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Author: Burns, John M.

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SPECIATION IN AN INSULAR SAND DUNE HABITAT:
ATRYTONOPSIS (HESPERIIDAE: HESPERIINAE)—MAINLY FROM THE SOUTHWESTERN
UNITED STATES AND MEXICO—OFF THE NORTH CAROLINA COAST

JOHN M. BURNS

Department of Entomology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 127,
Washington, DC, USA 20013-7012; email: burnsj@si.edu

ABSTRACT. Genus *Atrytonopsis* of the American Southwest and Mexico includes the distributionally anomalous species *Atrytonopsis hianna* of the eastern United States, which has given rise to a species that is, in addition, ecologically anomalous (not just for its genus but for US hesperiids generally): *Atrytonopsis quinteri* **new species** lives in sand dunes along a 50-km stretch of two North Carolina barrier islands (Bogue Banks and Bear Island) and on nearby man-made Radio Island. The oviposition site and larval foodplant of this skipper is the coastal grass *Schizachyrium littorale*, which thrives in the rigorous sand dune habitat. *Atrytonopsis quinteri* is bivoltine and locally abundant. Courtship can be cursory; larvae go through 6 instars; and adults have a notably distinctive facies but variable genitalia like those of *A. hianna* (except that some *A. quinteri* females more frequently express an extreme genitalic variant). Genitalia of this pair of species differ somewhat from those of their congeners, most of which are illustrated. Among these, female genitalia show that *A. margarita* **revised status** is a species separate from its current senior synonym, *A. python*. *Atrytonopsis quinteri* and *A. hianna* are geographically close to each other: at one point the intervening gap (mostly water and marsh) is no more than 5 km.

Additional key words: genitalia (male and female), life history, larval foodplant, *Schizachyrium littorale*, *Atrytonopsis quinteri* **new species**, *Atrytonopsis hianna*, *Atrytonopsis margarita* **revised status**

Breaking an ecologic mold may involve speciation. Of nearly 300 species of skipper butterflies (hesperiids) in the United States, a few are more or less coastal, frequenting salt to brackish marshes. But a notable differentiate of *Atrytonopsis* inhabits dry maritime sand dunes, primarily on Bogue Banks and Bear Island, North Carolina. This skipper's narrow, linear range is c. 50 km long (Fig. 1).

About 13 known congeners are mainland species occurring mostly in the southwestern United States and Mexico, with one of these species, *A. ovinia* (Hewitson), reaching Costa Rica, but also with an outlying species, *A. hianna* (Scudder), in most of the central and eastern United States and adjacent southern Canada. *Atrytonopsis hianna* includes geographic variants of debatable taxonomic rank, distribution, and designation (Hall 2004), i.e., *A. loammi* (Whitney) or *A. hianna loammi* or neither, in the Southeast; and *A. turneri* Freeman or *A. hianna turneri* or neither, in central and western Plains. Analysis of their mutual relationships is beyond the scope of this paper, in which use of the name *A. hianna* is inclusive.

The island skipper's limited range in a peculiar environment explains why it was overlooked for so long, despite its size, facies, abundance, bivoltinism, and presence on a populated strip of land (Bogue Banks). There, owing to natural phenomena and to human predilection for developing seashores, much of this skipper's requisite habitat has been modified or destroyed. But North Carolina's establishment of Fort Macon State Park (opened in 1936) and Hammocks Beach State Park (opened in 1961) chanced to preserve

significant areas of excellent habitat at opposite ends of the skipper's short range. The latter park, which occupies Bear Island, at the west end of the range, is especially beneficial because it is inaccessible by car or by other than a small boat and so is relatively unspoiled. At the east end of the range (Fort Macon), in 1978, Eric L. Quinter collected a pair of the ecologically restricted skipper, which he later passed on to me. Meanwhile, having been informed by Quinter of his odd catch, J. Bolling Sullivan verified it; and he and Richard A. Anderson brought several specimens to my attention in 1983.

MATERIALS AND METHODS

Armed with state permits, I went to Bogue Banks, Carteret County, North Carolina, and Bear Island, Onslow County, North Carolina, as well as to more or less adjacent islands and mainland, in late July 1983, late April/early May 1984, and late April 1985, collecting as much without as within the state parks. With special permission to collect, under supervision, at points along Onslow Beach in Camp Lejeune Marine Corps Base, Onslow County, North Carolina, I visited this locality on 26 April 1985. Using a Voigtländer Bessamatic 35mm camera, I photographed various prime areas harboring the dune skipper. I spread all specimens dorsal side up and, to document their size, measured the length of the right forewing (FW), from base of costa to apex, with a Helios vernier caliper calibrated to tenths of a millimeter. I defined each measured sample by locality, year of collection, generation, and sex of its specimens. To free genitalia, a separated abdomen was soaked for



FIG. 1. Islands along the North Carolina coast on four of which *A. quinteri* occurs, plus adjacent mainland harboring *A. hianna*.

5–10 minutes in a hot 10% solution of KOH, or overnight in that solution at room temperature; and the genitalia were dissected and cleaned with jeweler's forceps and a small paint brush. Using a Leitz Wetzlar stereomicroscope, I studied and compared, at all angles, a total of 285 dissected genitalia of the known species of *Atrytonopsis*, either in ethanol or in glycerol in 12-depression porcelain spotplates. In 1984 and 1985, starting with eggs seen laid in the field and, especially, with eggs obtained from caged females, I reared 18 adults from larvae that were individually housed in vials. Since reared adults average smaller than wild-caught ones, I discounted their measurements.

RESULTS

Atrytonopsis quinteri, new species

Description.—Size (Table 1): In both generations, FW length averages c. 17 mm in males and 18+ mm in females. As expected, females average a little larger than males; but, unexpectedly, at Fort Macon State Park, where sample sizes are biggest, males and females of the second generation average no larger than those of the first.

Facies (Figs. 2–14, 17–29): As is usual in hesperiids, wings of the female are broader and more rounded than those of the male. Pale spots of the FW are slightly yellowish cream both dorsally and ventrally, where they contrast with truly white spots of the ventral HW. Maximum expression of FW spots is (a) an irregular subapical to submarginal band of 8 spots, in which the 3 (usually elongate) subapical spots are offset inward and (unlike the 5 submarginal ones) tight together; and (b) a pair of spots, one above the other in the middle of the discal cell. The 8-spot band runs from cell R_1 – R_4 to cell CuA_2 – $1A+2A$. Spots are larger (a) in females than in males; and (b) ventrally than dorsally. Ventral HW spots form a nested pair of wide Vs lying on their side and pointing outward, with (a) one V submarginal and comprising 7 spots that run from cell $Sc+R_1$ – R_8 to cell CuA_2 – $1A+2A$, with the point of the V in cell M_1 – M_2 ; and (b) the other V basal and comprising only 3 spots, with the upper one in cell $Sc+R_1$ – R_8 , the middle one (which is the point of the V) in the discal cell, and the lower one in cell CuA_2 – $1A+2A$. Part of the submarginal V (especially its lower arm) often appears, more or less faintly, and especially in females, on the dorsal HW. Dorsal ground color of both wings is a medium brown with a touch of gray. Ventral ground color is more complex: a narrow marginal zone of pale lavender-gray shingle-like scales distad of the major bands gives the outer edge of the wings a hoary look; and the pale bands themselves disrupt a ground color that ranges through light to medium browns, overscaled with scales and hairs of dull yellow to beige.

Large samples of adults reveal lots of individual variation in wing spotting, not just between, but also within, the sexes. For example, the characteristic submarginal FW spots in cells M_1 – M_2 and M_2 – M_3 diminish in size and vanish in the series of four males in Figs. 2–5, 17–20; and in the same four males (which are all from one population), ventral HW spots vary greatly in size and shape (as the spots generally

TABLE 1. Length (mm) of right forewing of *Atrytonopsis quinteri* and *A. hianna* at six localities in Carteret and Onslow counties, North Carolina. (The *A. hianna* populations are univoltine.)

Species	Locality	Year	Brood	Sex	N	Range	Mean	SD
<i>A. quinteri</i>	Bear Island	1985	1	M	18	15.6–18.2	16.78	0.65
	Bear Island	1985	1	F	24	16.0–19.4	18.14	0.86
	Bear Island	1983	2	M	8	16.2–17.5	17.15	0.40
	Bear Island	1983	2	F	5	18.3–19.6	18.62	0.55
	Bogue Banks, Emerald Isle	1984, 1985	1	M	30	16.2–18.4	17.34	0.57
	Bogue Banks, Emerald Isle	1984, 1985	1	F	10	16.9–20.4	18.66	1.16
	Bogue Banks, Ft. Macon	1984	1	M	70	15.8–17.8	17.00	0.47
	Bogue Banks, Ft. Macon	1984	1	F	35	16.8–19.5	18.20	0.58
	Bogue Banks, Ft. Macon	1983	2	M	64	15.5–17.7	16.58	0.44
	Bogue Banks, Ft. Macon	1983	2	F	35	16.2–19.1	18.00	0.71
	Radio Island	1984, 1985	1	M	30	15.9–17.7	17.02	0.50
	Radio Island	1984, 1985	1	F	33	17.2–20.0	18.29	0.74
	<i>A. hianna</i>	Swansboro	1984, 1985	1	M	24	14.8–18.0	16.25
Holly Ridge		1984, 1985	1	M	40	15.0–17.7	16.70	0.63
Holly Ridge		1984, 1985	1	F	8	16.6–19.5	18.20	1.18

do). The FW spot in cell $CuA_2-1A+2A$ (which, unlike other spots, is diffuse) rarely shows dorsally in males but frequently does, to a variable extent, in females; present in both sexes ventrally, it is much better (although variably) expressed in females. The two FW discal cell spots may be missing or reduced to one, chiefly in males; both are usually present in females and, in either sex, may be joined in various ways (Figs. 2, 6, 7, 9–14, 17, 21, 22, 24–29).

The dorsal FW of the male bears an inconspicuous, slender, 3-part stigma (best seen in Figs. 5, 6, 11) that slants from a point at, or slightly proximad of, the union of veins M_3 and CuA_1 , downward and inward to the middle of vein $1A+2A$. One part of the stigma spans cell CuA_1-CuA_2 , and the other two parts span cell $CuA_2-1A+2A$.

Genitalia (Figs. 32, 43): Both sexes of *Atrytonopsis* closely reflect the genitalic template characterizing this genus. Interspecific expression is conservative (Figs. 33–42, 44–54). For species whose genitalia differ little from one another, isolated description is of little use. For appropriate treatment of *A. quinteri*, see “Genitalic context” in the Discussion.

Larval foodplant: *Schizachyrium littorale* (Nash) Bicknell; Poaceae.

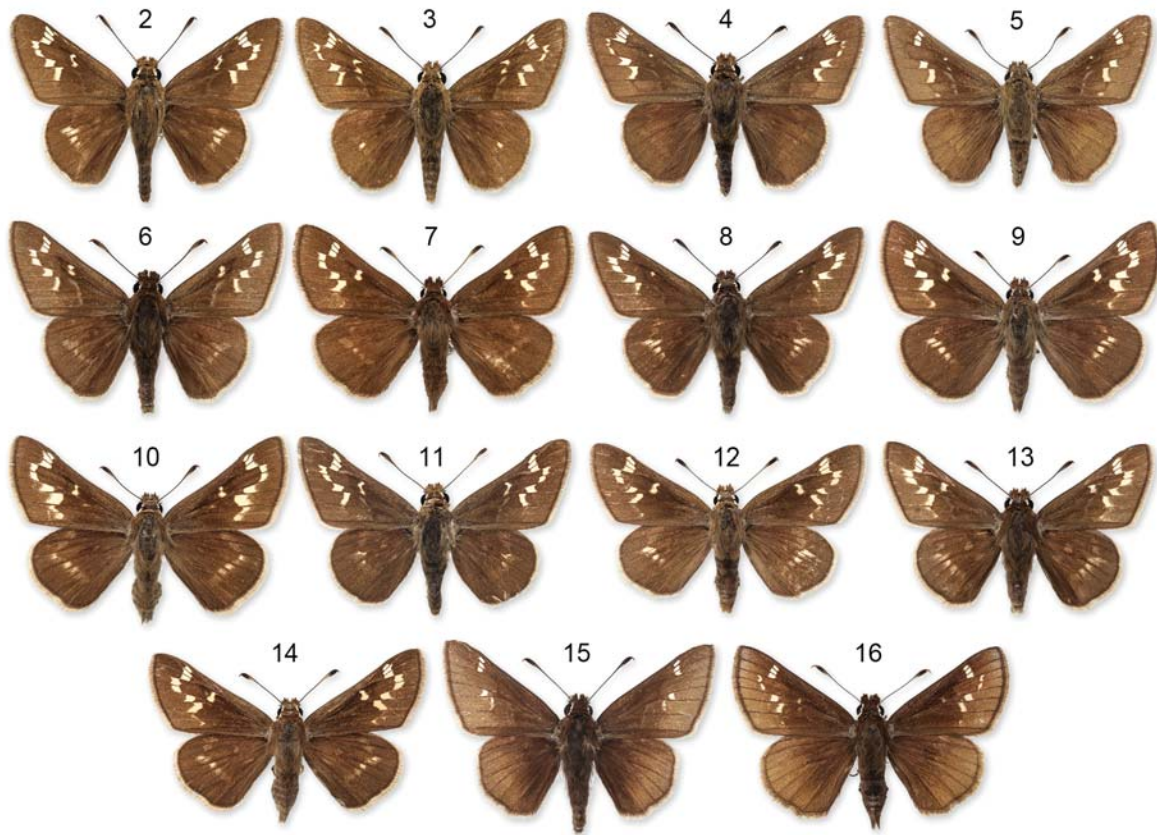
Number of larval instars: 6.

Generations per year: 2: midspring (mostly late April to early May) and midsummer (mostly late July to early August).

Range and habitat (Figs. 1, 56–61): Coastal North Carolina: primarily Bogue Banks in Carteret County and Bear Island in Onslow County; secondarily Radio Island and two or three other dredge spoil islands in Carteret County. In insular sand dunes that support the endemic larval foodplant; these dunes lie behind barrier dunes (a.k.a. primary dunes or foredunes), except on dredge spoil islands, which lack them. See “Distributional detail” and “Natural history” in the Discussion.

Type material.—Holotype: ♂ (Figs. 11, 26) Hammocks Beach State Park, Bear Island, Onslow County, North Carolina, 28-VII-1983, John M. Burns, collector. Deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Paratypes: Fort Macon State Park, Bogue Banks, Carteret Co., North Carolina: 26-VII-1978, 1♂, 1♀ (E. L. Quinter); 31-VII-1982, 2♂, 2♀ (R. A. Anderson); 10-V-1983, 3♂, 1♀ (J. B. Sullivan); 25-VII-1983, 5♂, 6♀; 26-VII-1983, 56♂, 28♀; 27-VII-1983, 4♂, 1♀; 25-IV-1984, 74♂, 36♀. Emerald Isle, Bogue Banks, Carteret Co., North Carolina: 1-V-1984, 21♂, 1♀; 24-IV-1985, 9♂, 9♀. Hammocks Beach State Park, Bear Island,



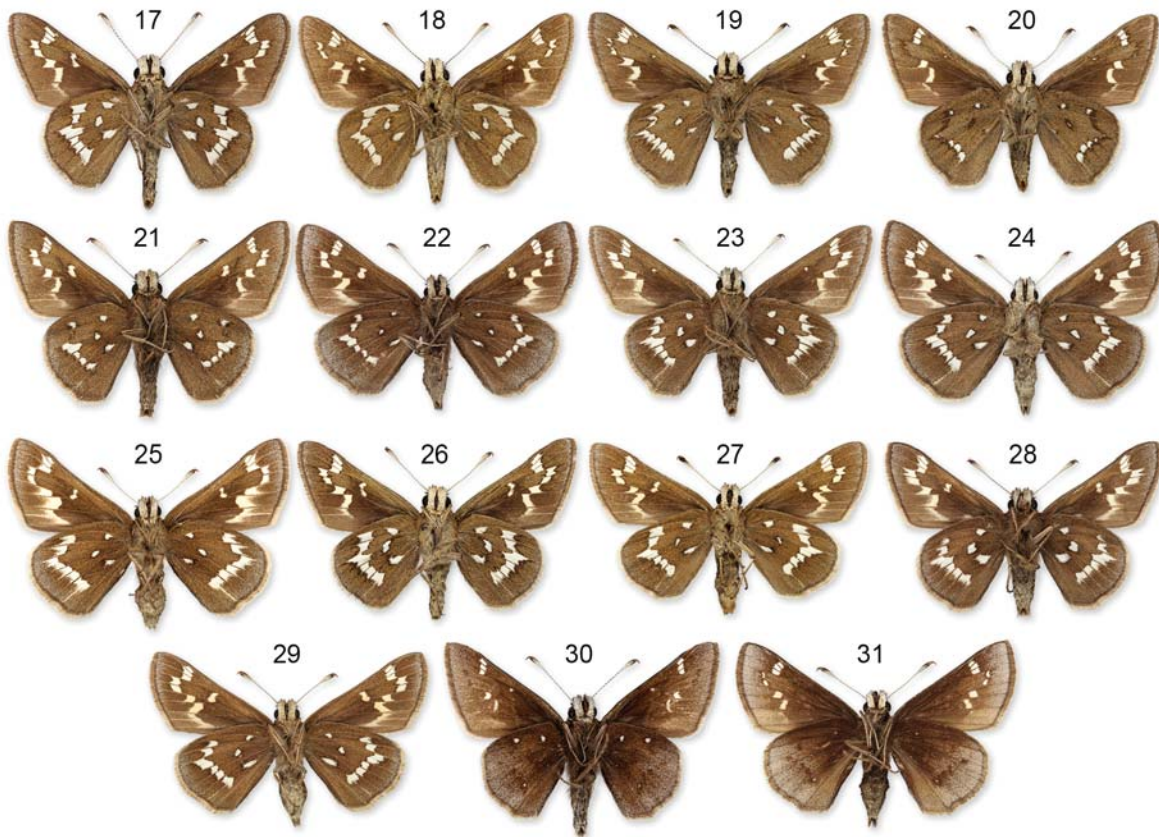
FIGS. 2–16. *Atrytonopsis* adults from Carteret and Onslow counties, North Carolina. Dorsal views. 2–14, *A. quinteri*; 15, 16, *A. hianna*. 2–6, 8, 11, 13, 15, Males; 7, 9, 10, 12, 14, 16, Females. 2–5, Ft. Macon State Park, Bogue Banks, 26 and 27-VII-1983. 6, 7, Radio Island, 2-V-1984. 8–10, Emerald Isle, Bogue Banks, 1-V-1984 and 24-IV-1985. 11–14, Hammocks Beach State Park, Bear Island, 27 and 28-VII-1983, 25-IV-1985. 15, 2 mi. N of Mill Creek, 5.5 mi. N of Morehead City, 3-V-1984. 16, 1 mi. W of Swansboro, 26-IV-1985. All specimens collected by J. M. Burns.

Onslow County, North Carolina: 27-VII-1983, 3♂, 3♀; 28-VII-1983, 4♂, 2♀; 25-IV-1985, 18♂, 24♀. Radio Island, Carteret Co., North Carolina: 2-V-1984, 19♂, 20♀; 29-IV-1985, 3♂, 4♀; 30-IV-1985, 10♂, 12♀. Except as noted at the beginning of this list, specimens collected by John M. Burns. Paratypes deposited in USNM (some to be distributed).

Etymology.—Named in honor of Eric L. Quinter, who discovered and first collected this skipper, perceived its significance, and generously provided his specimens.

Diagnosis.—All females of *A. quinteri* have FW spots in cells M_1 – M_2 and M_2 – M_3 and most males express both of them (though sometimes they are small). These spots also appear in well-sampled neighboring populations of *A. hianna*, but are far less frequent (present in only ¼ of 64 males examined, where they are rudimentary and, with three exceptions, only in cell M_2 – M_3 ; and present in 5 of 8 females, where they are small but in both cells [Figs. 16, 31]). However, other species of *Atrytonopsis* lack FW spots in cells M_1 – M_2 and M_2 – M_3 , except for two species from central Mexico—*A. llorentei* Warren 2009

and some females of the large species *A. frappenda* (Dyar)—and, just barely, for *A. pittacus* (W. H. Edwards) of west Texas, southwestern New Mexico, southeastern Arizona, and Mexico, in which 5 of 80 specimens examined show traces of a spot in one or both cells. Although the dorsal ground color of the wings is a medium brown in both *A. quinteri* and eastern populations of *A. hianna*, the brown usually looks grayer and colder in *A. quinteri*. This subtle difference is clearest when directly comparing large samples of each species. In *A. hianna*, far more than in *A. quinteri*, the dorsal brown is lighter distally than proximally so that the wing veins (which are darker) often stand out where they cross the light area; and, ventrally, the distal hoariness of the wings extends much more proximad than it does in *A. quinteri*. The ventral HW does not exhibit *A. quinteri*'s usually bold spotting. FW length in neighboring populations of *A. hianna* is like that of *A.*



FIGS. 17–31. *Atrytonopsis* adults from Carteret and Onslow counties, North Carolina. Ventral views of the same specimens as in Figs. 2–16 in the same sequence. 17–29, *A. quinteri*; 30, 31, *A. hianna*. 17–21, 23, 26, 28, 30, Males; 22, 24, 25, 27, 29, 31, Females. 17–20, Ft. Macon State Park, Bogue Banks, 26 and 27-VII-1983. 21, 22, Radio Island, 2-V-1984. 23–25, Emerald Isle, Bogue Banks, 1-V-1984 and 24-IV-1985. 26–29, Hammocks Beach State Park, Bear Island, 27 and 28-VII-1983, 25-IV-1985. 30, 2 mi. N of Mill Creek, 5.5 mi. N of Morehead City, 3-V-1984. 31, 1 mi. W of Swansboro, 26-IV-1985. All specimens collected by J. M. Burns.

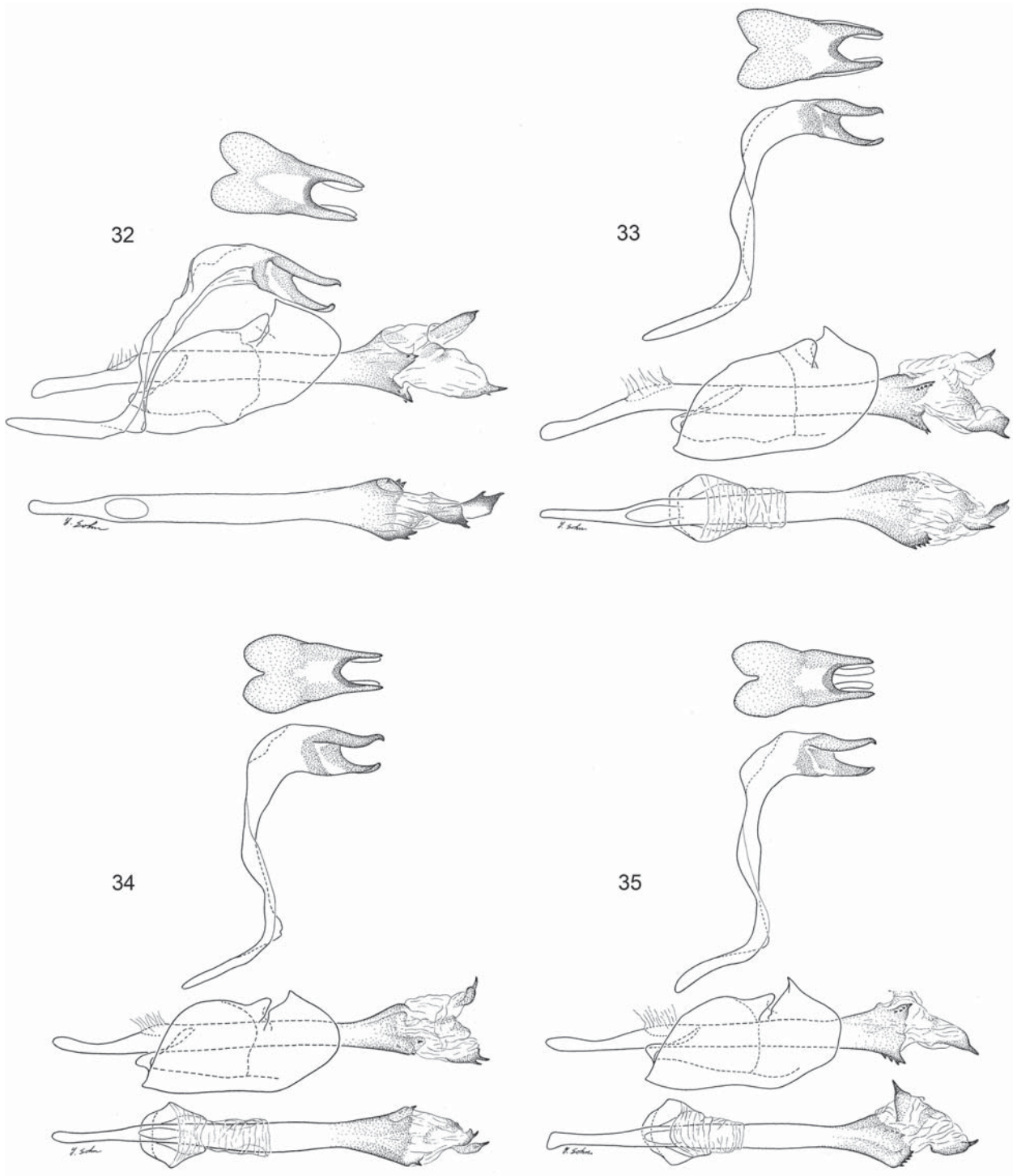
quinteri (Table 1). For consideration of an interspecific difference in the frequency of an odd variation in female genitalia, see “Genitalic context” in the Discussion. For differences in eggs and larvae of these two species, see “Natural history” in the Discussion. *Atrytonopsis quinteri* is extremely limited in distribution and habitat, abundant where it occurs, and not sympatric with any of its congeners.

DISCUSSION

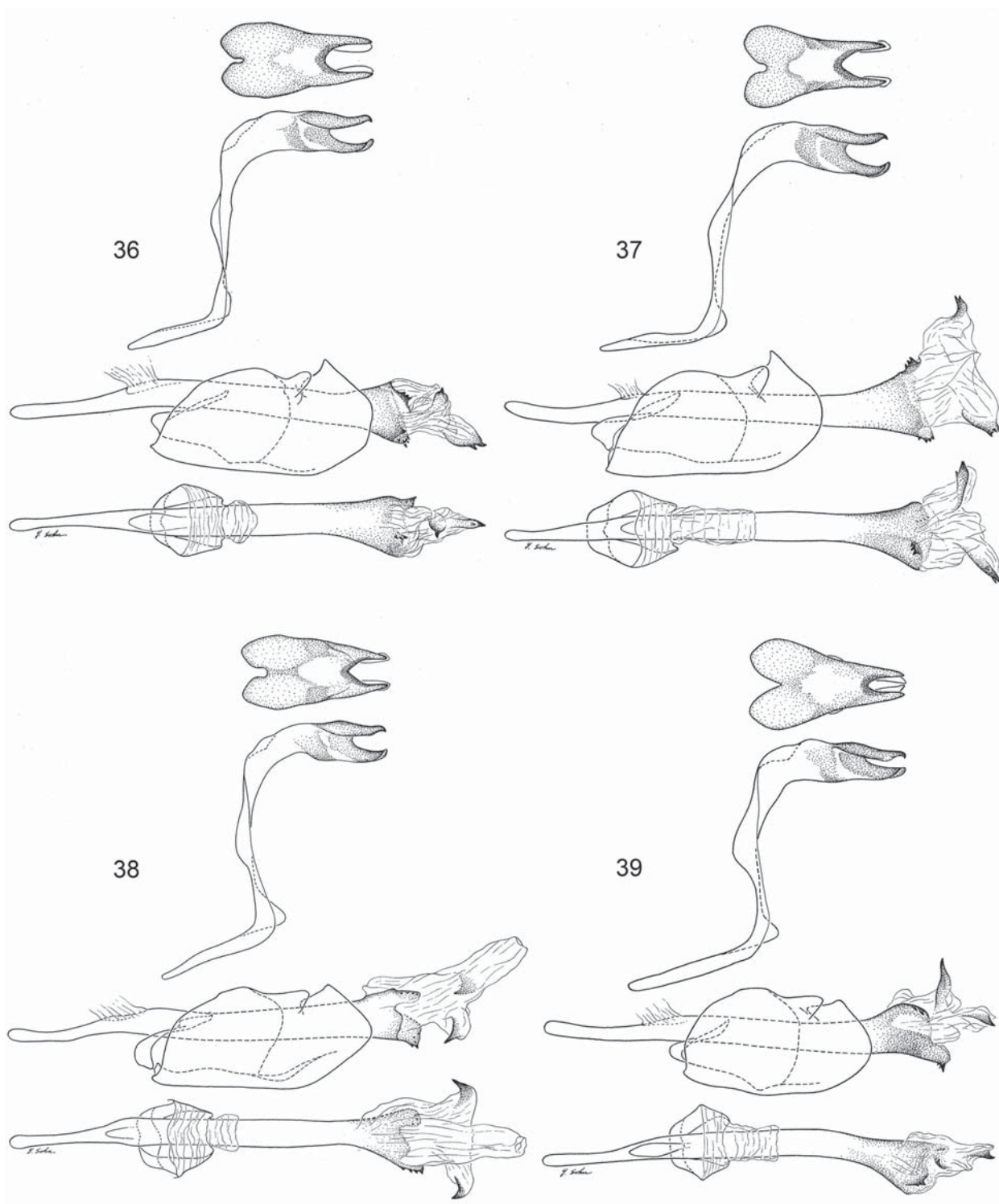
Distributional detail (Fig. 1). *Atrytonopsis quinteri* can cross water. I discovered a thriving population of the skipper, along with ample foodplant, when I drove onto Radio Island on 2 May 1984. This sandy island, aptly dubbed a “dredge spoil island,” surfaced in 1911 and mushroomed in the 1940s and 1950s, when material from deepening the channel between Morehead City and Beaufort was dumped on what had been no more

than a salt marsh island. As a result, Radio Island differs from Bogue Banks and Bear Island: it is lower, flatter, and devoid of barrier dunes and maritime forest. Because it lies between the two cities, with its south edge c. $\frac{3}{4}$ km north of the east end of Bogue Banks, it may be more protected from the elements—but not from human exploitation (some of which was already evident [Fig. 60] and is ongoing).

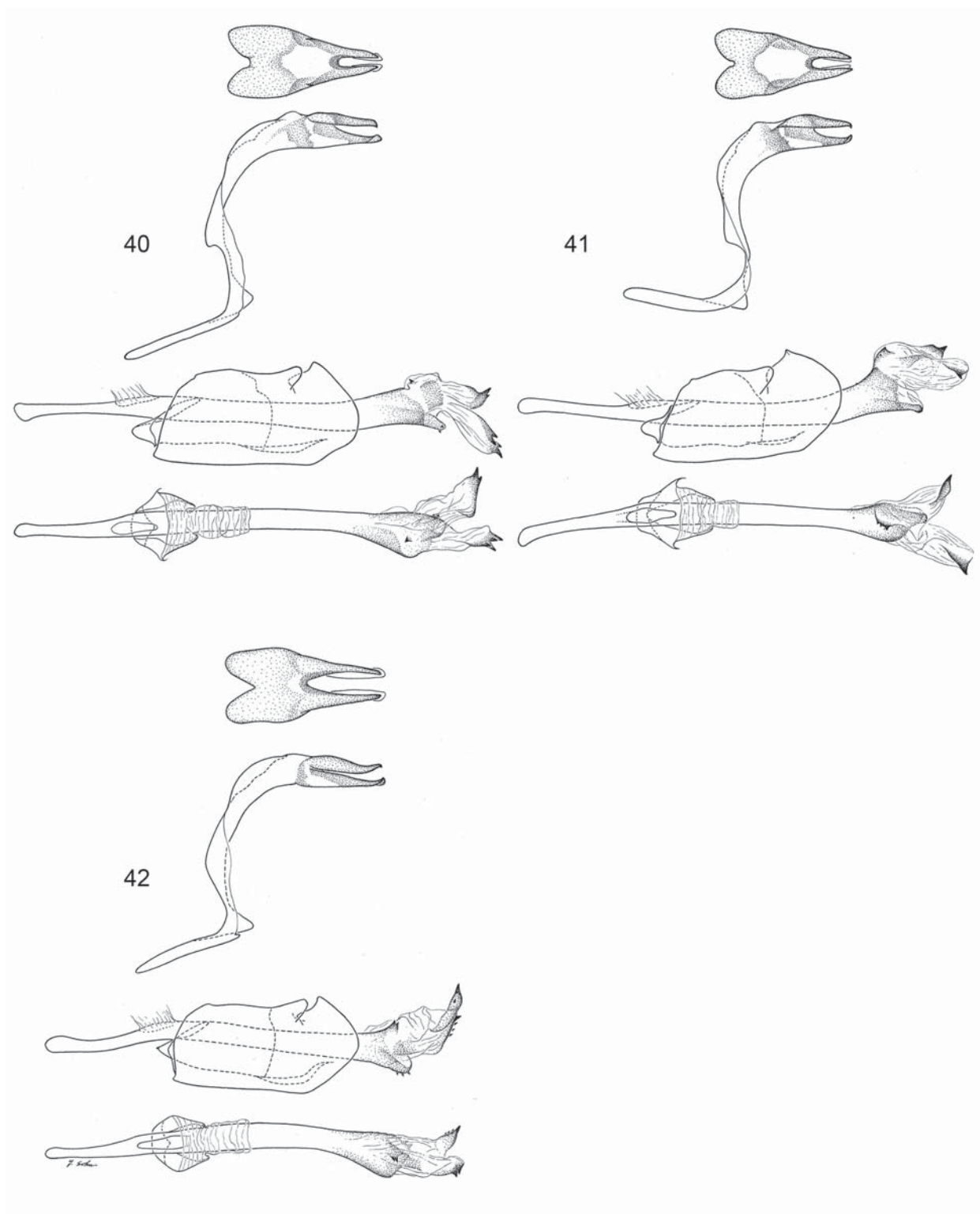
Although potentially accessible natural habitat extends beyond the documented range of *A. quinteri*, unnatural conditions may hamper the skipper. Having arranged passage to and from the west end of Shackleford Banks (a long-uninhabited island c. 1 km east of Fort Macon [a distance of this kind varies with storms, which constantly move and reshape the barrier islands—see below]), I spent a few hours on 2 May 1984 exploring that area: the physical habitat looked promising, but the larval foodplant was scarce and severely grazed by wild horses,



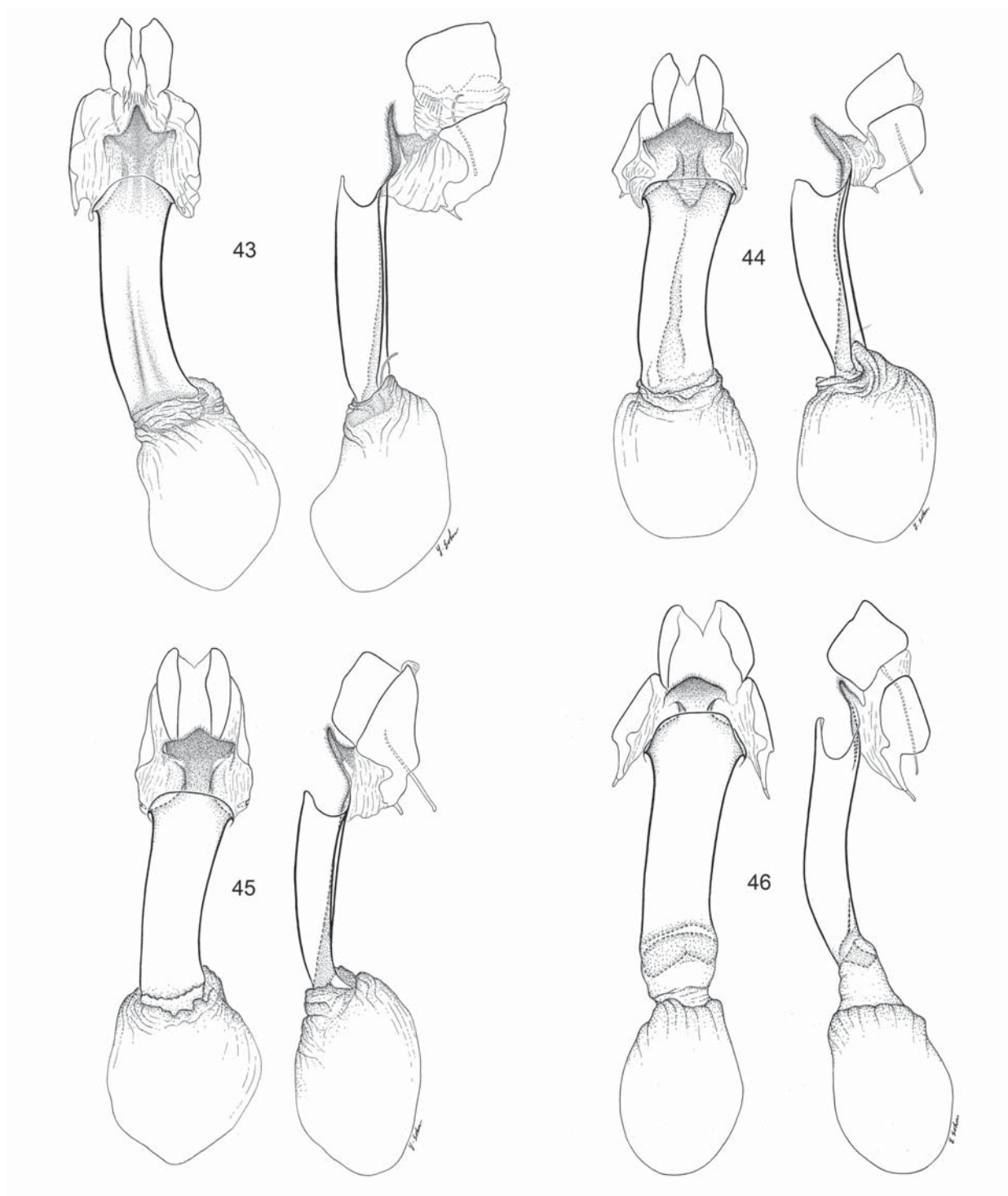
FIGS. 32–35. Male genitalia of *Atrytonopsis*. **32**, *A. quinteri*, Hammocks Beach State Park, Bear Island, Onslow Co., NC, 25-IV-1985, X-3554 (JMB). **33**, *A. hianna*, St. Petersburg, Pinellas Co., FL, 24-VI-1930, X-1196. **34**, *A. hianna*, Lexington (Grant St.), Middlesex Co., MA, 15-VI-1972, X-1199 (JMB). **35**, *A. hianna*, Bare Hills (area of serpentine outcrop just N of Baltimore city), Baltimore Co., MD, 29-V-1972, X-1096 (JMB). (X-codes designate genitalia dissections; JMB = John M. Burns, collector.)



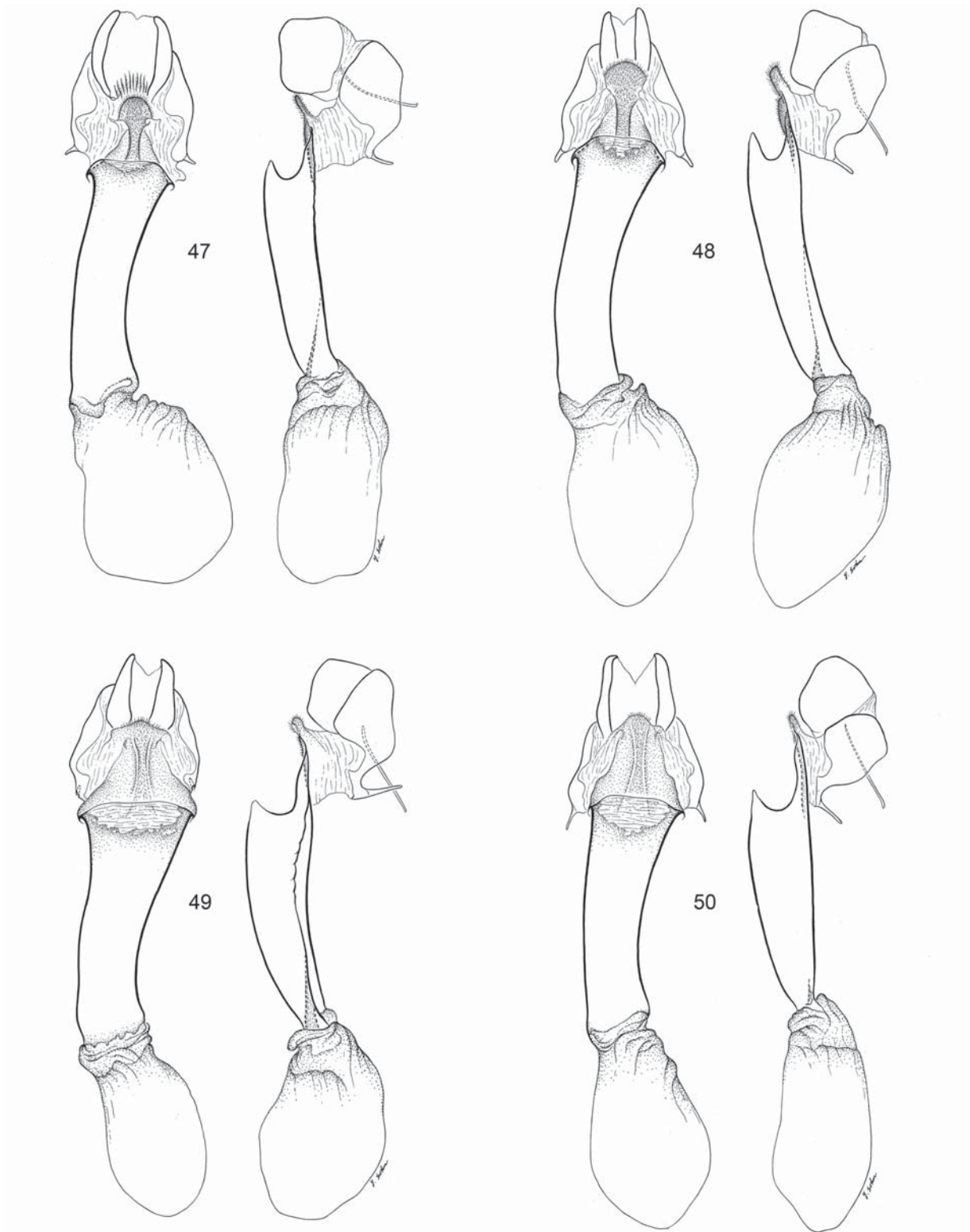
FIGS. 36-39. Male genitalia of *Atrytonopsis*. **36**, *A. vierecki*, Sitting Bull Falls, Guadalupe Mts., 4650 ft., Eddy Co., NM, 26-V-1959, X-1173 (JM & SNB). **37**, *A. deva*, 2 mi. ESE of Emory Pass, Black Range, 7000 ft., Sierra Co., NM, 27-V-1959, X-1189 (JM & SNB). **38**, *A. lunus*, Southwestern Research Station, Chiricahua Mts., Cochise Co., AZ, 6-VIII-1958, X-1179 (P. Opler). **39**, *A. pittacus*, HO Canyon, Davis Mts., 6000 ft., Jeff Davis Co., TX, 30-IV-1959, X-1181 (JM & SNB). (JM & SNB = John M. and Sarah N. Burns, collectors.)



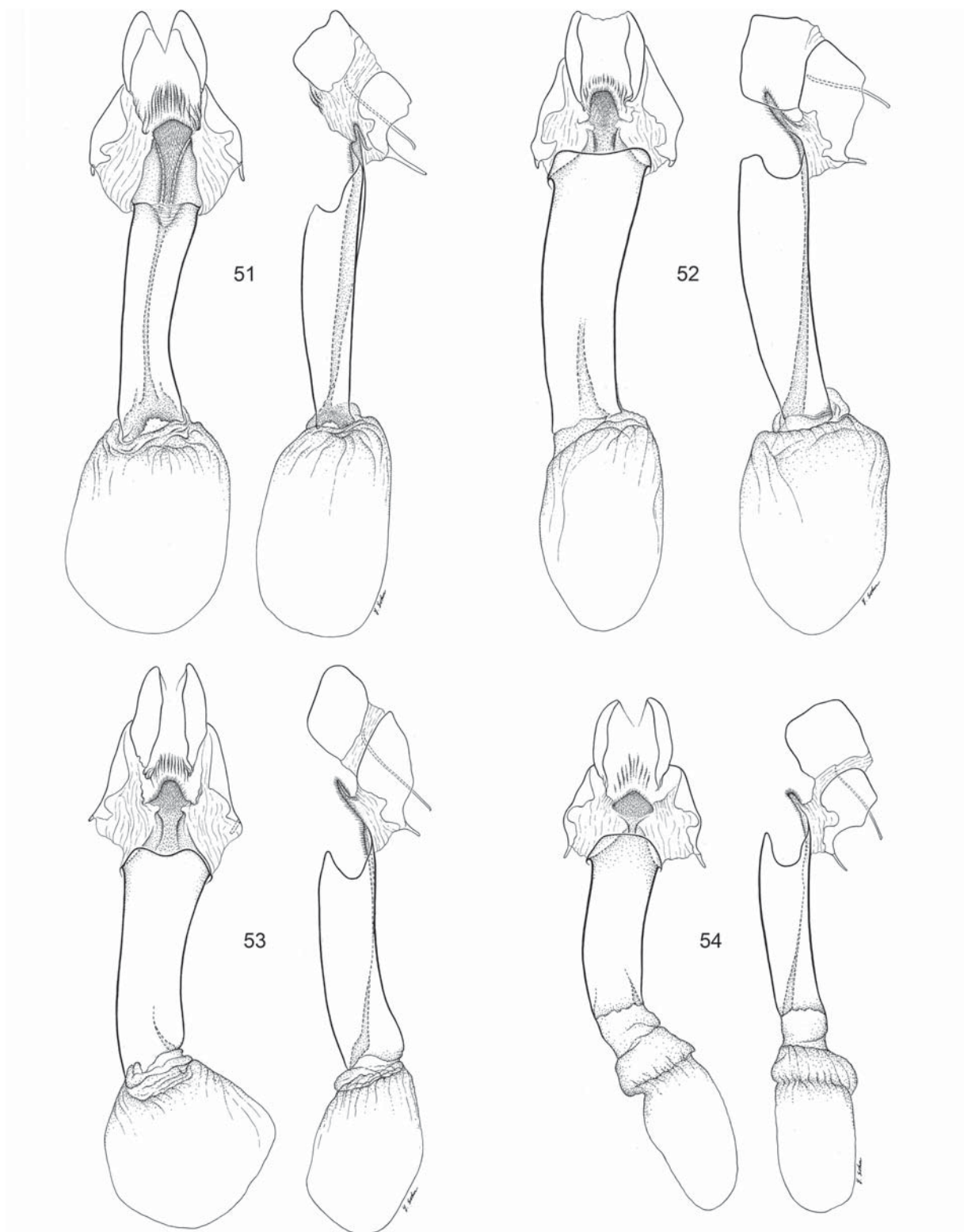
FIGS. 40–42. Male genitalia of *Atrytonopsis*. **40**, *A. python*, Palmerlee, Cochise Co., AZ, 8-V-1915, X-1131. **41**, *A. margarita*, Jemez Springs, Sandoval Co., NM, 24 to 31-V, X-1135. **42**, *A. cestus*, Baboquivari Mts., Pima Co., AZ, 15 to 30-V-1924, X-1144.



FIGS. 43–46. Female genitalia of *Atrytonopsis*. **43**, *A. quinteri*, Hammocks Beach State Park, Bear Island, Onslow Co., NC, 25-IV-1985, X-3560 (JMB). **44**, *A. hianna*, Lexington (Grant St.), Middlesex Co., MA, 2-VI-1975, X-1095 (JMB). **45**, *A. hianna*, New Berlin Rd. × Cedar Point Rd.: 0.5 mi. E of junction, northern Jacksonville, 24-III-1976, X-1195 (JMB). **46**, *A. lunus*, above Herb Martyr Camp and Dam, Cave Creek, Chiricahua Mts., 6000 ft., Cochise Co., AZ, 4-VIII-1974, X-1164 (JM & SNB).



FIGS. 47–50. Female genitalia of *Atrytonopsis*. **47**, *A. python*, 2.5 mi. NE of San Lorenzo, Black Range, 6200 ft., Grant Co., NM, 28-V-1959, X-1163 (JM & SNB). **48**, *A. python*, Southwestern Research Station of AMNH, Cave Creek Canyon, Chiricahua Mts., 5400 ft., Cochise Co., AZ, 14-VI-1958, X-1155 (JM & SNB). **49**, *A. margarita*, Mount Locke, Davis Mts., 6300–6791 ft., Jeff Davis Co., TX, 4-V-1959, X-1158 (JM & SNB). **50**, *A. margarita*, Jemez Springs, Sandoval Co., NM, 24 to 30-VI, X-1209.



FIGS. 51–54. Female genitalia of *Atrytonopsis*. **51**, *A. pittacus*, Limpia Canyon, 4 mi. WNW of Fort Davis, Davis Mts., 5000 ft., Jeff Davis Co., TX, 28-IV-1959, X-1183 (JM & SNB). **52**, *A. deva*, Treasure Park, Pinaleno Mts., 8900 ft., Graham Co., AZ, 4-VI-1959, X-1187 (JM & SNB). **53**, *A. vierecki*, Sitting Bull Falls, Guadalupe Mts., 4650 ft., Eddy Co., NM, 26-V-1959, X-1174 (JM & SNB). **54**, *A. cestus*, 1 mi. W of Elkhorn Ranch, Sabino Canyon, Baboquivari Mts., 4200 ft., Pima Co., AZ, 20-IV-1961, X-1165 (K. Roever).

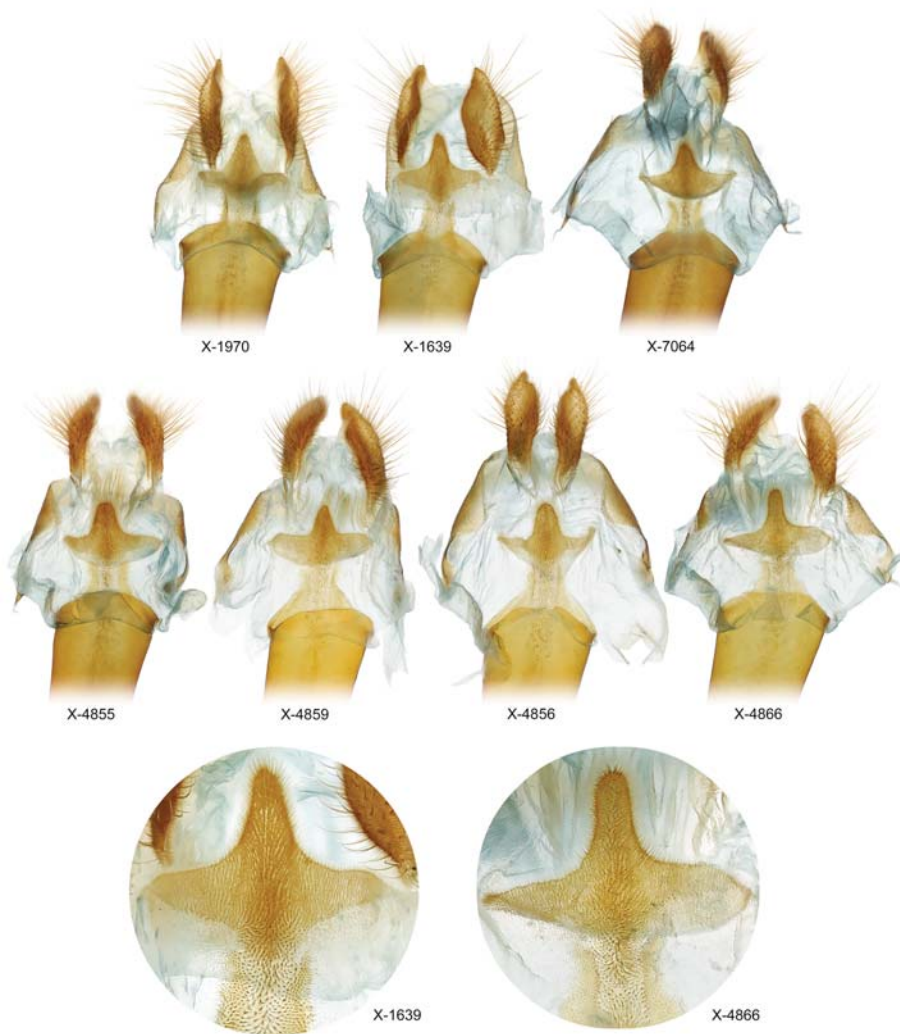


FIG. 55. Ultimate expressions of the narrow phenotype at the caudal end of the genitalia in seven females of *A. quinteri* (ventral view). Specimens denoted by their J. M. Burns genitalia dissection code. X-1970 from Hammocks Beach State Park, Bear Island, Onslow Co., NC; all others from Fort Macon State Park, Bogue Banks, Carteret Co., NC. Genitalia of two of the Ft. Macon specimens enlarged to show diverse microprojections.

as well as by cattle, goats, and sheep; I saw no skippers. On 26 and 27 August 2005, in the course of vegetation surveys on western Shackleford Banks, Leidner (pers. comm.) found the foodplant abundant in various horse enclosures that she examined; but earlier that year, when she visited the island during the spring and summer flight periods of *A. quinteri*, she did not find the skipper.

Atrytonopsis quinteri may occur c. ½ km west of Bear Island on Brown's Island, which is undeveloped. However, it belongs to the Camp Lejeune Marine Corps Base and is strictly off-limits because for decades it has been both a bombing range and a target for naval gunnery practice. (At times, when collecting on Bear Island, I flinched at the sound of nearby explosions and

hoped that the people responsible were reasonably accurate.) Having got permission from Camp Lejeune to collect in limited sections of Onslow Beach, farther southwest, I spent three hours on 26 April 1985 near Onslow North Tower and Risely Pier—areas with foodplant and suitable habitat (although it was narrower and somewhat damaged)—but saw no sign of *A. quinteri* whatsoever. On 4 and 6 May 1984, I checked much of Topsail Island, which lies even farther to the southwest in both Onslow and Pender counties, and found many areas of unspoiled habitat with much *Schizachyrium* but no *A. quinteri*.

Bogue Banks, Bear Island, and neighboring barrier islands are only 2,500–3,000 years old and extremely

dynamic (S. R. Riggs pers. comm., O. H. Pilkey pers. comm.). However, relative to their neighbors, Bogue Banks and Bear Island are tough, i.e., in the course of rapid changes in barrier islands, better able to persist (S. R. Riggs pers. comm.). In this region, major threats are erosion and/or sand deposition from frequent sizeable storms and accompanying surges, hurricanes, various human activities (which include residential and commercial development and shoreline augmentation or “stabilization”—plus, from the skipper’s point of view, use of insecticides), and global warming.

In 2001 and 2002, in connection with the status and conservation of *A. quinteri*, Hall (2004) sought the skipper not only on Bear Island, Bogue Banks, and Radio Island, but also along the length of the North Carolina coast. His survey sites stretched from almost the Virginia border to the South Carolina border; and he, too, went to Shackleford Banks, Onslow Beach, and Topsail Island. Nevertheless, his study did not expand the known limits of the skipper’s range. Many survey sites along the Outer Banks lacked the larval foodplant. Additional territories for *A. quinteri*—discovered in 2000 and 2003, respectively—are two more dredge spoil islands: Brandt Island, just north of Fort Macon State Park and virtually in contact with it, so that the Brandt Island skipper population is, in effect, no more than an extension of the Ft. Macon one; and Marsh Island, right next to the north edge of Morehead City. However, it is questionable whether there ever was a population on Marsh Island (only one individual was seen there) and, if so, whether it could survive recent destruction of the requisite habitat (Hall 2004). On dredge spoil high enough to support *S. littorale* at the west end of Bird Shoal (which is between Radio Island and Beaufort [and part of the Rachel Carson Reserve of the National Estuarine Research Reserve]), Leidner (pers. comm.) saw one example of *A. quinteri* on 25 April 2008 and three on 30 July 2014.

The barrier islands inhabited by *A. quinteri* closely parallel the mainland, with unsuitable salt marshes and water in between (except for some dredge spoil islands). In seeking proximate populations of *A. hianna*, I found and sampled it c. 1½ km west of Swansboro, Onslow County, a mainland locality that is only c. 5 km north of Bear Island (with some intervening dredge spoil islands, at least two of which support the larval foodplant [Hall 2004]), and at another mainland locality that is c. 9 km north of Morehead City, Carteret County. Besides those specimens of *A. hianna* (two of which appear in Figs. 15, 16, 30, 31), I took 40 males, 8 females of *A. hianna* at Holly Ridge, c. 4 km from the water in far southern Onslow County, which are also typical.

Genitalic context. Male. Setting the genitalia of *A. quinteri* in context, Figs. 32–54 show *Atrytonopsis*

genitalic morphology in both sexes of most species. The figures of male genitalia (Figs. 32–42)—with the posterior end to the right—are (except for Fig. 32) exploded views: uppermost are the uncus, gnathos, and tegumen in dorsal view; then the uncus, gnathos, tegumen, vinculum, and saccus in left lateral view (with the uncus, gnathos, and tegumen rotated 90° from their dorsal aspect); followed by the left valva, phallus (with cornuti exerted beyond its dentate distal end), and juxta in left lateral view; and finally the phallus and juxta in dorsal view.

The genitalia of *Atrytonopsis* are interspecifically conservative. Essentially, in males, the valvae (in lateral view) suggest a “roundish rectangle,” with a very rounded distal end that terminates dorsally in a sharply to bluntly pointed projection, which is almost always higher than the body of the valva; the body of the valva itself ends dorsoposteriorly in a separate, rounded, thumb-like projection, which is slightly lateral to, and usually slightly overlapping, the pointed projection. Both the uncus and gnathos are divided. The distal end of each uncus prong is curved slightly downward to a pointed tip. The phallus is slender and long (longer than the valva and saccus combined), flared at the distal end, and finely dentate there, with two sizable cornuti that are sharply pointed, each with one or two (sometimes three) sharp points. The most obvious differences between a number of species involve the uncus and gnathos: the length of the prongs of the divided uncus, the horizontal distance between them, and their vertical distance from the underlying gnathos vary. Closer study indicates other, smaller interspecific differences. Some of them are obscure owing to intraspecific variation but emerge when series of genitalic dissections are compared. To make this point, I illustrated individual variation in both male and female genitalia of four species of *Atrytonopsis*: *A. lunus* (Edwards) and *A. frappenda*, which constitute the *lunus* group of *Atrytonopsis* (Burns 1982, figs. 17–28); and *A. ovinia* and *A. edwardsi* Barnes and McDunnough, which constitute superspecies *A. ovinia* (Burns 1983, figs. 28–55). These published figures and those of two recently described Mexican species of *Atrytonopsis* (*A. llorentei* and *A. austinorum* Warren 2011) are not duplicated here. Warren and Grishin (2012) showed that the Mexican species *A. zweifeli* Freeman—which Freeman described from two males, and which I included in the *lunus* group—is simply a synonym of *A. frappenda*. Male genitalia of the two species in superspecies *A. ovinia* depart significantly from the general description given above with respect to both the uncus (shallowly notched) and the phallus (great length, slight distal flare) (Burns 1983, figs. 19–27).



FIGS. 56–61. Sand dune habitat of *A. quinteri*, in which its larval food, *Schizachyrium littorale*, is the dominant plant. **56**, Fort Macon State Park, Bogue Banks, Carteret Co., NC, 27-VII-1983. **57–59**, Hammocks Beach State Park, Bear Island, Onslow Co., NC, 27-VII-1983. **60, 61**, Radio Island (a dredge spoil island), Carteret Co., NC, 29-IV-1985. (**60**, Motorcycles have worn bare paths through vegetation.)

The male genitalia of *A. quinteri*—with a deeply divided uncus, whose prongs are both widely spaced (producing a U in dorsal view) and well above the gnathos—resemble not only those of its nearest relative, *A. hianna*, but also those of other species: *A. vierecki* (Skinner), *A. deva* (W. H. Edwards), *A. lunus*, *A. frappenda*, and *A. llorentei*. Despite their genitalic similarity, these species differ in facies and size. In still

other superficially separable species, *A. python* (W. H. Edwards), *A. pittacus*, *A. cestus* (W. H. Edwards), and *A. austinorum*, the uncus prongs are closer together so that the U is squeezed (it is also deeper in *A. cestus*), and the uncus is closer to the gnathos. But small interspecific differences in valval shape apparent in the various figures are generally attributable to individual variation. Given the degree of conservatism overall, it is not

surprising that the male genitalia of *A. quinteri* are like those of *A. hianna*.

Female. The figures of intact female genitalia (Figs. 43–54)—with the posterior end at the top—show the ovipositor lobes, lamella postvaginalis, and bursa copulatrix in ventral view (on the left) and in right lateral view (on the right). Always, the ostium bursae is large and the ductus bursae is wide and heavily sclerotized, and it curves a little to the left in ventral view. Obvious differences between species of *Atrytonopsis* involve a distal central strip together with the distal end of the lamella postvaginalis, which are more or less sclerotized and roughened with microprojections that range from hairs to spines to teeth (see especially Figs. 55: X-1639 and X-4866).

In both *A. quinteri* and *A. hianna*, the sclerotized distal end of the lamella postvaginalis is generally wide (Figs. 43–45)—much as it is in the *lunus* group (Fig. 46)—and, midventrally, it almost always extends to form a sort of triangle that varies greatly from wide to narrow, and from short to long, with a caudal tip that ranges from pointed to (more often) rounded or (rarely) blunt. (For a good example of an *A. lunus* female that develops a midventral triangle in the lamella postvaginalis similar to that in many females of *A. hianna* and *A. quinteri*, see Burns 1982, fig. 22.) In *A. quinteri* (43 females dissected) narrowing of the triangle may be conspicuous (Fig. 43). Figure 55 shows ultimate expressions of the narrow phenotype. However, at least half of the triangles in dissected *A. quinteri* females are within the range of expression in *A. hianna* (36 females dissected), and *A. hianna*'s triangles occasionally narrow, so that the more frequent and more extreme narrowness in *A. quinteri* is a modest difference. Despite extensive individual variation, the female genitalia of these species differ from those of other species of *Atrytonopsis* (Figs. 47–54), in which the central strip is notably narrow and its expansion into a caudal projection at the posterior end of the lamella postvaginalis, although laterally limited, is medially pronounced.

Taxonomic tangent (Figs. 47–50). However, *A. margarita* (Skinner) **revised status** is an exception (and it is not, as it has variously been called, a synonym, form, variety, race, or subspecies of *A. python* [Mielke 2005, vol. 4, p. 853]). In the female genitalia of *A. python*—the sister species of *A. margarita*—both the caudal expansion and especially the central strip are sclerotized, and the caudal expansion is usually wide enough for the two, in combination, to suggest a paddle (Figs. 47, 48). In *A. margarita*, both parts look relatively pale, despite their microprojections; and a lessening to lack of sclerotization makes the distal end of the lamella postvaginalis look relatively formless. It is particularly

significant that sclerotization flanking the central strip is wider and longer in *A. margarita* (Figs. 49, 50) than it is in *A. python* (Figs. 47, 48). Male genitalia are not helpful (taxonomically).

Superficially, these two species express to varying degrees the wingspot pattern common to most species of *Atrytonopsis*, including *A. quinteri*. Wingspots are white in *A. margarita* instead of light yellow, as they are on both wings dorsally and the forewing ventrally, in *A. python*. The brown ground color of both wings is warmer in *A. python* because their overscaling (particularly the long hairs of the dorsal hindwing) are yellower, at times imparting a faintly orange tinge. The colder brown ground color of *A. margarita* stems from overscaling that varies within individuals from paler yellow to gray. At least in the United States, these species may replace each other geographically: *A. margarita* occurs in west Texas (e.g., Big Bend, Davis Mountains, Guadalupe Mountains) and in much of New Mexico; *A. python*, in southwestern New Mexico and Arizona.

Natural history. Mating: On Bear Island at 1045 h EDT on 25 April 1985, I saw a male and female *A. quinteri* fluttering about each other below the tops of sea oats, *Uniola paniculata* L., Poaceae, and rushed over to find the pair already united, less than 60 sec. later, on the sand to which the female had dropped. On Radio Island at 1200 h EDT on 30 April 1985, I watched a female *A. quinteri* in direct flight, at a height of c. 1 m. When a perched male flew up at her, she instantly dropped, alighting on a *Schizachyrium* blade c. 5 cm aboveground. The male followed at once, lit beside her, and promptly engaged. Their speedy courtship—if any—was not elaborate. After observing them for less than 2 min., I netted and cyanided them, and their union was already firm: they remained in copula instead of coming apart.

Oviposition and ova (Fig. 62): From 1983 to 1985, in Fort Macon State Park, at Emerald Isle, and on Radio Island, I saw 15 different females oviposit: always a single egg on either the dorsal or ventral surface of a blade of *S. littorale*, c. 2–20 cm above the sand. Oviposition took place at any time of day (specific records ranged from 0848 h to 1658 h EDT). Eggs have a nubby surface and are pale greenish cream or pale yellowish cream when laid. Within a day, they become pale orange; and in the second day, the orange intensifies (through reddish-orange to red), appearing as a spot at the micropyle and as a narrow to wide, regular to irregular, belt around the egg, all against a tan (or pale yellowish) ground. The red may shade toward a purplish-red, and the belt may cover almost all of the egg. Color fades in the last three days to tan, with the dark head of



FIG. 62. Immature stages of *A. quinteri*. a–c, egg (newly laid [pale] and older). d–x, Larval Instars: d–i, first; j, k, second; l, m, third; n–q, fourth; r–u, fifth; v, w, sixth; x, prepupa. y–z1, pupa. Note, on the front of the head in latter larval instars, the development of an odd W whose central pointed apex extends dorsad in a wide midcranial line longer than the sides of the W. In this plate, black lines within white ones demarcate three groups of photos; in each group, photos are to the same scale. (Courtesy N. V. Grishin)

the larva becoming visible beneath the micropylar area. Eclosion of first instar larvae from eggs seen laid on 25-VII-1983 occurred 9 days later. A newly eclosed larva eats most of its egg shell.

Eggs that I got from a caged female *A. hianna* from Holly Ridge, NC, were very pale green when laid and promptly developed a pale orange tinge. Then, on day two, they became uniformly light orange (and, still later,

uniformly darker orange), except for a more intense orange or red spot at the micropyle. But unlike eggs of *A. quinteri*, they never developed a belt of any kind. Heitzman and Heitzman (1974), who reared *A. hianna* many times in Missouri and Arkansas, did not see a belt either.

Development (Fig. 62): There are 6 larval instars. The shiny black head of the first instar gives way to a

matte pale brown and then light brown, on which, in latter instars, there appears a darker brown marking that looks (especially in head-on view) like a **W** whose central pointed apex extends dorsad in a wide midcranial line that is longer than the sides of the **W**. The body, fuzzy with short white hairs, becomes pink; but in the last instar the body becomes yellowish ventrolaterally. From 1 to 2½ weeks (average c. 11 days) into the last instar, wax glands appear on the ventral abdomen, traversing an anterior part of both A7 and A8. The larva coats the inside of its shelter with bright white, powdery wax.

Unlike the larvae of *A. quinteri*, those that I reared from a female of *A. hianna* did not develop the odd **W** marking on the head; and, in a late instar, the dense white hairs of the body were longer than those of *A. quinteri*. Heitzman and Heitzman (1974) described the head of the last instar larva of *A. hianna* as “unmarked” and the body as “covered with long yellowish white hair.”

Speciation. The following scenario stresses the possibility of a novel, rigorous environment exerting strong selective pressure on a colonizer. Presumably, by whatever means, at least one fertilized female from an eastern or southeastern population of *Atrytonopsis* reached an island in the dynamic complex of barrier islands and founded a population that was genetically less variable than its source population (see, e.g., Mayr 1963), as well as geographically isolated from it to a slight but relevant extent. The new environment was bizarre because barrier islands—instead of separating from mainland—form offshore and offer harsh, unstable, sandy habitat. Some mainland species successfully invade such ecologically meager habitat, adapting to it rapidly and even differentiating to the level of new species in a short time. *Schizachyrium littorale*, which is endemic to coastal sands and rather wide-ranging today, may well have existed already on the barrier island that *A. quinteri*'s ancestor reached. It was an attractive foodplant for the immigrant skipper. (Foodplants of *A. hianna* are species of *Schizachyrium* and its close relative *Andropogon*.) Where *S. littorale* flourishes (Figs. 56–61), so does *A. quinteri*. The grass is so adjusted to hot, dry, shifting sand dunes, as well as to windblown salt spray, that it is the dominant dune plant and an abundant, concentrated food source. The skipper withstands similar conditions. Although from a broad perspective *A. quinteri* is considered rare, Leidner and Haddad (2010, 2011) estimate that local populations range in size from hundreds to thousands of adults.

Given that the combination Bogue Banks + Bear Island is only c. 2,500 to 3,000 years old (S. R. Riggs pers. comm., O. H. Pilkey pers. comm.), evolution of *A. quinteri* may have been rapid; and differentiation continues. No later than 1585 (Fisher 1962), an inlet

split Bogue Banks from Bear Island. Leidner and Haddad's (2010, 2011) use of amplified fragment length polymorphisms for genetic analysis of population differentiation across 8 and 10 sampling sites reveals three populations of *A. quinteri*, separated by natural inhibitors of dispersal. The two populations on Bogue Banks are genetically more similar to each other than they are to the population on Bear Island, which is not as genetically variable. As expected, degrees of genetic difference relate to the efficacy and age of the two dispersal inhibitors: the lesser one is an eroded 8-km stretch of Bogue Banks wherein beach abuts maritime forest (which runs along the inner side of the island) because intervening dunes and shrub thickets have been washed away; the greater one is the inlet between the two islands (Leidner & Haddad 2010, 2011).

The origin of *A. quinteri* may have been lengthier and more complex. Fuller understanding of history and relationships calls for molecular comparison of *A. quinteri* with populations of *A. hianna* from the southeastern United States as well as from the rest of that skipper's extensive range. At the very least, DNA barcodes from sizable samples would help. In general, barcodes are a powerful taxonomic tool at the species (and generic) level in hesperiids. As an example of barcodes at their best, they were the first clue that a common and widespread species of *Perichares* described in 1775 actually comprises four species with similar facies and genitalia; as it turns out, small interspecific differences in larval and pupal color patterns and big differences in foodplant selection support the barcode data (Burns et al. 2008). However, at the other extreme (which is rare), barcodes barely separate two species of *Polyctor* with distinctly different genitalia, facies, and ecosystem choice (Burns et al. 2007). Whether barcodes are helpful or not, data from nuclear DNA would be desirable for thorough analysis of the eastern American *Atrytonopsis*.

Evolution of new species in ecologically outré, often severe, sandy habitats is a common phenomenon in both plants and animals. Currently, in Lepidoptera, Metzler (2014) is documenting local differentiation in seven families of moths. In material he has amassed during six years of collecting in the gypsum dunes of White Sands National Monument, an ecologic island in the Tularosa Basin of New Mexico, he has discovered 30 new species (many now formally named). Here again, selection is strong, and differentiation has been recent and rapid: decisive geologic evidence shows that the white sands formation is only c. 8,000 years old. It seems that in some cases, speciation has occurred with the divergent population in its peculiar habitat remaining in contact with its progenitor.

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