

PHYLOGENY AND ZOOGEOGRAPHY OF THE BIGGER AND BETTER GENUS *ATALOPEDES* (HESPERIIDAE)

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ABSTRACT. What makes *Atalopedes* bigger and better is the addition of two tropical species, *A. clarkei*, new species and *A. bahiensis* (Schaus), and the subtraction of another, *nabokovi* (Bell & Comstock), which belongs in *Hesperia*. Comparison of genus *Atalopedes* with its sister *Hesperia*, using characters of size, antenna, facies, stigma, and, especially, male and female genitalia, precedes comparisons among the species of *Atalopedes*, using these same characters. The five species form three highly distinct groups, whose phylogenetic sequence is (1) *A. campestris* (Boisduval), which ranges from equator to USA; (2) the *mesogramma* group—*A. mesogramma* (Latreille), on most Greater Antilles, Isle of Pines, and some Bahama Islands including New Providence, and *A. carteri* Evans, New Providence Island; and (3) the *clarkei* group—*A. clarkei*, Margarita Island, Venezuela, plus Cartagena, Colombia, and *A. bahiensis*, coastal central Brazil. The far-out *clarkei* group has switched its ecologic niche to seashore grass; habitat is very restricted. The older the species of *Atalopedes*, the wider its geographic range.

Additional key words: genitalia (male and female), *Hesperia*, *H. nabokovi*, taxonomy, evolution.

What makes *Atalopedes* bigger and better is the addition of two tropical species, an undescribed one plus its misplaced sister, and the subtraction of another, *nabokovi* (Bell & Comstock), which belongs in *Hesperia* (Burns 1987).

Because the five resulting species form three highly distinct clusters, *Atalopedes* seems riddled by extinctions—far more than sister genus *Hesperia*, which, with four times as many species, is still relatively compact.

Atalopedes is American; *Hesperia*, mostly so—but it also spans the Palearctic, an extension of range considered rather recent (Scudder 1874, MacNeill 1964). Though basically northern in modern distribution, *Hesperia* turns out, with the inclusion of *H. nabokovi*, to be lowland Hispaniolan as well as Holarctic, which raises questions about area of origin, particularly since *nabokovi* is among the oldest species of *Hesperia* (Burns 1987). The idea that *Hesperia* may have arisen in the Neotropics becomes less astonishing in light of the fact that sister *Atalopedes* occurs from the middle of South America to the middle of North America and in much of the West Indies.

As currently known, the few species of *Atalopedes* tend to replace one another geographically. The only species in the continental United States is widespread and weedy and thus (for a skipper) familiar. *Atalopedes campestris* (Boisduval) ranges from about the equator, through northern South America (up to at least 3100 m in Colombia), through Central America, and through Mexico, to most of the United States

below Canada. Across the southern United States, this multivoltine grass-eater flourishes, especially in disturbed open habitats, becoming scarcer toward higher latitudes and altitudes. It commonly invades various northern states in which it fails to overwinter: records typically reflect the mid- to latter warm season. To many temperate lepidopterists (such as Clark & Clark 1951, Shapiro 1966, 1974, Opler & Krizek 1984), this mobile skipper is a classic immigrant.

Three of the four remaining species of *Atalopedes* are emigrants, wholly or partly on islands. Only one has much of an insular distribution: *A. mesogramma* (Latreille) extends through all the Greater Antilles except Jamaica, as well as south of Cuba to the Isle of Pines and north of it to some of the Bahama Islands. By contrast, *A. carteri* Evans occurs on New Providence Island in the Bahamas; and *A. clarkei*, new species, on Margarita, an island (68 km east to west) roughly 25 km north of the Venezuelan mainland and 250 km west of Trinidad.

Beyond that, this new skipper hails from the Caribbean coast of Colombia (Cartagena); and its sister, *A. bahiensis* (Schaus), from the Atlantic coast of central Brazil (Bahia and Espirito Santo)—though, surely, neither is quite so localized.

The last reviser of *Atalopedes* (Evans 1955) saw one species, *A. mesogramma*, as polytypic. Two subspecies, *A. m. mesogramma* and *A. m. apa* Comstock, are real, but apparently minor, differentiates of no special concern here: the latter (with broader light markings that make it brighter overall) occurs on Puerto Rico and Hispaniola; the former (with narrower light markings that leave it darker), to the west. But what Evans (1955:339) described as a third subspecies, *A. m. carteri*, differs more sharply from the others in both size and facies; and, to quote Evans, it “occurs [at Nassau on New Providence in the Bahamas] with *mesogramma*, which probably is a visitor from Cuba, while *carteri* breeds locally.” Presumably taking this as evidence of sympatry between differentiates without breakdown of their sizeable differences, Riley (1975:186) called *carteri* a full species. The situation points to double invasion, with complete speciation on the part of the first invader (see Mayr 1963:504–507 for discussion of multiple invasions).

The sistership of *Atalopedes* and *Hesperia* (Burns 1987) has mostly been missed. Lindsey (1921) and Lindsey et al. (1931), in treating the skippers of North America north of Mexico, inserted one genus (*Hy-lephila*) between *Atalopedes* and *Hesperia*; and Evans (1955), in treating the entire New World fauna, five (*Appia*, *Linka*, *Polites*, *Wallengrenia*, and *Pompeius*), though all these workers, in attempting to characterize *Atalopedes*, compared it with *Hesperia*, Evans (1955:338) even going so far as to say, “Palpi as *Hesperia*. . . . Resembles *Hesperia* in facies.” MacNeill (1975) set the two genera side by side, noting a

relation. Yet, in the subsequent spate of North American butterfly books and checklists, only Stanford (1981) and Pyle (1981) followed his arrangement (both consulted MacNeill).

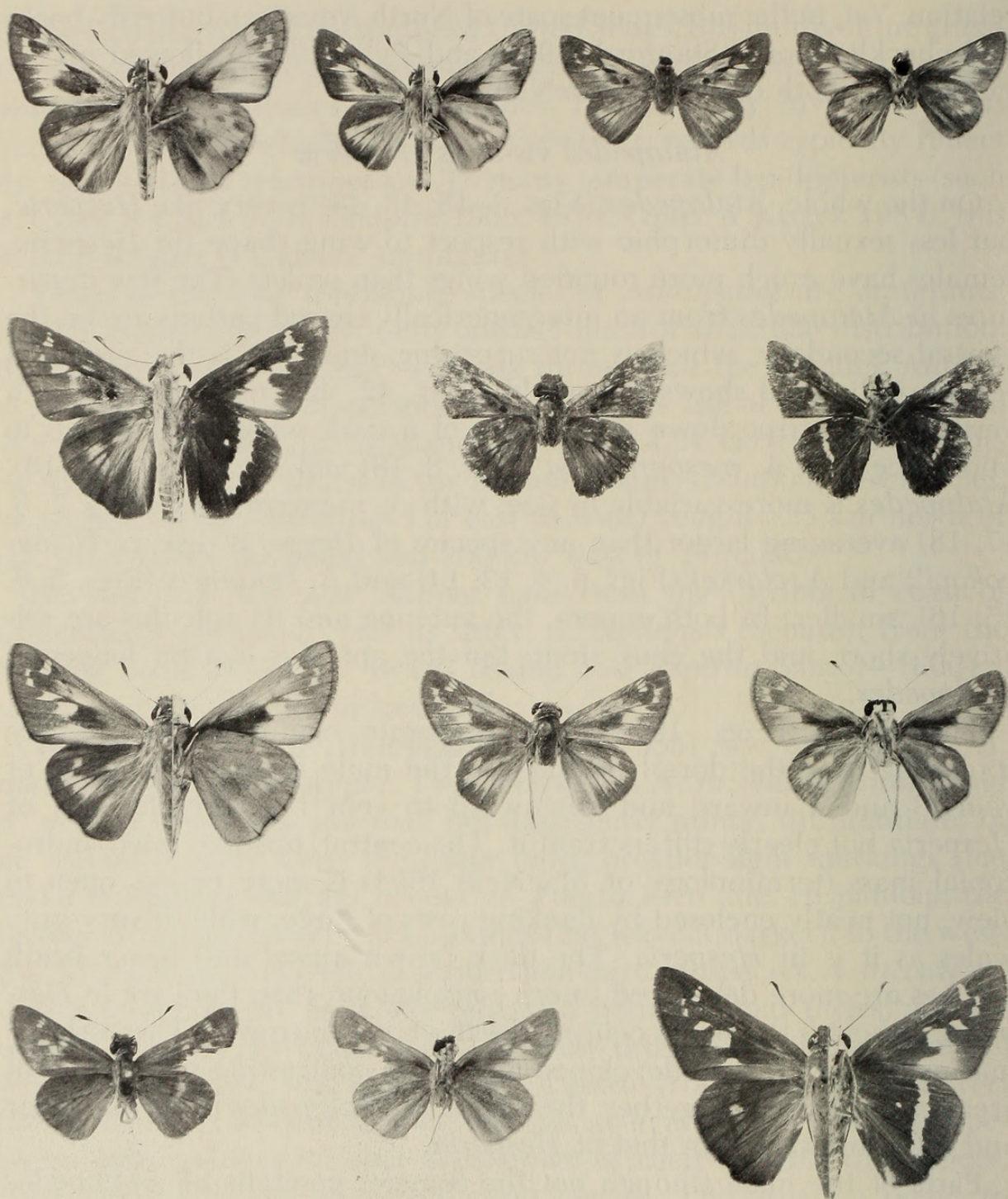
Atalopedes vis-à-vis Hesperia

On the whole, *Atalopedes* (Figs. 1–18, 42, 43) is very like *Hesperia*, but less sexually dimorphic with respect to wing shape (in *Hesperia*, females have much more rounded wings than males). The few departures in *Atalopedes* from an intergenerically shared pattern are on the ventral secondary, which is not surprising since this is the surface a resting individual shows the world (Figs. 42, 43): most extreme is a vertical pale stripe down the middle of a dark wing from vein 8 to mid-space lc in *A. mesogramma* (Figs. 8, 18) and *A. carteri* (Fig. 10). *Atalopedes* is more variable in size, with *A. mesogramma* (Figs. 7, 8, 17, 18) averaging larger than any species of *Hesperia* (except *H. nabokovi*!) and *A. clarkei* (Figs. 3, 4, 13, 14) and *A. bahiensis* (Figs. 5, 6, 15, 16), smaller. In both genera, the antenna and its apiculus are relatively short, and the club, stout; but the apiculus is a bit longer in *Atalopedes*.

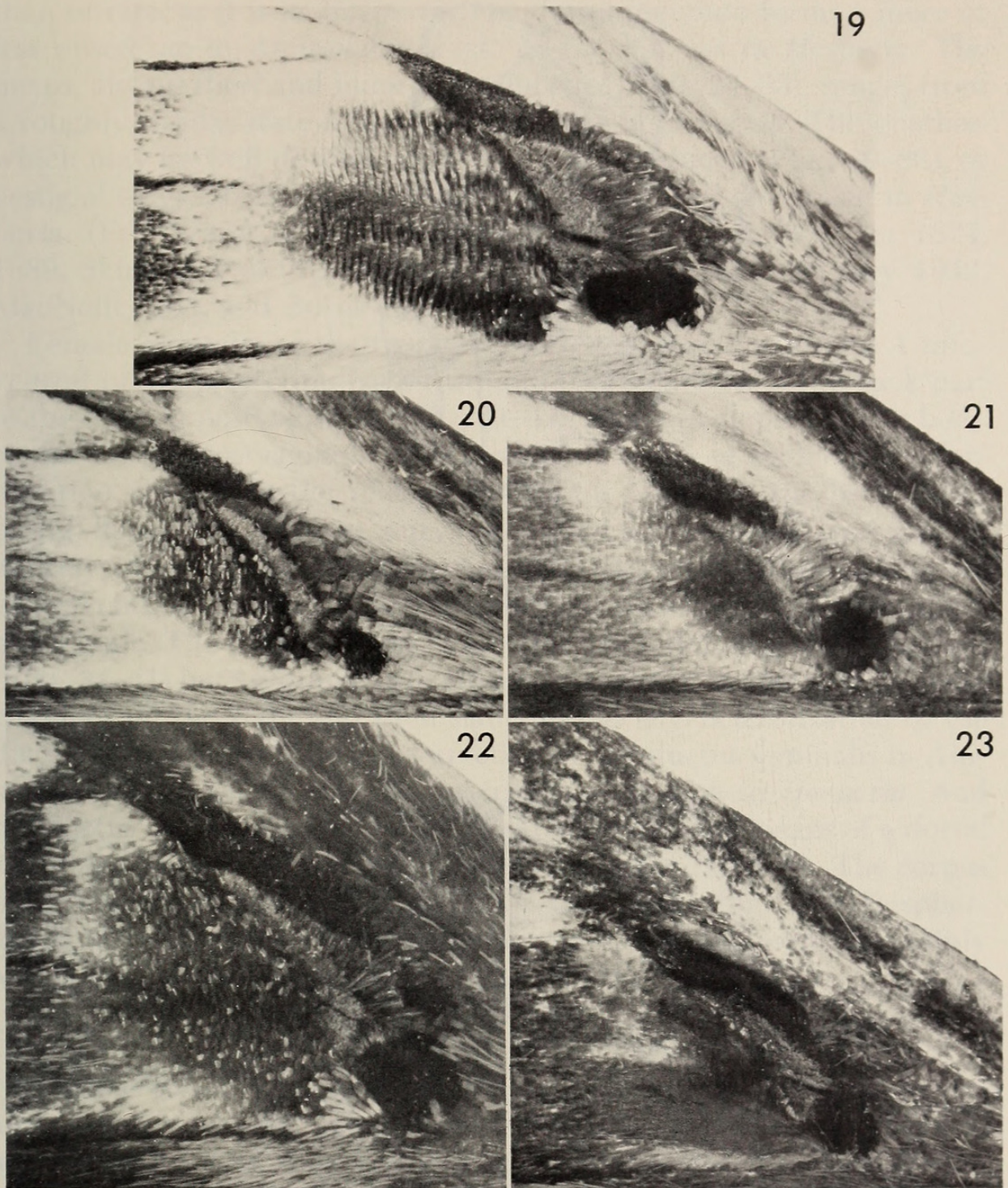
The stigma (Figs. 19–23)—an elaborate communicative device spreading over the dorsal primary of the male from the junction of veins 3 and 4 inward and downward to vein 1—resembles that of *Hesperia* but clearly differs from it. The central, dustlike microandroconial mass (terminology of MacNeill 1964) is more or less open to view, not neatly enclosed by flanking rows of large, wide, silvery-gray scales as it is in *Hesperia*. The dark brown apical and lower brush patches are more developed, more conspicuous, than they are in *Hesperia*, although the scales comprising them are narrower. The poststigmatal patch, too, is well developed and dark, contrasting with adjacent areas of the wing. Altogether, the stigma of *Atalopedes* looks less linear and more massive than that of *Hesperia*.

Parts of the male (though not the female) genitalia of *Atalopedes* hint at those of *Hesperia*. In both genera the valva ends in two large, pointed, more or less dorsally-directed projections whose bases join on the lateral valval surface by way of a smooth, U-shaped edge. This U, narrow in *Atalopedes* (Figs. 24–33), varies from narrow to wide in *Hesperia*. The more distal projection is the more complex, almost always extending forward, medial to the proximal projection. In both genera the aedeagus is slender and comparatively simple—quite unlike the formidable one bristling with bizarre, often outsized, titillators and cornuti in such related genera as *Yvretta*, *Polites*, *Ochlodes*, *Poanes*, and *Paratrytone*.

Many genitalic features divide *Atalopedes* from *Hesperia* (Burns



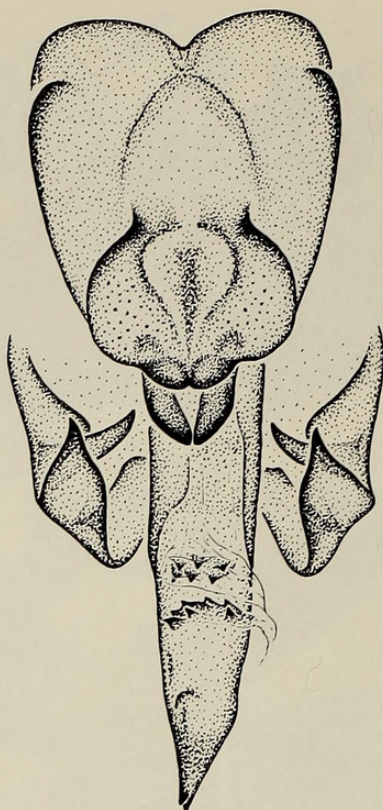
FIGS. 1-18. Adults of *Atalopedes* (all $\times 1$) (in USNM unless otherwise indicated): 1-10, males; 11-18, females; odd numbers, dorsal views; even numbers, ventral views. 1, 2, *campestris*, Charleson St., Annandale, Fairfax Co., Virginia, USA, 1 September 1979, J. M. Burns; 3, 4, *clarkei*, El Morro, Margarita Island, VENEZUELA, 12 February 1985, J. F. G. Clarke; 5, 6, *bahiensis*, holotype, Bahia, BRASIL; 7, 8, *mesogramma*, Tánamo, CUBA, March 1902; 9, 10, *carteri*, Nassau, BAHAMAS, 1 February 1898, H. G. Dyar; 11, 12, *campestris*, Austin, Travis Co., Texas, USA, 3 June 1967, J. M. Burns; 13, 14, *clarkei*, Cartagena, COLOMBIA, 14 July 1969, J. Herrera (collection of C. D. MacNeill); 15, 16, *bahiensis*, Conceição da Barra, Espírito Santo, BRASIL, 25 March 1969, C. & C. T. Elias (collection of O. H. H. Mielke); 17, 18, *mesogramma*, Matanzas, CUBA, October.



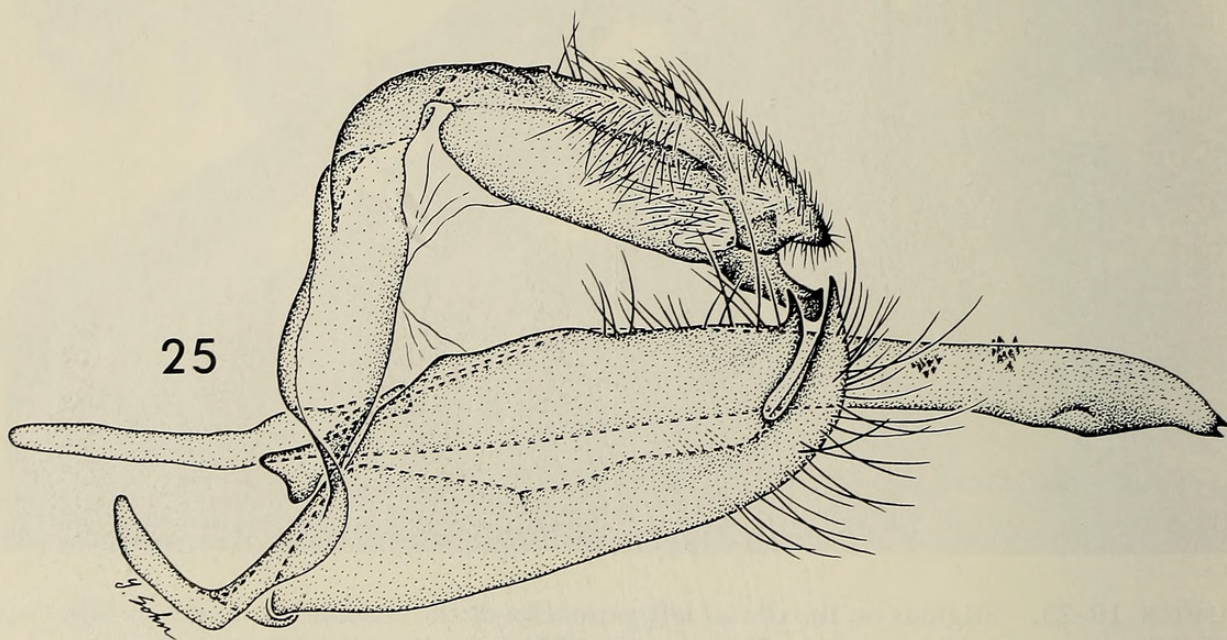
FIGS. 19–23. Stigmas on the dorsal left primaries of the *Atalopedes* males in Figs. 1–10. 19, *campestris*; 20, *clarkei*; 21, *bahiensis*; 22, *mesogramma*; 23, *carteri*.

1987). The aedeagus is longer than the rest of the intact genitalia in *Atalopedes* (Figs. 25, 27, 29, 31, 33) but not in *Hesperia*; and it bears either two multidentate cornuti (Figs. 24, 25) or none (Figs. 26–33) in *Atalopedes* compared with a single bidentate cornutus in *Hesperia*. Paired prongs projecting forward from the front end of the juxta are short and stout in *Atalopedes* (Figs. 25, 27, 29, 31, 33) but long and delicate in *Hesperia*. The valva is elongate and its top and bottom about

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FIGS. 24, 25. Male genitalia of *Atalopedes campestris* from Skippers, Greensville Co., Virginia, USA, 25 July 1983, J. M. Burns (genitalic dissection no. X-2107). **24**, Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **25**, Complete genitalia (minus right valva) in left lateral view.

parallel in *Atalopedes* (Figs. 25, 27, 29, 31, 33), whereas the top of the valva is usually quite humped in *Hesperia*; and the distal projection of the valva, apart from its one (Figs. 24, 25) or two (Figs. 26–33) big points, is smooth along its dorsal edge in *Atalopedes* (Figs. 24–33) rather

than serrate, as it is in *Hesperia*. The dorsal tegumen forms a more or less raised sac in *Atalopedes* (Figs. 24–33) but not in *Hesperia*. The uncus, always short and blunt in *Atalopedes* (Figs. 24–33), ranges from a roughly similar state to long and pointed in *Hesperia*. The gnathos, which may be well developed (Figs. 24, 25), reduced (Figs. 30–33), or vestigial (Figs. 26–29) in *Atalopedes*, is always well developed in *Hesperia*. (For figures of male genitalia of *Hesperia*, see Scudder 1874, 1889, Skinner & Williams 1924, Lindsey et al. 1931, Lindsey 1942, MacNeill 1964, and Burns 1987.)

Female genitalia of the two genera are thoroughly distinct. A mid-ventral prong projecting backward and downward from the back part of the lamella postvaginalis (Figs. 34–41) marks *Atalopedes*. The body of the lamella postvaginalis in *Atalopedes* consists of midventral sclerotization (extending the roof of the ductus bursae to the base of the prong) flanked by surfaces (curving upward and outward) that may be entirely (Figs. 34, 35, 40, 41) or scarcely (Figs. 36–39) sclerotized. In ventral outline the simpler lamella postvaginalis of *Hesperia* approaches a rectangle. The ductus bursae is more or less symmetric in *Atalopedes* (Figs. 34–41) but asymmetric in *Hesperia*, where it begins with a caudal chamber on the right and then slants to the left. Sclerotization of the ductus bursae stops before the junction of the ductus seminalis in *Atalopedes* (Figs. 35, 37, 39, 41) but after its junction in *Hesperia*. And the ductus bursae connects with the corpus bursae by means of a dorsal jog in *Atalopedes* (Figs. 35, 37, 39, 41) but not in *Hesperia*. The corpus bursae itself is essentially cylindrical in *Atalopedes* (Figs. 34–41), spherical in *Hesperia*. (For figures of female genitalia of *Hesperia*, see mainly MacNeill 1964 but also Gillham 1954 and Burns 1987.)

Additions to *Atalopedes*

Full and formal treatment of all included species (which would swell an ordinary taxonomic text) is not essential. I have introduced them all already by way of their peculiar distributions and gone on, in connection with strict definition of the genus, to provide comparative figures of their facies, stigmas, and genitalia—a wealth of information useful at the specific level, as well as above. The species are few enough and diverse enough to stand out. Their characters flood the upcoming discussion of phylogeny anyway. Ritual is therefore restricted to the two species in nominal need.

These, the South American sisters, are the most southern in distribution and the smallest in size. Because the sample of the new species is far larger than that of the old—37 males and 3 females as opposed to 1 male and 1 female—and because a larger sample affords a better description, the new species comes first.

***Atalopedes clarkei*, new species**
(Figs. 3, 4, 13, 14, 20, 26, 27, 36, 37, 42, 43)

Length of right primary (mm).

Sample	Sex	N	Range	Mean \pm SE	SD	CV
Margarita I., Venezuela	♂	28	11.0–13.4	12.28 \pm 0.09	0.46	3.70
	♀	1	12.7			
Cartagena, Colombia	♂	8	11.0–13.0	11.88 \pm 0.27	0.78	6.53
	♀	2	13.2–14.0			

Antenna. Club shorter and thicker in males than in females; anterodorsally, from base to (or close to) start of apiculus, club scaled orange in males, blackish brown in females. (This marked sexual dimorphism involving size, shape, and color of the antennal club is of general occurrence in *Atalopedes*—not to mention *Hesperia* and some other genera—though details of expression can vary between species: for instance, the anterodorsal orange stripe of males extends farther out the club in *A. clarkei* and *A. campestris* than it does in *A. mesogramma* and *A. carteri*.) Nudum usually 7/5: of 34 specimens with at least one antenna intact, 3 are 7/4; 27, 7/5; and 4, 7/6. (Nudum usually 7/7 in *campestris*, 8/8 in *mesogramma*.)

Facies. Much as in *campestris* (compare Figs. 3, 4 with 1, 2; and 13, 14 with 11, 12) except for the ventral secondary, where a yellow ray from the cell through most of spaces 4 and 5 divides two yellow spots in spaces 2 and 3 from a third (not always present) in space 6 (Figs. 4, 14, 42, 43). This distinctive ventral secondary relates readily to that of many *campestris* males (compare Figs. 4 and 2) but not to that of *campestris* females (compare Figs. 14 and 12). (It suggests the ventral secondary of marsh-dwelling species of *Poanes*.) Spots of the primary (which become hyaline in females of *campestris* and *mesogramma*) opaque in both sexes.

Stigma. Well developed (Fig. 20) but not hypertrophied as it is, slightly, in *mesogramma* (Fig. 22) and, grossly, in *campestris* (Fig. 19).

Male genitalia. Valva similar to that of *mesogramma* and *carteri* (compare Figs. 26, 27 with 30–33), with the more distal of the two large, terminal projections expanded into two major, dorsally directed points just mediad of the one-pointed proximal projection. Tip of uncus broadly notched (Fig. 26) and roughly textured (Figs. 26, 27). Gnathos vestigial (Figs. 26, 27). No cornuti, but tooth present on left side of aedeagus before the single, backward pointing, terminal tooth (Figs. 26, 27).

Female genitalia. Midventral prong projecting from back of lamella postvaginalis short (compare Figs. 36, 37 with 34, 35 and 40, 41). Much of lamella postvaginalis unsclerotized (Figs. 36, 37). Simple, sclerotized ductus bursae modestly and rather evenly tapered from ostium bursae forward (Fig. 36).

Material examined. Holotype: Male. VENEZUELA, [Nueva Esparta], Margarita I[slan]d, El Morro, [ca. 4 km E Porlamar], on seashore grass, 12 Feb[ruary] 1985, J. F. G. Clarke. Deposited in National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes (39): 27 males with same data as holotype, plus 7 genitalia dissections (USNM). 1 male, 1 female, VENEZUELA, Nueva Esparta, Margarita Island, near Pampatar, between Playa Moreño and Playa El Angel, 19 August 1987, J. Glassberg & J. Scott, plus 2 genitalia dissections (USNM). 2 females, COLOMBIA, Cartagena, 14 July 1969, J. Herrera, plus 2 genitalia dissections (collection of C. D. MacNeill). 8 males with same data except 15 July 1969, plus 4 genitalia dissections (collection of C. D. MacNeill).

***Atalopedes bahiensis* (Schaus), new combination**
(Figs. 5, 6, 15, 16, 21, 28, 29, 38, 39)

Thymelicus [sic] *bahiensis* Schaus (1902:436).
[The brief, verbal original description of nothing but facies and wing-

spread is so vague that Evans (1955:337) questioningly assigned *bahiensis* to the synonymy of *Pompeius amblyspila* (Mabille).]

Length of right primary (mm). Male, 11.8; female, 13.2; so probably about as in *A. clarkei*.

Antenna. [Male, missing.] Female, club scaled blackish brown anterodorsally; nudum 7/5 or 7/6 (count equivocal owing to incomplete suture).

Facies. Reminiscent of *clarkei* but darker, without the pale ray (parallel to veins through the middle of the ventral secondary) characteristic of that species (compare Figs. 5, 6 with 3, 4; and 15, 16 with 13, 14); chiefly in female, brown background encroaches upon pale pattern elements (compare Figs. 15, 16 with 13, 14). Spots of the primary opaque in female as well as in male, as in *clarkei* (but not *campestris* and *mesogramma*).

Stigma. Similar to that of *clarkei* (Fig. 20), but lower brush patch perceptibly larger and poststigmatic patch, smaller (Fig. 21).

Male genitalia. Overall, very like those of *clarkei*, but with scattered differences (compare Figs. 28, 29 with 26, 27). In lateral view (Fig. 29 versus 27), one-pointed, laterally placed, proximal terminal projection of valva more nearly horizontal, extending farther back to about end of valva; two-pointed, medially placed, distal terminal projection of valva with its proximal point higher than its distal point, rather than the reverse; posterior edge of valva not curved prominently backward the way it is in *clarkei*; anterior end of tegumen more angular, less rounded. In dorsoposterior view (Fig. 28 versus 26), tegumen-uncus usually narrower; left lateral tooth near end of aedeagus longer and basally much broader.

Female genitalia. Similar to those of *clarkei*, but midventral prong projecting from back of lamella postvaginalis even shorter, lamella postvaginalis still more narrowly sclerotized, and ductus bursae more (and more abruptly) flared around level of ostium bursae (compare Figs. 38, 39 with 36, 37).

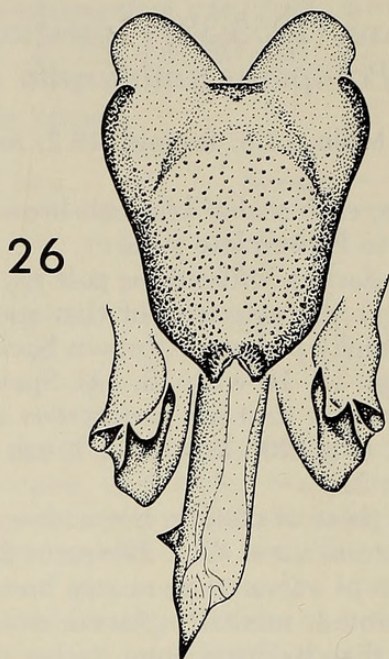
Material examined. Male. Holotype: Bahia, Brazil; Collection W. Schaus; *Thymelicus Bahiensis* Sch[au]s Type [handwritten in black]; Type No. 5999 U.S.N.M. [label red]; Genitalia No. X-2357 J. M. Burns 1987.

Female. Conceicao [da] Barra, E[spirito] S[anto], Brasil, 25 March 1969, C. & C. T. Elias; DZ 3081; Genitalia No. X-2390 J. M. Burns 1987; [collection of O. H. H. Mielke].

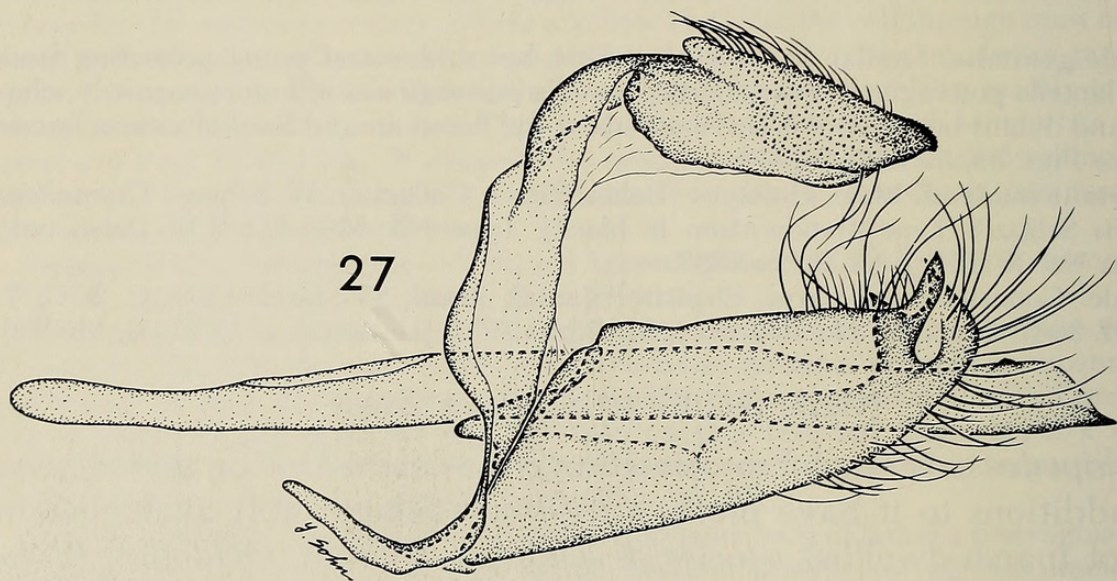
Niche Switch to Seashore Grass

Atalopedes is a genus of multivoltine grass-eaters. One or, more likely, both additions to it have made a striking ecologic shift analogous to those of marsh-dwelling species of *Euphyes*, *Poanes*, *Ochlodes*, *Problema*, and *Panoquina*. *Atalopedes clarkei* lives in a peculiar and relatively simple community dominated by short grass growing in sand behind sandy marine beach (Figs. 42–44). This physically harsh environment may offer fewer biotic pressures. At any rate, as in marsh-dwelling skippers whose foodplant is local but sometimes locally abundant, populations can be extremely local (and thus hard to find), but the density of a population can be high. It was certainly high at El Morro on Margarita when J. F. G. Clarke found *A. clarkei* (see Material examined). In that area, man is the worst enemy of *A. clarkei* now because he is rapidly wrecking its limited seashore habitat with hotels and such (J. Glassberg pers. comm.).

The habitat must have been basically similar, and the population density more or less high, when J. Herrera found *A. clarkei* at the Colombian seaport of Cartagena (see Material examined). During his



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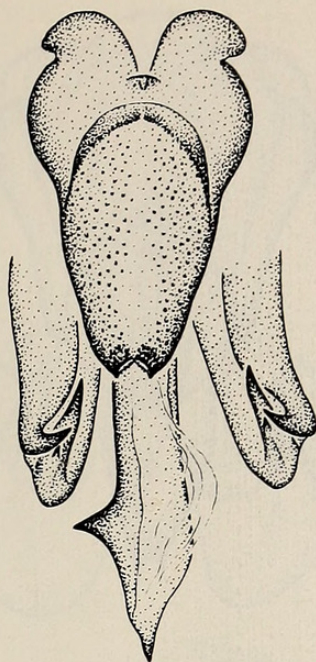
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FIGS. 26, 27. Male genitalia of *Atalopedes clarkei* from El Morro, Margarita Island, VENEZUELA, 12 February 1985, J. F. G. Clarke (X-2104). **26**, Tegumen, uncus, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **27**, Complete genitalia (minus right valva) in left lateral view.

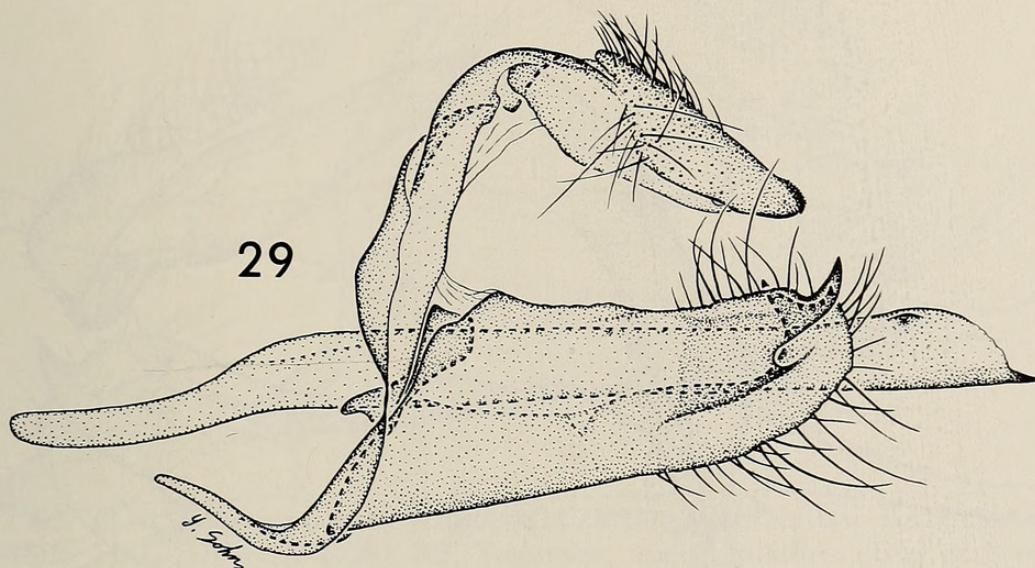
brief time in Cartagena, Herrera collected at the airport, which is right by the water (C. D. MacNeill pers. comm.).

Indirect evidence suggests that seashore grass is also the habitat of *A. clarkei*'s close Brazilian sister. The female of *A. bahiensis*, taken rather recently, is without question from a town on the coast. The male, collected before 1902, is labelled "Bahia Brazil" which may mean the large coastal state of Bahia but probably refers to its capital, a seaport

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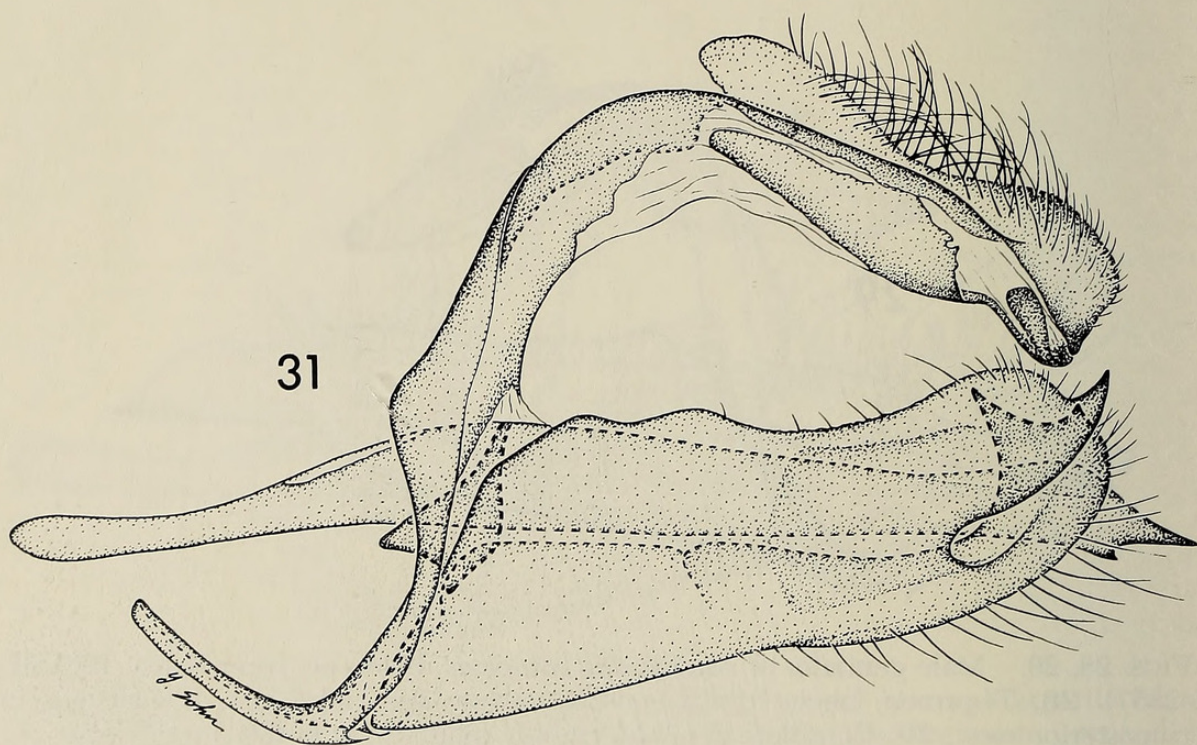
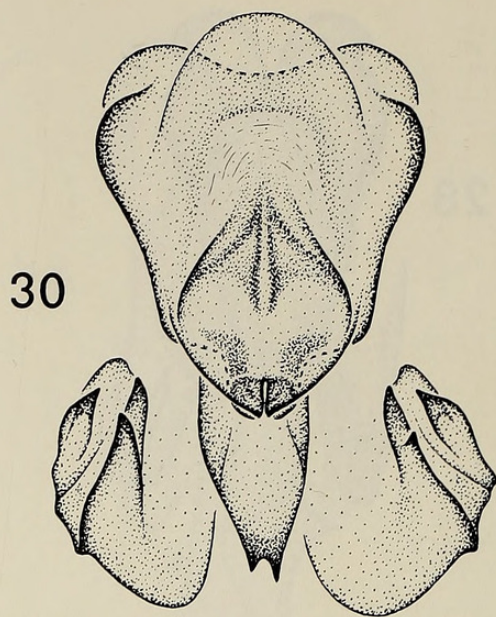


FIGS. 28, 29. Male genitalia of *Atalopedes bahiensis*, holotype, from Bahia, BRASIL (X-2357). **28**, Tegumen, uncus, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **29**, Complete genitalia (minus right valva) in left lateral view.

now called Salvador but formerly called Bahia. Restriction to special habitat could explain the scarcity of the skipper in collections.

Phylogeny of *Atalopedes*

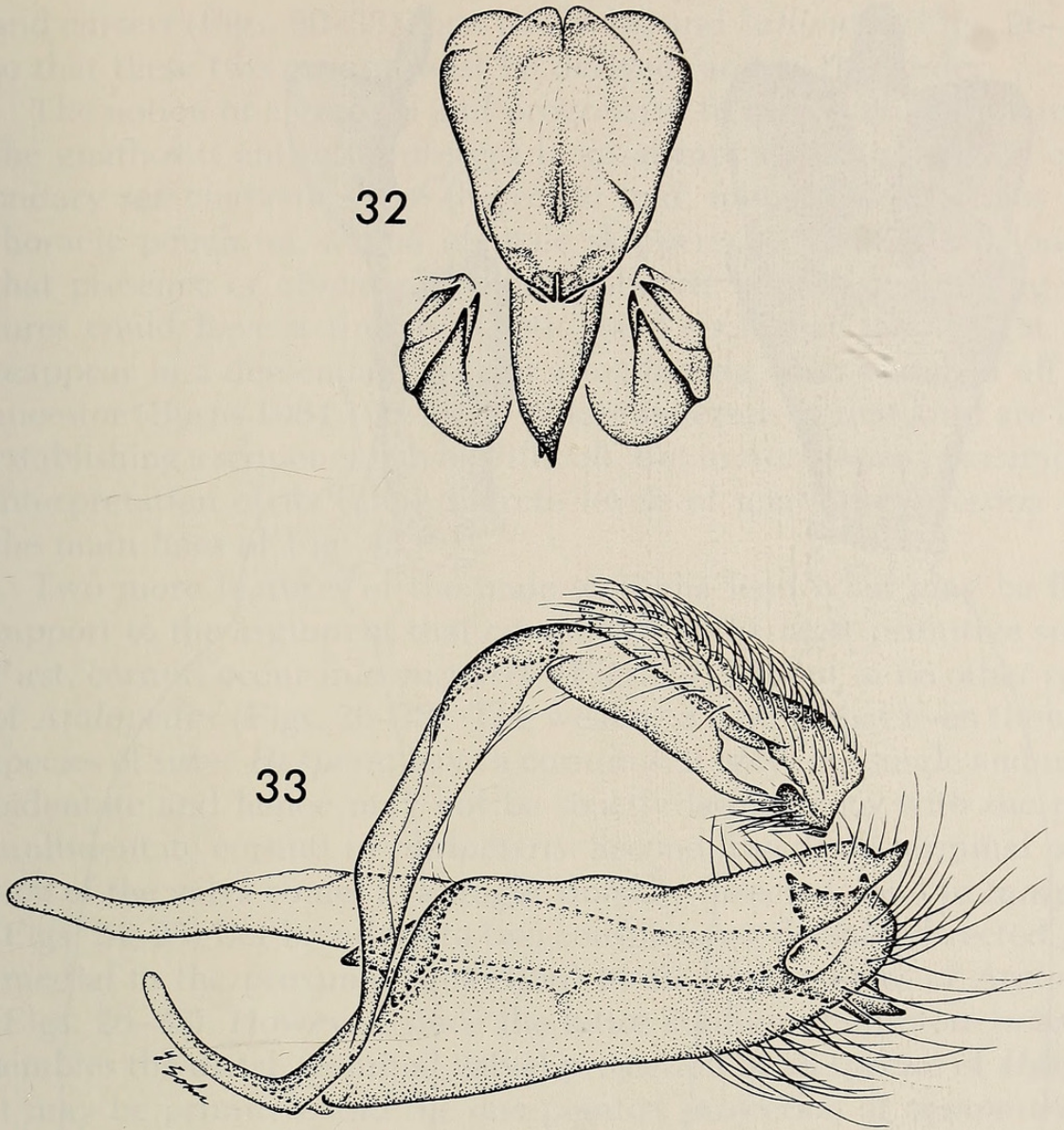
The species of *Atalopedes* form three obvious groups: (1) *campestris*, (2) *mesogramma* and *carteri* (the *mesogramma* group), and (3) *clarkei* and *bahiensis* (the *clarkei* group). Between these groups, differences are large; within them, small—so small that, when I think about the



FIGS. 30, 31. Male genitalia of *Atalopedes mesogramma* from Guantánamo Bay, CUBA, 14 September 1943, W. H. Wagner (X-2115). **30**, Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **31**, Complete genitalia (minus right valva) in left lateral view.

genus as a whole, it comes down to a trio of widely spaced points, which beg for connection. Drawing those real but unseen lines of phylogenetic relationship (Fig. 45) is trying.

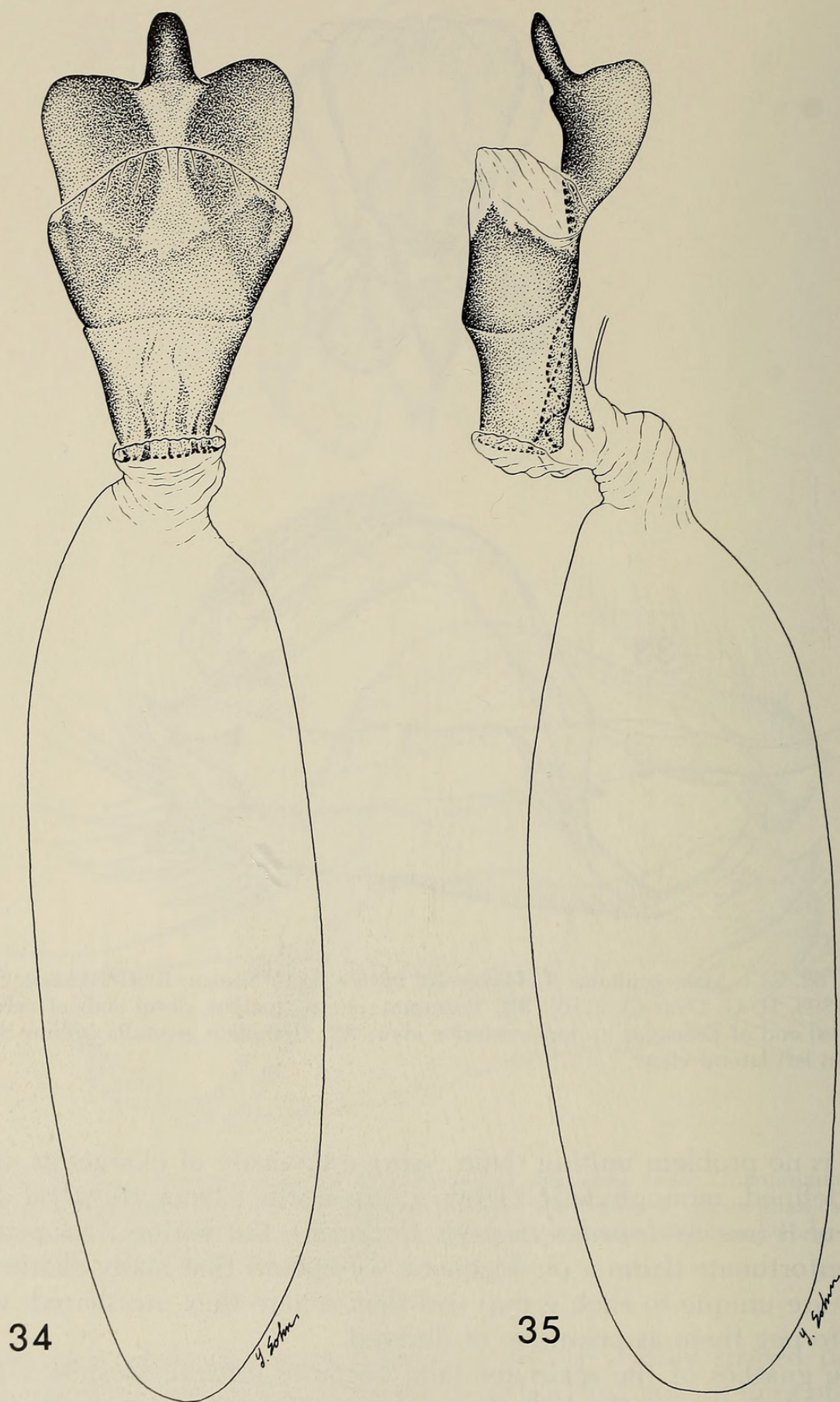
Though extinction seems to have obliterated most of the record so that the surviving species groups stand out and apart from one another,



FIGS. 32, 33. Male genitalia of *Atalopedes carteri* from Nassau, BAHAMAS, 1 February 1898, H. G. Dyar (X-2116). **32**, Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **33**, Complete genitalia (minus right valva) in left lateral view.

there is no problem uniting them, using a diversity of characters, in a well-defined, monophyletic higher group distinct from *Hesperia* and sister of it (see *Atalopedes vis-à-vis Hesperia*). But within *Atalopedes*, it is unfortunate (from a phylogenetic viewpoint) that many character states are unique to each group and that, where they are shared, it is hard to peg them as primitive or derived.

The gnathos of the male genitalia becomes critical. Despite a hypertrophied stigma (Fig. 19), the most primitive species of *Atalopedes* must be *campestris* because its gnathos is fully developed (Figs. 24, 25) as it is in every species of sister genus *Hesperia*. In the remaining species of *Atalopedes*, the gnathos is reduced—less severely in *mesogramma*



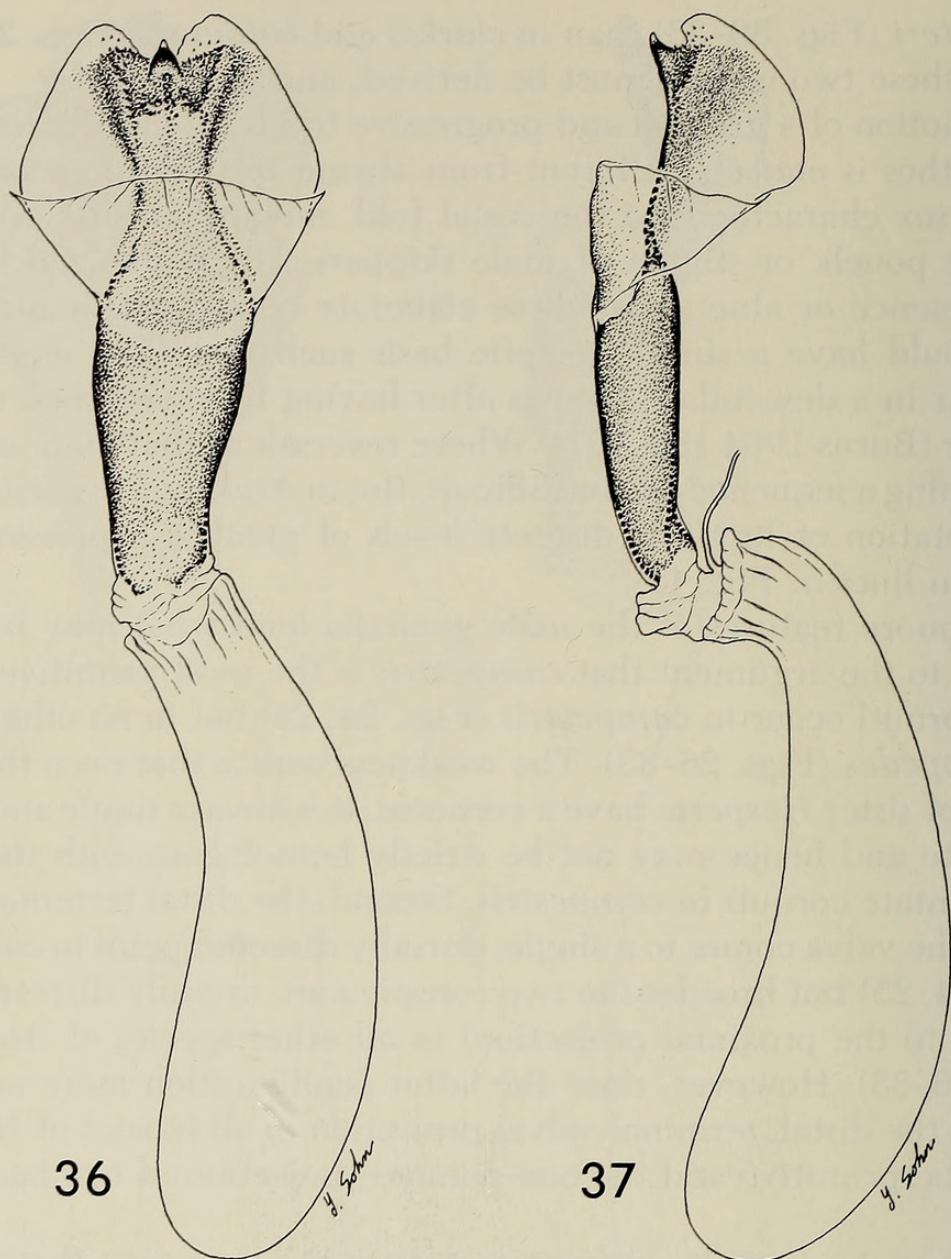
FIGS. 34, 35. Female genitalia of *Atalopedes campestris* from Skippers, Greenville Co., Virginia, USA, 30 September 1981, J. M. Burns (X-2169). **34**, Sterigma and bursa copulatrix in ventral view; **35**, The same, plus part of the ductus seminalis, in right lateral view.

and *carteri* (Figs. 30–33) than in *clarkei* and *bahiensis* (Figs. 26–29)—so that these two groups must be derived, and in that order.

The notion of a gradual and progressive trend toward elimination of the gnathos is entirely different from abrupt total suppression of secondary sex characters like the costal fold, metatibial tufts plus metathoracic pouch, or stigma of male skippers. I hypothesized long ago that presence or absence of those elaborate odor-disseminating structures could have a simple genetic basis such that they might easily reappear in a descendant species after having been switched off in an ancestor (Burns 1964:196–197). Where reversals of that kind are likely, establishing a sequence can be difficult. But in *Atalopedes*, parsimonious interpretation of its three discrete levels of gnathos expression yields the main lines of Fig. 45.

Two more features of the male genitalia lend what may be flawed support to the argument that *campestris* is the most primitive species. First, cornuti occur in *campestris* (Figs. 24, 25) but in no other species of *Atalopedes* (Figs. 26–33). The weakness here is that even though all species of sister *Hesperia* have a cornutus, it is always single and usually bidentate and hence may not be strictly homologous with the paired multidentate cornuti in *campestris*. Second, the distal terminal projection of the valva comes to a single, dorsally directed point in *campestris* (Figs. 24, 25) but broadens to two conspicuous, dorsally directed points (medial to the proximal projection) in all other species of *Atalopedes* (Figs. 26–33). However, since the latter configuration more nearly resembles the distal, terminal valval projection in all species of *Hesperia*, it may be primitive and the one-pointed projection of *campestris*, derived.

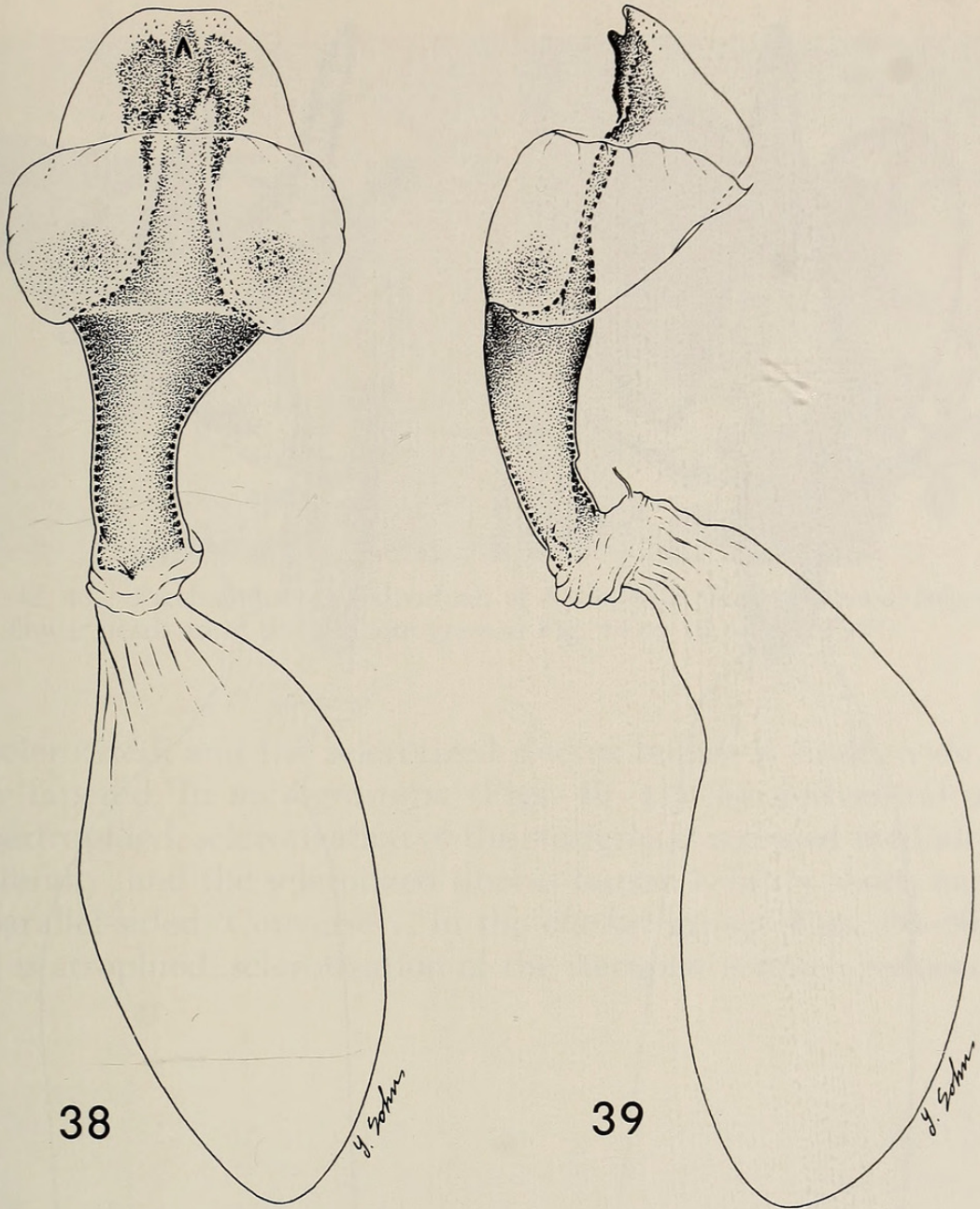
Other male genitalic characters bolster the sequence that puts the *mesogramma* group between *campestris* and the *clarkei* group. The strangely protuberant uncus of the *mesogramma* group (Figs. 30–33) relates clearly to that of *campestris* (Figs. 24, 25), though differing in many details and appearing, as a whole, rather less extreme. (Among the figures just cited, the protuberance shows better in the dorsoposterior views.) The protuberance is wanting in the *clarkei* group (Figs. 26–29). On the other hand, the posterior tip of the uncus is more deeply notched in the *mesogramma* group (Figs. 30, 32) than it is in *campestris* (Fig. 24); and the deep notch persists in the *clarkei* group where, moreover, its sides diverge widely (Figs. 26, 28). The very tip of the aedeagus is finely dentate in *campestris* (Figs. 24, 25) and more coarsely bidentate in the *mesogramma* group, where, in addition, one tooth is decidedly more anterior than the other (Figs. 30–33); in the *clarkei* group, the anterior tooth appears to have moved upward and forward along the left side of the aedeagus and to have grown bigger still (Figs. 26–29).



FIGS. 36, 37. Female genitalia of *Atalopedes clarkei* from Cartagena, COLOMBIA, 14 July 1969, J. Herrera (X-2267) (collection of C. D. MacNeill). **36**, Sterigma and bursa copulatrix in ventral view; **37**, The same, plus part of the ductus seminalis, in right lateral view.

All parts considered, the male genitalia set the *clarkei* group farthest out (which is reasonable from an ecologic perspective, considering the shift to seashore grass). Admittedly, some far-out facies mark the *mesogramma* group (compare Figs. 7-10, 17, 18, particularly the ventral secondaries, with Figs. 1-6, 11-16, and the entire genus *Hesperia*); but facies can be much more labile even than genitalia. When such data conflict, favor the genitalia.

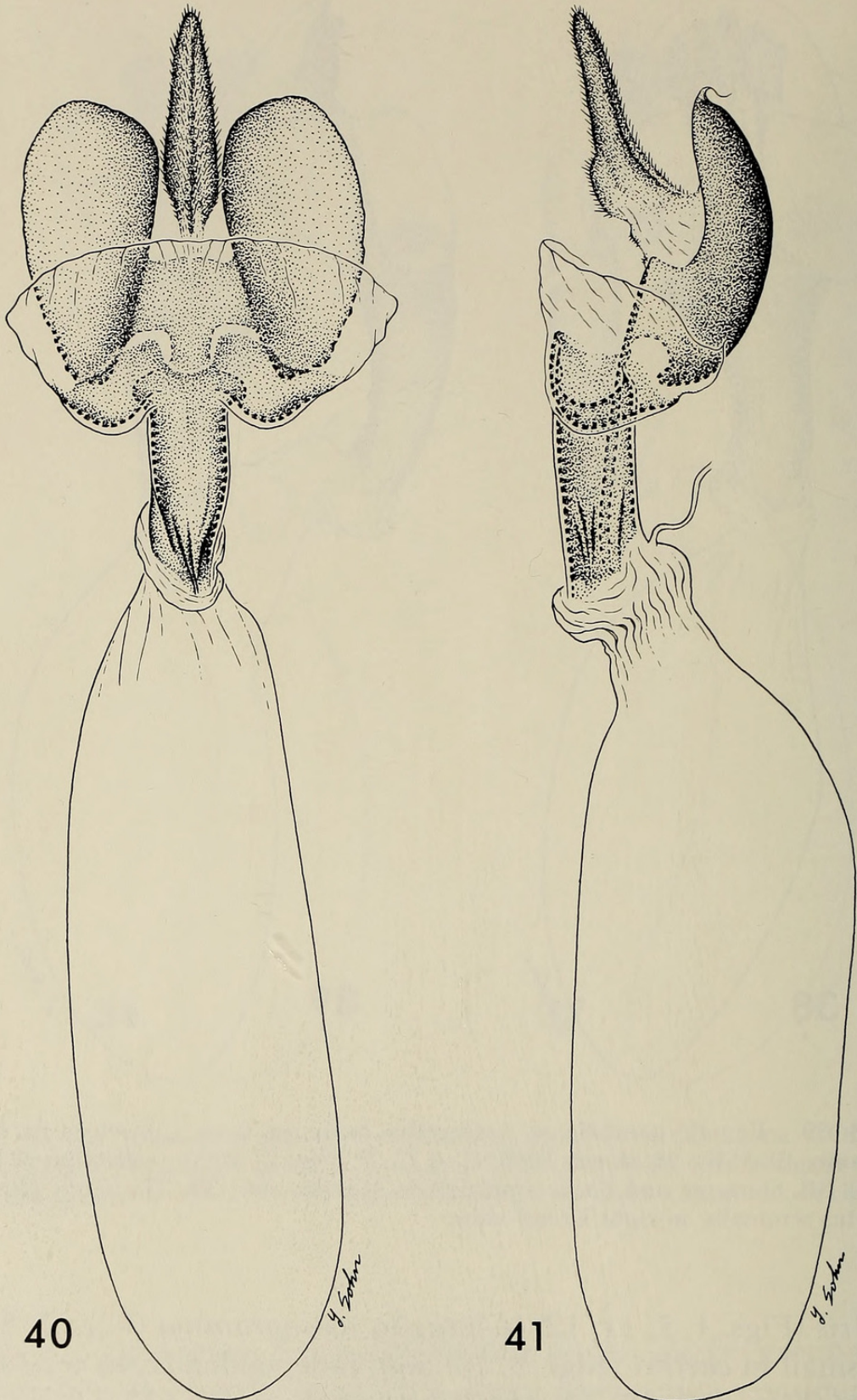
Size is another labile character of little value in working out low-level skipper phylogeny. In *Atalopedes* size varies from medium in



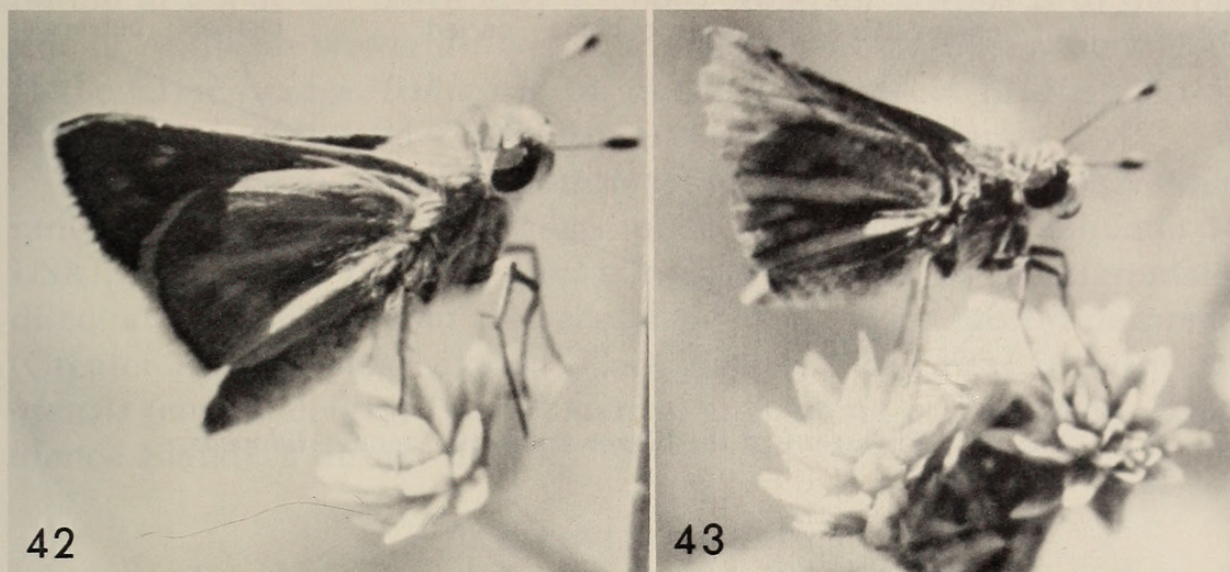
FIGS. 38, 39. Female genitalia of *Atalopedes bahiensis* from Conceição da Barra, Espírito Santo, BRASIL, 25 March 1969, C. & C. T. Elias (X-2390) (collection of O. H. H. Mielke). **38**, Sterigma and bursa copulatrix in ventral view; **39**, The same, plus part of the ductus seminalis, in right lateral view.

campestris (Figs. 1, 2, 11, 12) to large in *mesogramma* (Figs. 7, 8, 17, 18) but small in *carteri* (Figs. 9, 10) and, independently, to very small in *clarkei* (Figs. 3, 4, 13, 14) and *bahiensis* (Figs. 5, 6, 15, 16).

Female genitalia neither help nor hurt the case built from male genitalia, except that *campestris* does seem to reflect a more generalized morphology from which the disparate expressions of the *mesogramma* and *clarkei* groups could readily come. In *campestris* (Figs. 34, 35) the midventral prong projecting backward and downward from the back of the lamella postvaginalis is of medium length, the whole sterigma is



FIGS. 40, 41. Female genitalia of *Atalopedes mesogramma* from Guantánamo Bay, CUBA, 15 September 1943, "caught laying eggs on *Poa* lawn," W. H. Wagner (X-2172). **40**, Sterigma and bursa copulatrix in ventral view; **41**, The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 42, 43. Fresh and worn individuals of *Atalopedes clarkei* perched, larger than life, on flower heads amid the seashore grass in Fig. 44 on 19 August 1987.

well sclerotized, and the sclerotized ductus bursae is short, wide, and evenly tapered. In *mesogramma* (Figs. 40, 41) the midventral prong is hypertrophied, sclerotization of the sterigma is reduced medially but not laterally, and the sclerotized ductus bursae is fairly short, narrow, and parallel-sided. Conversely, in the *clarkei* group (Figs. 36–39) the prong is atrophied, sclerotization of the sterigma is much reduced lat-



FIG. 44. Seashore grass habitat of *Atalopedes clarkei* between Playa Moreño and Playa El Angel, near Pampatar, Margarita Island, Nueva Esparta, VENEZUELA, 19 August 1987. Caribbean Sea shows at upper right through crescentic gap in barrier dune.

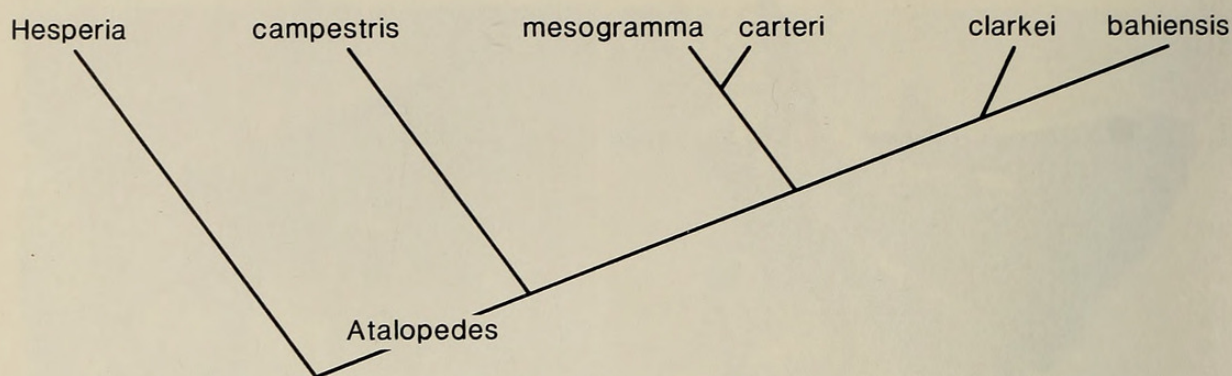


FIG. 45. Phylogeny of the bigger and better genus *Atalopedes*.

erally but not medially, and the sclerotized ductus bursae is long, wide, and tapered.

Within each group of two species, which species is primitive and which derived? Geographic distribution indicates that *mesogramma* must have given rise to *carteri*: *mesogramma* is complexly widespread (Puerto Rico, Hispaniola, Cuba, Isle of Pines, and some of the Bahamas, including New Providence) whereas *carteri*, so far as known, is limited to one small, low island (New Providence); furthermore, *mesogramma* is somewhat differentiated across its discontinuous range. I should note tangentially that *mesogramma* may be even more widely distributed: Evans (1955) lists one female in the British Museum (Natural History) from Costa Rica, and I find in the National Museum of Natural History, Smithsonian Institution, one male labelled "Mex" and three males labelled "Yucat."—but all of these mainland records need verification. Except for its small size and reduced pattern elements, daughter species *carteri* (Figs. 9, 10, 23) is very like mother *mesogramma* (Figs. 7, 8, 17, 18, 22). I have seen only one example of *carteri*, a male whose genitalia (Figs. 32, 33) are essentially those of *mesogramma* (Figs. 30, 31; Comstock 1944:606, pl. 1, fig. 4)—the slight differences between figures may reflect nothing more than individual variation.

Ancestral-descendant relations in the *clarkei* group (whose species differ more from each other) are not obvious. To judge from genitalic form, *clarkei* (Figs. 26, 27, 36, 37) probably preceded *bahiensis* (Figs. 28, 29, 38, 39). In the male the narrow tegumen-uncus and the enlarged anterior tooth of the aedeagus that mark *bahiensis* (Fig. 28) appear more derived. In the female the more atrophied midventral prong of *bahiensis* (Figs. 38, 39) seems farther out.

Zoogeography

Geographically, too, it is the derived species of each two-species group which is farther out—in this case from some generic center of distri-

bution at about the north end of South America: *carteri* is to the far side of Antillean *mesogramma*, on a small island on the northern edge of the latter's range; *bahiensis*, on the central coast of Brazil, is far to the southeast of coastal Colombian and Venezuelan *clarkei*.

The older the species of *Atalopedes* (Fig. 45), the wider its geographic range: *campestris*, the oldest, has much the widest range (equator to USA), even when the vast area temporarily taken by immigrants is discounted; *mesogramma*, the second oldest, is second most widespread (Greater Antilles plus); *clarkei* (Cartagena to Margarita) is third; *bahiensis* (coastal central Brazil), fourth; and young *carteri* (New Providence Island), a distant fifth.

ACKNOWLEDGMENTS

Thanks to J. F. G. Clarke who provoked this study by collecting a long series of a Venezuelan skipper that kept reminding me of North American kinds while continually eluding placement; to C. D. MacNeill, O. H. H. Mielke, and J. B. Sullivan for lending or giving crucial South American material; to Jeffrey Glassberg and Jane Scott for donating not only a pair of specimens but also the color photographs of live adults and their habitat which became Figs. 42-44; to Lee-Ann Hayek for calculating statistics; to Adrienne Venables for meticulously KOH-dissecting numerous genitalia; to Young Sohn for tastefully rendering genitalia, as well as mounting drawings and photographs; to Victor Krantz for photographing dead adults and their stigmas and making black-and-white prints from color slides; and, again, to Don MacNeill for just plain seeing.

MacNeill and A. M. Shapiro thoughtfully reviewed the manuscript.

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Received for publication 18 July 1988; accepted 27 September 1988.



Burns, John McLauren. 1989. "PHYLOGENY AND ZOOGEOGRAPHY OF THE BIGGER AND BETTER GENUS ATALOPEDES HESPERIIDAE." *Journal of the Lepidopterists' Society* 43, 11–32.

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