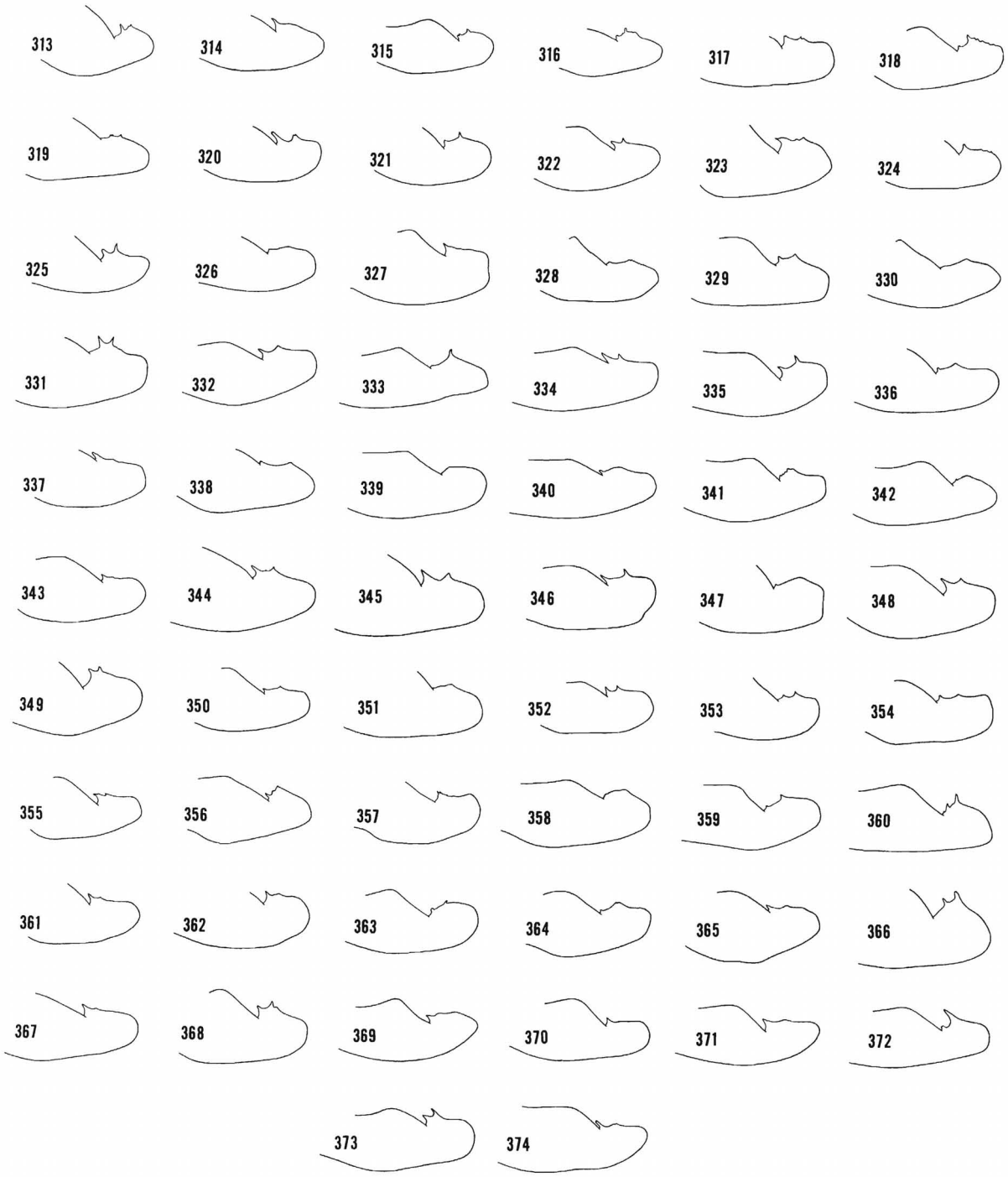
prongs (Figs. 35, 71). Although this variable expression of one or, more often, two teeth on the low distal end of the valve is perfectly normal for *albescens*, it has regularly been mistaken for intergradation toward the elevated, two-prong process of *communis*. The five valval figures called "intermediates" by Austin (1986:fig. 1), for example, are all unadulterated *albescens*.

Despite the bimodal variation, some will ask, How do you know that many of the more extreme variants are not intergrades reflecting genetic exchange between *communis* and *albescens*? The answer comes from studying and comparing genitalic variation throughout each species' geographic range. In so doing, I have found, within each species, fully as much genitalic variation in areas of separation as in areas of contact or overlap. In other words, wherever it occurs, *P. communis* runs the gamut of variation on its specific genitalic theme, whether *P. albescens* is present or not—and vice versa. The high level of genitalic variation is not the result of hybridization between differentiates; rather, it is inherent in each.

I can convey all this best by showing genitalic variation in sizable samples from a variety of situations. For *P. communis*, these are northeastern South Carolina (Figs. 142–183) and western South Dakota (Figs. 184–220), both of which are well removed (in different directions) from any contact with *albescens* (Fig. 21); plus Austin, Texas (Figs. 221–267), where *communis* predominates but *albescens* does occur. For *P. albescens*, these are Harlingen (Figs. 268–288), a town almost 300 mi (480 km) due south of Austin in southernmost Texas where *albescens* predominates but *communis* does occur; plus San Diego, California (Figs.



FIGS. 289–312. Genitalia of 24 ♂ *Pyrgus albescens* from San Diego, San Diego County, California, USA, 30 August 1891 to 25 May 1959, F. E. Blaisdell, G. H. Field, F. M. Jones, J. Powell, W. S. Wright (CAS, UCB, USNM); distal end of left valva in lateral view.



FIGS. 313–374. Genitalia of 62 ♂ *Pyrgus albescens* from the region of Laguna Chapala, Punta Prieta, Bahia de Los Angeles, Rancho Rosarito, and Mission San Borja in southern Baja California Norte, MEXICO, 28 March to 2 April 1973, J. Donohoe, J. Doyen, D. Patterson, J. Powell (CAS); distal end of left valva in lateral view.

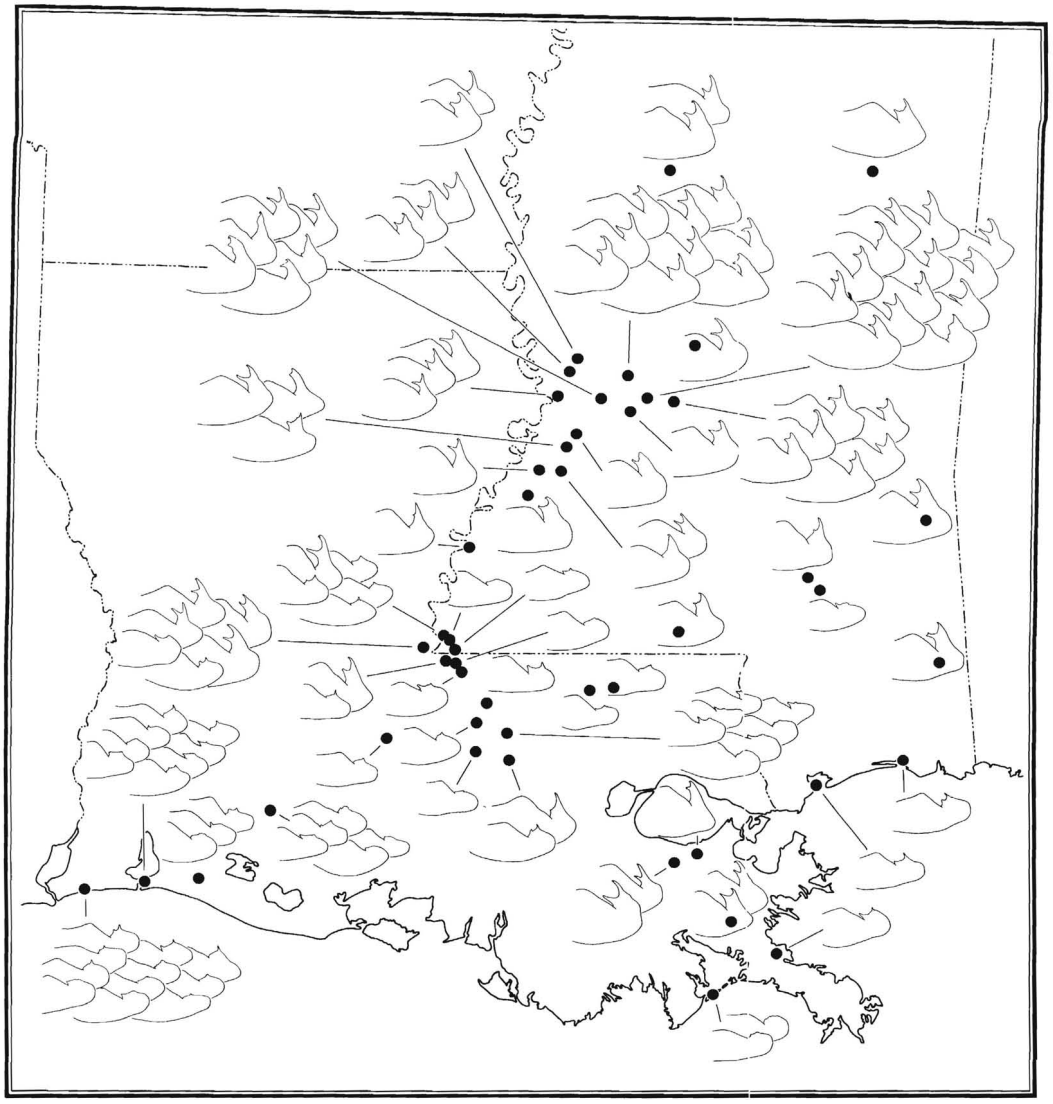
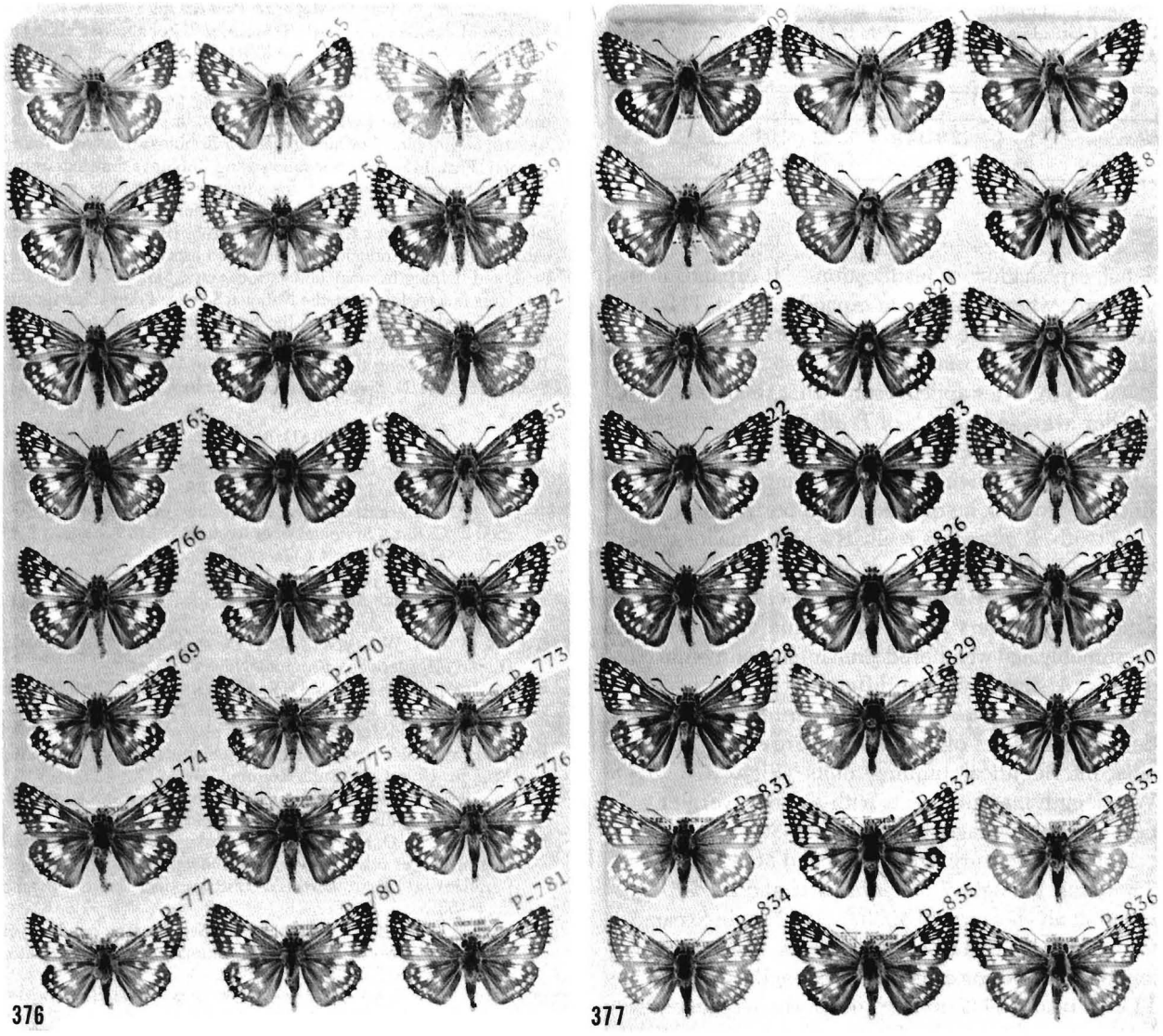


FIG. 375. Detailed geographic distribution of *Pyrgus communis* and *P. albescens* in Louisiana and Mississippi, USA, based on male genitalia, which appear (distal ends of left valvae) in lateral view.

289–312), and southern Baja California Norte (Figs. 313–374), both of which are well removed from any contact with *communis* (Figs. 21, 22). And, finally, for both species where they are in contact and narrowly sympatric, these are Louisiana and Mississippi (Fig. 375).

Most extreme among *P. communis* genitalic variants are those that have more or less lost the lower of the two prongs on the long valval process. Because I encountered a number of these individuals (Figs. 23, 50, 87, 113, 120, 124, 129, 139) in the Portal sample of mixed *Pyrgus*, it might be argued that loss of the prong reflects genetic input from *albescens*. But nothing would be further from the truth. Such one-prong variants have surfaced again and again in many different populations of *communis*—including not only those that are sympatric with *albescens* (as at Austin, Texas [Figs. 225, 228, 248]) but also those that are decidedly allopatric (as in South Carolina [Fig. 169] and, most notably, South Dakota [Figs. 191, 192, 196, 197, 212, 215, 217]).

Genitalic variants of *P. albescens* that tend most toward *P. communis* are those whose two teeth at the distal end of the valve are appreciably elevated as, for example, at Portal, Arizona (Figs. 36, 39, 58, 59, 67), and Harlingen, Texas (Figs. 269, 279)—both areas of



FIGS. 376, 377. 24 ♂ *Pyrgus albescens* (left) and 24 ♂ *P. communis* (right) from the same time and place (midsummer 1974, Portal, Chiricahua Mountains, 4800 ft [1465 m], Cochise County, Arizona, USA, J. M. & S. N. Burns [USNM]) arranged in pinning units of the same size to show the greater average wingspread of *P. communis*.

sympatry with *communis* and therefore of potential influence from it. But similar variants appear where *albescens* is well separated from *communis*, as at San Diego, California (Figs. 291, 294, 296, 311). Indeed, the most extreme variants of this kind have turned up in southern Baja California Norte (Figs. 325, 335, 344, 345, 348, 368, 373 and especially Figs. 331, 349, 366), where *albescens* is about as far removed and isolated from *communis* as it can be.

In light of this analysis, the picture of genitalic variation in Louisiana and Mississippi (Fig. 375) clearly shows *P. communis* and *P. albescens* meeting and slightly overlapping in space without genetically merging.

SIZE DIFFERENCE

It is always more satisfying to be able to bolster a difficult species separation based on subtle genitalic distinctions with evidence of another kind.

In his minimal original description of *P. occidentalis* (=*albescens*), Skinner (1906a:96) said, "This is a smaller . . . species than *tessellata*" (=*communis*); and, soon after, he claimed (Skinner 1906b:278)—with no

TABLE 1. Length (mm) of right forewing in *Pyrgus* males from Portal, Chiricahua Mountains, 4800 ft (1465 m), Cochise County, Arizona, USA, July to August 1974, J. M. & S. N. Burns (USNM).

Species	N	Range	Mean ± SE	SD	CV
albescens	63	12.0–14.9	13.72 ± 0.08	0.61	4.45
communis	54	13.2–15.6	14.58 ± 0.07	0.54	3.70

detail, explanation, or justification—"It expands in the ♂ 25 mm.; whereas *tessellata* expands 32 mm. This is an average size for the two." Tilden (1965:92) observed, "In long series, *P. communis* appears a bit larger. . . . *P. albescens* in series appears somewhat smaller. . . . The smaller average size . . . of *P. albescens* might be expected of a desert population, as compared with a related population living in a more temperate climate." But, like Skinner, he offered no supporting data.

In truth, *P. albescens* really is a little smaller than *P. communis*. The 1974 Portal, Arizona, sample is ideal for comparing size in these species because both were caught in numbers at the same time and place and presumably had weathered similar environmental conditions. A slight average difference in size becomes readily perceptible when the mounted, genitalically determined males of each species are segregated into adjacent, identical pinning units (Figs. 376, 377). Winglength measurements with a pair of vernier calipers show an average difference of 0.86 mm (Table 1).

A quarter century later, on 15 and 16 August 1999, Sarah and I caught 7 ♂ *P. albescens* and 21 ♂ *P. communis* at an elevation of 4000 ft (1220 m) in Sycamore Canyon, Santa Cruz County, Arizona. Mean forewing lengths of these coexisting *albescens* and *communis* are 13.41 mm and 14.25 mm, respectively—for an equivalent average difference of 0.84 mm.

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