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GENITALIA AT THE GENERIC LEVEL: *ATRYTONE* RESTRICTED, *ANATRYTONE* RESURRECTED, NEW GENUS *QUASIMELLANA*—AND YES! WE HAVE NO *MELLANAS* (HESPERIIDAE)

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ABSTRACT. Some prior opinion notwithstanding, both male and female genitalia are exceedingly valuable in delimiting genera of skippers and in grouping species within genera. Even such small genitalic parts as the cornutus and juxta of the male can have value out of all proportion to their size.

The New World genera *Atrytone* Scudder and *Mellana* Hayward are polyphyletic. *Atrytone* genitalically sorts out into (1) *Atrytone*, with the one species *Atrytone arogos* (Boisduval & Leconte) from the central and eastern United States, and (2) the old synonym *Anatrytone* Dyar, with eight species, ranging from southern Canada to Argentina. Half of these species were in *Mellana* (and in synonymy besides); and they include the type species of *Mellana*, which thus becomes a new synonym of *Anatrytone*. For much of what was in *Mellana*, plus five new species, I genitalically define the **new genus *Quasimellana*,** with a total of 24 species, ranging from the far southern United States to northern Argentina. Despite superficial similarities between some species, *Anatrytone* and *Quasimellana* are not closely related.

All names in *Anatrytone*, except those of the type species *Anatrytone logan* (Edwards) and the new species *A. sarah*, and all names in *Quasimellana*, except those of the new species *Quasimellana siblinga*, *Q. antipazina*, *Q. andersoni*, *Q. imperfida*, and *Q. mielkei*, are new combinations. The type species of *Quasimellana* is *Q. mexicana* (Bell). In the following lists, eight new synonyms appear in brackets.

I genitalically define two species groups in *Anatrytone*, each of which (a) ranges widely (Canada to Argentina/Mexico to Argentina) and (b) comprises four species that tend to replace one another geographically: (1) the *logan* group with the North American *logan* subgroup comprising *Anatrytone logan* (Edwards) and *A. mazai* (Freeman) and the South American *barbara* subgroup comprising *A. barbara* (Williams & Bell) and *A. flavens* (Hayward); and (2) the compact *mella* group comprising *A. potosiensis* (Freeman), *A. mella* (Godman), ***A. sarah* n. sp.**, and *A. perfida* (Möschler) [= *gladolis* (Dyar)].

I genitalically define three species groups in *Quasimellana*: (1) the *eulogius* group (southern United States to Brazil and Paraguay, but mainly North American) with the five species *Q. mexicana* (Bell), *Q. eulogius* (Plötz) [= *agnesae* (Bell), = *oaxaca* (Freeman)], ***Q. siblinga* n. sp.**, *Q. balsa* (Bell) [= *balsa freemani* (Steinhauser)], and *Q. mulleri* (Bell); (2) the *sethos* group (Mexico to Bolivia and Brazil, and equally North and South American) with the 12 species *Q. aurora* (Bell) [= *tecla* (Steinhauser)], *Q. nayana* (Bell) [= *tamana* (Steinhauser)], *Q. noka* (Evans), *Q. pazina* (Evans), ***Q. antipazina* n. sp.**, *Q. sista* (Evans),

***Q. andersoni* n. sp.**, *Q. sethos* (Mabille), *Q. myron* (Godman), *Q. verba* (Evans), *Q. inconspicua* (Hayward), and *Q. angra* (Evans); and (3) the *nicomedes* group (Mexico to Argentina, but mainly South American) with the seven species *Q. amicus* (Bell), *Q. fieldi* (Bell) [= *montezuma* (Freeman)], *Q. nicomedes* (Mabille) [= *monica* (Plötz)], ***Q. imperfida* n. sp.**, ***Q. mielkei* n. sp.**, *Q. meridiani* (Hayward), and *Q. pandora* (Hayward).

Four species put in *Mellana* by Evans belong neither in *Quasimellana* nor in *Anatrytone*: *gala* Godman, *helva* Möschler, *rivula* Plötz, and *clavus* Erichson, which is the differentiate of *Wallengrenia* currently going by the junior name *Wallengrenia otho curassavica* (Snellen).

Additional key words: systematics, species groups and sister species, New World, geographic distribution, *Wallengrenia*.

Genitalia are the best means to an end—for the holder, of course, but also, at quite another level, for the thoughtful beholder. Long exploited for separating species from one another, genitalia are just as good for pulling related species together in higher groups like genera.

Although Scudder and Burgess (1870, plus later work summarized in Scudder 1889) and Godman and Salvin (1879–1901) were way ahead of their time because they examined and illustrated the male genitalia of many of the skipper butterflies that they treated, they erred by placing species with similar genitalia in different genera and species with disparate genitalia in the same genus. For example, the twelve species of *Atrytone* whose genitalia grace plate 94 in Godman and Salvin actually belong to five distinct genera.

In North America, illustration of skipper genitalia continued with Barnes and McDunnough (1912), Skinner (1914), and especially Skinner and Williams (1922, 1923a, 1923b, 1924a, 1924b, 1924c) who figured the males of almost all the species then known from north of Mexico. When Lindsey, Bell, and Williams in 1931 updated Lindsey's 1921 treatment of this fauna, they incorporated the Skinner and Williams figures.

An overly guarded paragraph in Lindsey (1921:11) on the taxonomic uses of genitalia reappeared nearly verbatim in the collaborative revision (Lindsey et al. 1931:10), but with a couple of addenda (here set in italics):

> The genitalia, especially in the males, are of great value in making specific identifications and similarity of genitalic structure often affords an index of generic relationship. We have found several apparent contradictions of the latter statement and are therefore inclined to use the principle cautiously until more is known about the skippers, but still we hesitate to include in the same genus species whose genitalia are of widely different forms *unless other structures indicate close relationship. Genitalia are obviously more erratic in their variation than other structures.*

These italic afterthoughts took a huge leap backward.

Though it soon became standard, in this country and abroad, to illustrate male genitalia in descriptions of new skipper species, the enormous store of information in published tails was—and is—relatively untapped. Authors would dutifully show a new tail but often say little or nothing about it, even with respect to the species from which it came, much less compare it critically with others for clues to higher affinities. Despite exploitation by Barnes and McDunnough (1912) in megathymines, female genitalia were mostly ignored until MacNeill (1964) in *Hesperia* and Burns (1964) in *Erynnis* made heavy, comparative use of them. Female genitalia can be as helpful as those of the male.

We are still seduced by outward appearance: *simius* Edwards looks like an *Amblyscirtes*—but its genitalia, in both sexes, spurn the *Amblyscirtes* mold; reexamination of "other structures" shows that the palpi and especially the antennal apiculus also deviate significantly; and *simius* must go elsewhere (Burns 1990). Again, *nabokovi* Bell & Comstock (1948) superficially looked like an *Atalopedes* to its describers, who routinely figured the tail of the male—but those genitalia, in both sexes, are unabashed variations on the *Hesperia* (not the *Atalopedes*) theme; the stigma, too, comes straight from *Hesperia*; and that is where *nabokovi* goes (Burns 1987, 1989). Despite appearances (and convention), genitalia clearly show that *snowi* (Edwards) belongs in *Paratrytone* rather than *Ochlodes* and that two-thirds of the species currently in *Paratrytone* belong somewhere else—mostly with the non-marsh-dwelling species of *Poanes*, which, in turn, harbor a pair of outwardly acceptable genitalic misfits (Burns 1992).

Granted, genitalia are far more difficult, tedious, and time-consuming to study and compare rigorously. But their morphologic complexity in skippers yields a wealth of potential characters (often enriched through asymmetry). Being hidden and serving quite other functions, they escape many of the pressures bombarding the external, visual phenotype and tend to reflect relationship better than facies.

During the last eight years I have been genitalically reviewing nearctic hesperiine skippers, a relatively well-studied fauna whose long-stable genera seem to be gaining authority—yea, rigidity—through constant repetition in a spate of state, provincial, seminational, and national butterfly books and checklists (e.g., Harris 1972, Irwin & Downey 1973, Hooper 1973, Shapiro 1974, MacNeill 1975, Dornfeld 1980, Stanford 1981, Pyle 1981, Miller & Brown 1981, 1983, Opler & Krizek 1984, Scott 1986, Tilden & Smith 1986, Heitzman & Heitzman 1987, Shull 1987, Klassen et al. 1989, Bailowitz & Brock 1991, Opler & Malikul 1992, Iftner et al. 1992). Unfortunately, as I have intimated, our genera are a mess. Problems generally spread into the neotropics, where they ramify—but where specimens and data are so much scarcer that sophisticated generic revision dealing fully with all relevant species is not practical. Even if it were, I am finding mistakes at the generic level too rapidly to give each affected species anything like the time and attention I have lavished on pairs of close and confusing differentiates within *Erynnis, Celotes, Atrytonopsis, Autochton, Wallengrenia,* and *Pyrgus* (Burns 1964, 1974, 1983, 1984, 1985, unpublished). Such detail is dispensable because problems of grouping species in genera are different from problems of delimiting species and analyzing speciation.

I aim here and in some related papers (e.g., Burns 1992, 1994) to redefine certain genera strictly by means of genitalia. Many short generic descriptions—including those of Evans (1955)—that omit genitalic characters really fail to characterize. Some recent long descriptions manage to drown a few useful genitalic observations in an indiscriminate sea. At the very least, my corrected generic limits will lead to better evolutionary, ecologic, ethologic, and biogeographic generalizations about American hesperiines.

Since my examination of their genitalia has shown that some type specimens are not what others thought, I have had to make some jolting changes in nomenclature. The abbreviations I use in citing museums are spelled out at the beginning of Acknowledgments (p. 334). All X-rated genitalia dissections are mine.

Atrytone Scudder vis-à-vis *Anatrytone* Dyar
(Figs. 1–3, 16, 17) (Figs. 4–15, 18–27, 83–86)

Scudder (1872) "defined" his new genus *Atrytone* merely by designating *Hesperia iowa* Scudder (= *Hesperia arogos* Boisduval & Leconte) type species and by including three other species originally described in *Hesperia*: *logan* Edwards, *conspicua* Edwards, and *zabulon* Boisduval & Leconte. Because this largely nearctic assemblage is heterogeneous, interpretation of *Atrytone* varied. Over the next eight decades, chiefly Godman, Dyar, Williams, Bell, and Hayward described many and various neotropical species in *Atrytone*. Hayward (1948) made one of them, *mella* Godman, the type of his monotypic new genus *Mellana*. Meanwhile, Barnes and McDunnough (1916) removed *zabulon* (plus a few of its congeners) to *Poanes*; and, eventually, Evans (1955) removed *conspicua* (plus what by then were seven related congeners) to *Euphyes* and all of the modern neotropical species of *Atrytone* to *Mellana*, leaving *Atrytone* with just two nearctic species from the eastern and central United States and adjacent Canada: *arogos* and *logan*. Later, Freeman (1969) described two new species of *Atrytone* from Mexico: *mazai* and *potosiensis*.

Dyar (1905) "characterized" his heterogeneous new genus *Anatry-*

tone in four and a half lines of undiagnostic text, designated *Hesperia delaware* Edwards (= *Hesperia logan*) type species, and included also *lagus* Edwards (now considered a subspecies of *logan*), *vitellius* Fabricius (now in *Choranthus*), and, of all things, *arogos*—the type species of *Atrytone*! (Dyar placed in *Atrytone* four skippers congeneric with one another though not with *arogos*.) Skinner (1905) lost no time in pointing out this grand idiocy, and *Anatrytone* has been called a synonym of *Atrytone* ever since (e.g., Barnes & McDunnough 1916, Lindsey 1921, Lindsey et al. 1931, Evans 1955, dos Passos 1964, Miller & Brown 1981, 1983).

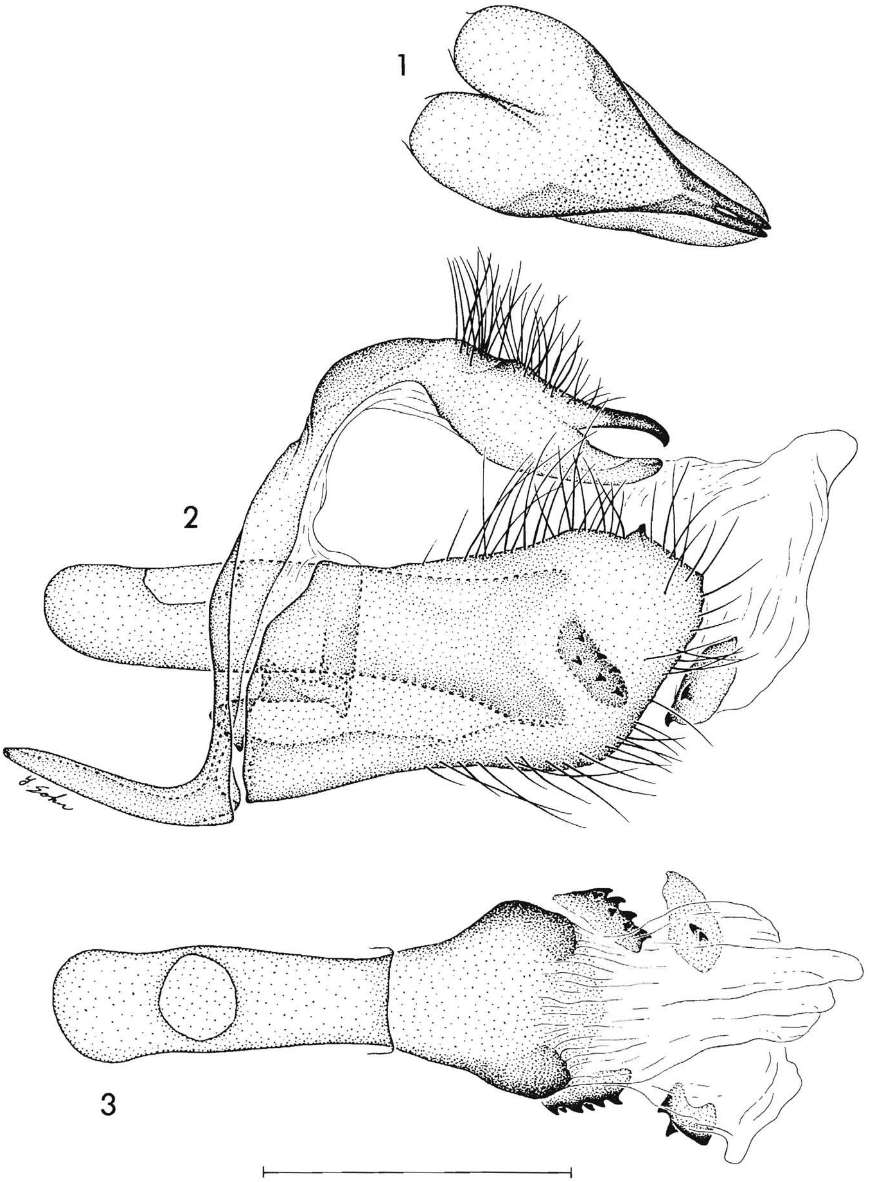
But the two genera do have different types, *arogos* and *logan*; and, as I demonstrated in great genitalic detail at the annual meetings of The Lepidopterists' Society in 1990 and 1991, these two fairly similar looking species (which have always been grouped—even by Dyar) really belong in separate genera. We must refer to *Atrytone arogos* and *Anatrytone logan*. Seizing mostly on differences in immature stages and life history, Scott (1992) reached the same conclusion.

For the record, I wish to emphasize that male tails of these skippers have been adequately shown in the past (though improperly read): *logan* by Scudder (1889:pl. 37, fig. 11) and, more completely, by Godman (1900:pl. 94, fig. 6); both *arogos* and *logan* by Skinner and Williams (1924a:figs. 12, 13—reprinted in Lindsey et al. 1931 on plates 27 and 28).

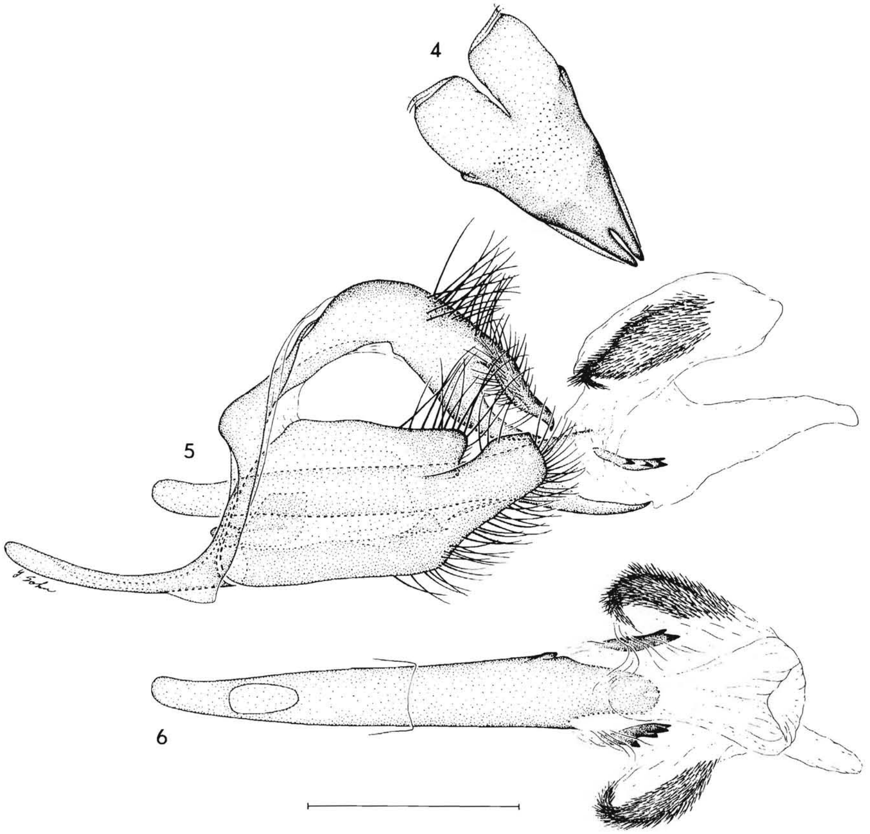
How do the genitalia of *Atrytone* and *Anatrytone* differ? Not with the "saccus longer" in *Anatrytone*, as claimed by Scott (1992:135).

An answer requires more than comparing the type species. Although, with the loss of *logan*, *Atrytone* is currently monotypic, *Anatrytone* is decidedly polytypic, containing not just *logan* and the above mentioned Freeman species, *mazai* and *potosiensis*, but five other species that collectively range from Mexico to Paraguay and Argentina. Evans (1955) put four of those species in *Mellana*—and in synonymy besides! Scott (1992:136) wrongly asserted "that based on adult morphology '*Atrytone*' *potosiensis* Freem. obviously belongs to genus *Mellana potosiensis new combination*." In characterizing *Anatrytone*, I have studied and compared the genitalia of all eight species, and have chosen to figure fully those of *potosiensis*, *barbara* Williams & Bell, and *flavens* Hayward, as well as *logan*, because they are as different from *logan* as any in the genus. However, in showing extremes of genitalic variation within *Anatrytone*, I am more interested in conveying a sense of the resemblance among the species than of the differences between them. Once this essential similarity is grasped, the larger and qualitatively different gap between *Anatrytone* and *Atrytone* should be obvious.

In males of *Atrytone* (Figs. 1–3), the valva is simple: its only em-



FIGS. 1–3. Male genitalia of *Atrytone arogos* from loess hills, 1460 ft (445 m), 4½ mi (7¼ km) SE Westfield, Plymouth County, Iowa, USA, 1 July 1980, J. M. Burns (genitalic dissection no. X-2569) (USNM). Scale = 1.0 mm. **1,** Tegumen, uncus, and gnathos in dorsal view. **2,** Complete genitalia (minus right valva), with vesica everted, in left lateral view. **3,** Aedeagus, with vesica everted, in dorsal view.



FIGS. 4–6. Male genitalia of *Anatrytone logan* from loess hills, 1150–1300 ft (350–395 m), 2.8 mi (4.5 km) W Ticonic, T85N, R44W, sect. 18 and 19, Monona County, Iowa, USA, 2 July 1980, J. M. Burns (X-2567) (USNM). Scale = 1.0 mm. **4,** Tegumen, uncus, and gnathos in dorsal view. **5,** Complete genitalia (minus right valva), with vesica everted, in left lateral view. **6,** Aedeagus, with vesica everted, in dorsal view.

bellishment is a small, toothlike flange on the distal dorsal rim (Fig. 2). The tegumen/uncus, in lateral view (Fig. 2), is dorsally concave above the point at which the gnathos diverges, and, in dorsal view (Fig. 1), is unevenly tapered to an extremely delicate pair of uncus prongs so that much of the underlying gnathos shows. The aedeagus (Figs. 2, 3) is short (distinctly shorter than the rest of the intact genitalia), stout, and distally flared. The everted vesica (Figs. 2, 3), which is short, sports two pairs of rigid cornuti below—the pair at the distal end of the aedeagus with more teeth than the pair beyond it.

In males of *Anatrytone* (Figs. 4–15, 24–27), the valva is more complex: a large notch in the dorsal rim splits a prominent dorsodistal extension from the body of the valva (Figs. 5, 8, 11, 14, 27); toward and at the base of this extension are modest medial protrusions (Figs. 5, 8, 11, 14). The tegumen/uncus, in lateral view (Figs. 5, 8, 11, 14, 27), is dorsally convex above the point at which the gnathos diverges, and, in dorsal view (Figs. 4, 7, 10, 13), is more or less evenly tapered to a heavier pair of uncus prongs so that most (Fig. 4) or all (Figs. 7, 10, 13) of the underlying gnathos is concealed. The aedeagus (Figs. 5, 6, 8, 9, 11, 12, 14, 15, 24–27) is nearly as long as, or longer than, the rest of the intact genitalia; and its floor is caudally prolonged. The everted vesica (Figs. 5, 6, 8, 9, 11, 12, 14, 15, 24–26), which is long, sports one pair of rigid cornuti below, near the caudally prolonged floor of the aedeagus, plus (in all species but *barbara* [Figs. 11, 12] and *flavens* [Figs. 14, 15]) a pair of flexible, spinulose cornuti above (which suggest scouring pads).

The female genitalia look more immediately distinct: they are shorter in *Atrytone* than in *Anatrytone*. In females of *Atrytone* (Figs. 16, 17), the lamella postvaginalis is short (in ventral view, wider than long) and arched dorsad (see lateral view); its posterior margin is usually well notched at the midline. The ductus bursae is short, almost uniformly wide, and well sclerotized, with many longitudinal wrinkles, especially dorsally. The adjacent, posterior part of the corpus bursae is lightly sclerotized, with more (chiefly longitudinal) wrinkles.

In females of *Anatrytone* (Figs. 18–21) other than *barbara* (Figs. 22, 23) and perhaps *flavens* (whose female I have not seen), peculiar, roughly linear sclerotization occurs midventrally in membrane between the ovipositor lobes, posterior and dorsal to the lamella postvaginalis and separate from it. The lamella postvaginalis itself (Figs. 18–23) is long (in ventral view, longer than wide) and ventrally about flat, with its lateral edges bent dorsad (see both ventral and lateral views); its posterior margin varies from outwardly rounded to shallowly notched at the midline. The ductus bursae—though ranging from short to long and from well to poorly sclerotized—reflects a basic pattern that involves some tapering toward the ostium bursae (Figs. 18, 20, 22), some dorsal concavity (Figs. 19, 21, 23), and some tendency for its roof to become membranous anteriorly where it meets the corpus bursae. The corpus bursae is entirely membranous.

THE SPECIES OF *ANATRYTONE* (INCLUDING THE TYPE OF *MELLANA*)

The *logan* Group

(Figs. 4–6, 10–15, 18, 19, 22, 23)

Anatrytone logan is the northernmost member of a loose, four-species group extending from southern Canada to Peru, Brazil, and northern Argentina.

In males of the *logan* group, the saccus is long (Figs. 5, 11, 14); titillators are totally absent (Figs. 12, 15) or, in about half the individuals of *logan*, present in rudimentary form on just the right side of the aedeagus (Fig. 6); the rigid cornuti are more or less linear and long and parallel with the caudal prolongation of the aedeagal floor so as to suggest dorsolateral extensions of the aedeagal roof (Figs. 5, 6, 11, 12, 14, 15); and the valvae are usually low (Figs. 11, 14) to medium (Fig. 5) in height.

In *logan* group females (*flavens* not seen), the sclerotization in membrane between the ovipositor lobes is wide (Fig. 18) or, in *barbara*, absent (Figs. 22, 23); the lamella postvaginalis, moderately long; the ventral lip of the ostium bursae, relatively simple; and the ductus bursae, long (see Figs. 18, 19, 22, 23 for all the above characters).

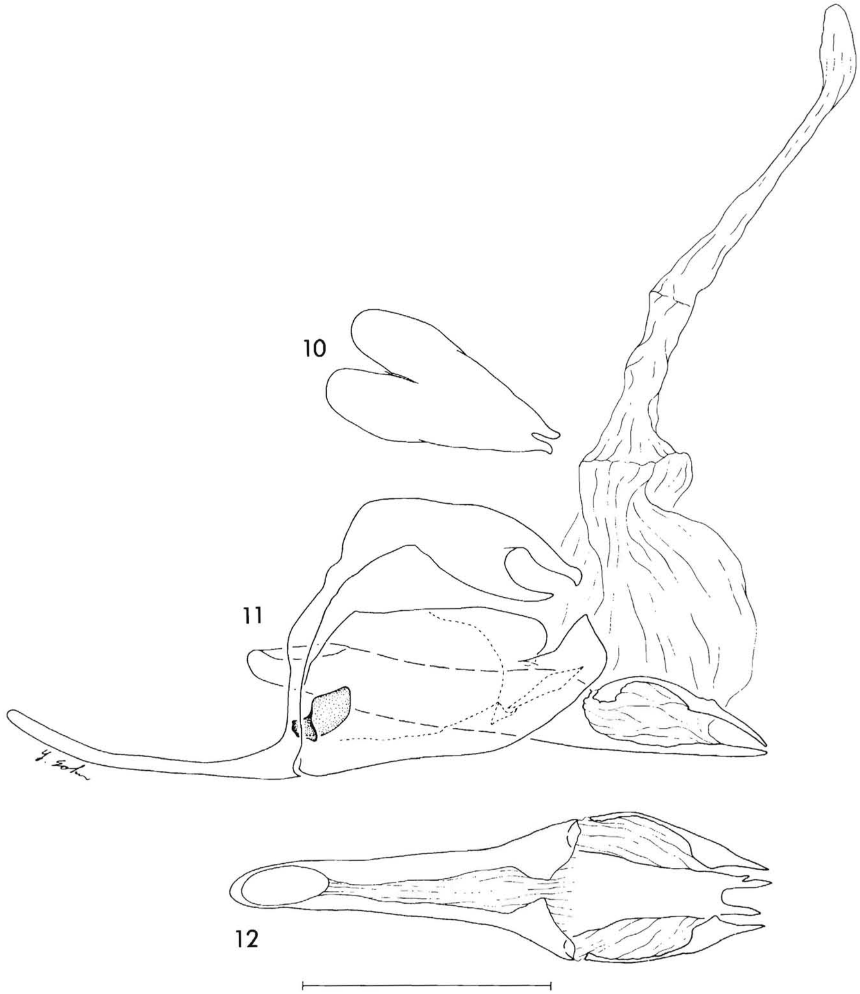
Although well differentiated from one another, these species are more or less allopatric: *A. logan* occurs from extreme southcentral Canada, through most of the eastern and central United States, to extreme northeastern Mexico; *A. mazai*, from extreme southern Texas (Laredo [Freeman 1969]) and northeastern Mexico, through El Salvador, to Costa Rica (Guanacaste); *A. barbara*, from Colombia, through Ecuador, Venezuela, and the Guianas, to Peru and Brazil (Amapá, Pará, Rondônia); and *A. flavens*, in northern Argentina (Tucumán, Salta). This far-flung quartet forms two subgroups of two species each—a North American *logan* subgroup comprising *logan* and *mazai* and a South American *barbara* subgroup comprising *barbara* and *flavens*. *Anatrytone logan* and *A. mazai* are closer to each other, both morphologically and geographically, than are *A. barbara* and *A. flavens*. However, *logan* and *mazai* are not subspecies, as claimed by Scott (1986) and echoed by Opler and Malikul (1992). Indeed, though virtually allopatric, they are too different from each other even to be grouped in a superspecies.

In *A. logan* and *A. mazai*, the dorsodistal extension of the valva, viewed from the side, is dorsally broad (Fig. 5); the flexible "scouring-pad" cornuti are large and long and well sclerotized (Figs. 5, 6); the straight rigid cornuti have at least two to as many as five points (Figs. 5, 6); and the caudal prolongation of the aedeagal floor is blunt at its distal end (Fig. 6).

This prolongation is greater in *A. mazai* than it is in *A. logan*; the rigid cornuti of *mazai* are more than twice as long as those of *logan*; and the thin, platelike protrusion from the inner side of the dorsodistal extension of the valva is much larger—and arises much higher—in *mazai* than in *logan*.

In *A. barbara* and *A. flavens*, the dorsodistal extension of the valva, viewed from the side, is dorsally narrow (Figs. 11, 14); flexible cornuti are lacking (Figs. 11, 14); the long, curved rigid cornuti have either a

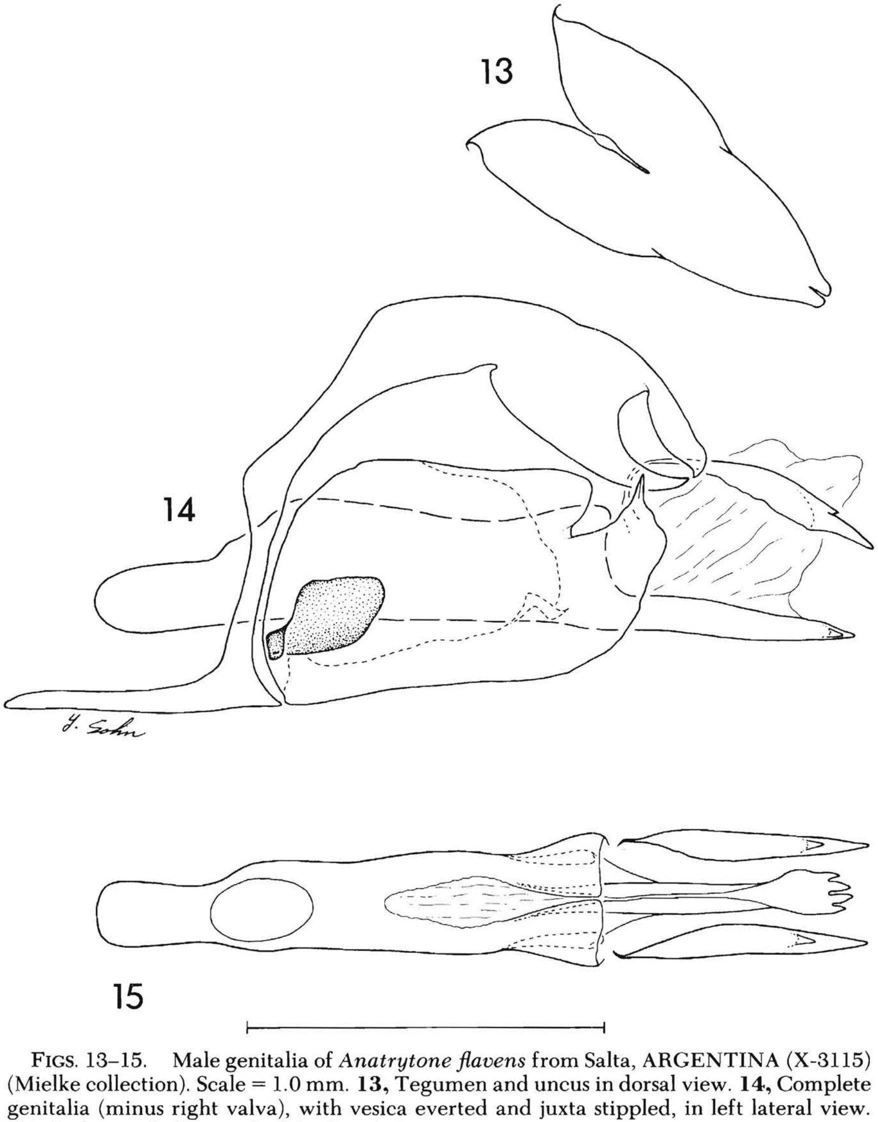
FIGS. 7–9. Male genitalia of *Anatrytone potosiensis* from San Pedro Sula, HONDURAS, 17 July 1979, R. D. Lehman (X-2573) (USNM). Scale = 1.0 mm. **7,** Tegumen, uncus, and gnathos in dorsal view. **8,** Complete genitalia (minus right valva), with vesica everted, in left lateral view. **9,** Aedeagus, with vesica everted, in dorsal view.



FIGS. 10–12. Male genitalia of *Anatrytone barbara* from 20 km SW Puerto Maldonado, 300 m, Madre de Dios, PERU, 25 October 1983, S. S. Nicolay (X-2585) (USNM). Scale = 1.0 mm. **10,** Tegumen and uncus in dorsal view. **11,** Complete genitalia (minus right valva), with vesica everted and juxta stippled, in left lateral view. **12,** Aedeagus (minus vesica) in dorsal view.

single (terminal) point (Figs. 11, 12) or such a point plus one small accessory point (Figs. 14, 15); and the caudal prolongation of the aedeagal floor is forked at its distal end (Figs. 12, 15).

The saccus is far shorter in *A. flavens* (Fig. 14) than it is in *A. barbara,* where it is nearly or quite as long as the valva (Fig. 11); the gnathos is



FIGS. 13–15. Male genitalia of *Anatrytone flavens* from Salta, ARGENTINA (X-3115) (Mielke collection). Scale = 1.0 mm. **13,** Tegumen and uncus in dorsal view. **14,** Complete genitalia (minus right valva), with vesica everted and juxta stippled, in left lateral view. **15,** Aedeagus (minus vesica) in dorsal view.

much shorter than the uncus in *A. barbara* (Fig. 11) though not in *A. flavens* (Fig. 14); the dorsodistal extension of the valva, viewed from the side, is dorsally extra narrow in *A. flavens* (Fig. 14); the caudal prolongation of the aedeagal floor is shallowly forked, with four tines at its distal end, in *A. flavens* (Fig. 15) but deeply and widely forked, with two main tines (often equipped with one [Fig. 12] or occasionally two small secondary teeth), in *A. barbara* (Fig. 12); the sides of the caudal prolongation are distinctively rolled upward in *A. flavens* (Fig. 15) while the distal end of the aedeagus is more expanded in *A. barbara* (Fig. 12).

In both *A. logan* and *A. mazai*, as already noted, there is wide sclerotization in membrane between the ovipositor lobes (Figs. 18, 19); the ventral lip of the ostium bursae is not notably enhanced (Figs. 18, 19); the ductus bursae is not strongly flattened dorsoventrally, and its dorsal concavity is pronounced (Fig. 19); at most, the anterior quarter of the roof of the ductus bursae gives way to membranous corpus bursae (Fig. 19); and the tapering of the ductus bursae toward the ostium bursae looks prosaic (Fig. 18).

The dorsal concavity of the ductus bursae is simple throughout its length in *A. mazai* whereas a more or less anterior part of the dorsal concavity is divided longitudinally by a middorsal keel in *A. logan* (Figs. 18, 19); the ventral lip of the ostium bursae is unreinforced in *mazai* but lightly reinforced in *logan* (Figs. 18, 19).

In *A. barbara*, there is no sclerotization in membrane between the ovipositor lobes (Figs. 22, 23); the ventral lip of the ostium bursae is well reinforced and turned strongly downward and backward (Figs. 22, 23); the ductus bursae is quite flattened dorsoventrally, and its dorsal concavity is slight (Fig. 23); at least the anterior half of the roof of the ductus bursae gives way to membranous corpus bursae (Figs. 22, 23); and the ductus bursae tapers toward the ostium bursae with style (Fig. 22).

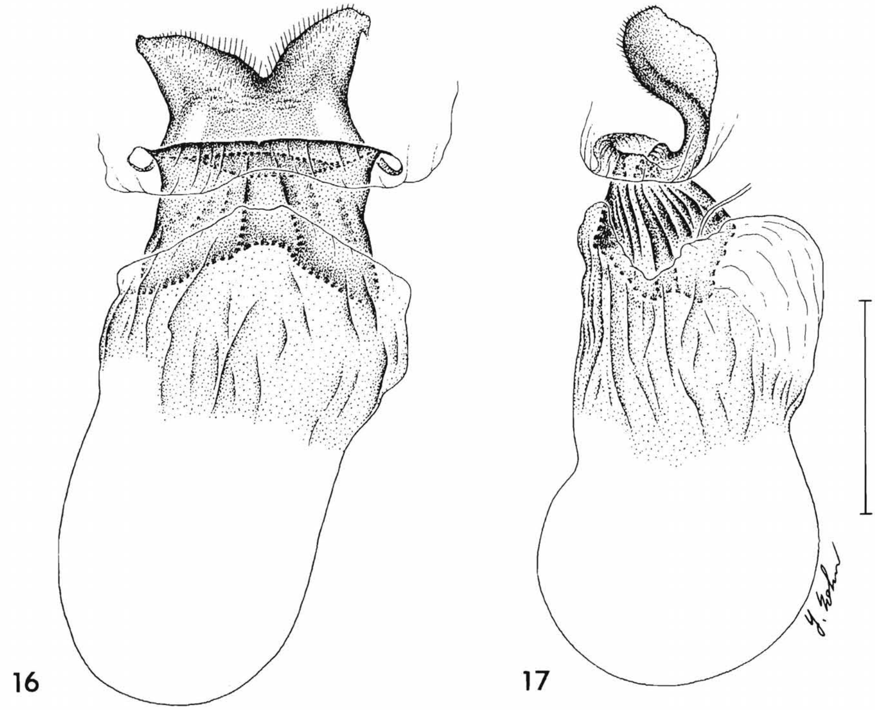
The *mella* Group
(Figs. 7–9, 20, 21, 24–27, 83–86)

Anatrytone potosiensis is the northernmost member of a compact, four-species group extending from Mexico to Argentina.

In males of the *mella* group, the saccus is short (Figs. 8, 27); conspicuous, paired titillators project from the sides of the aedeagus about where the caudal prolongation of the aedeagal floor begins (Figs. 8, 9, 24–27); the rigid cornuti are short (Figs. 8, 9, 24, 25) or lengthened by a peculiar base (Fig. 26); and the valvae are usually medium to extra high (Figs. 8, 27).

In *mella* group females, the sclerotization in membrane between the ovipositor lobes is narrow; the lamella postvaginalis, extra long; the ventral lip of the ostium bursae, well arched caudally and heavily sclerotized; and the ductus bursae, short (see Figs. 20, 21 for all the above characters).

Records of these closely related species indicate some sympatry with no breakdown in genitalic differences: *Anatrytone potosiensis* occurs



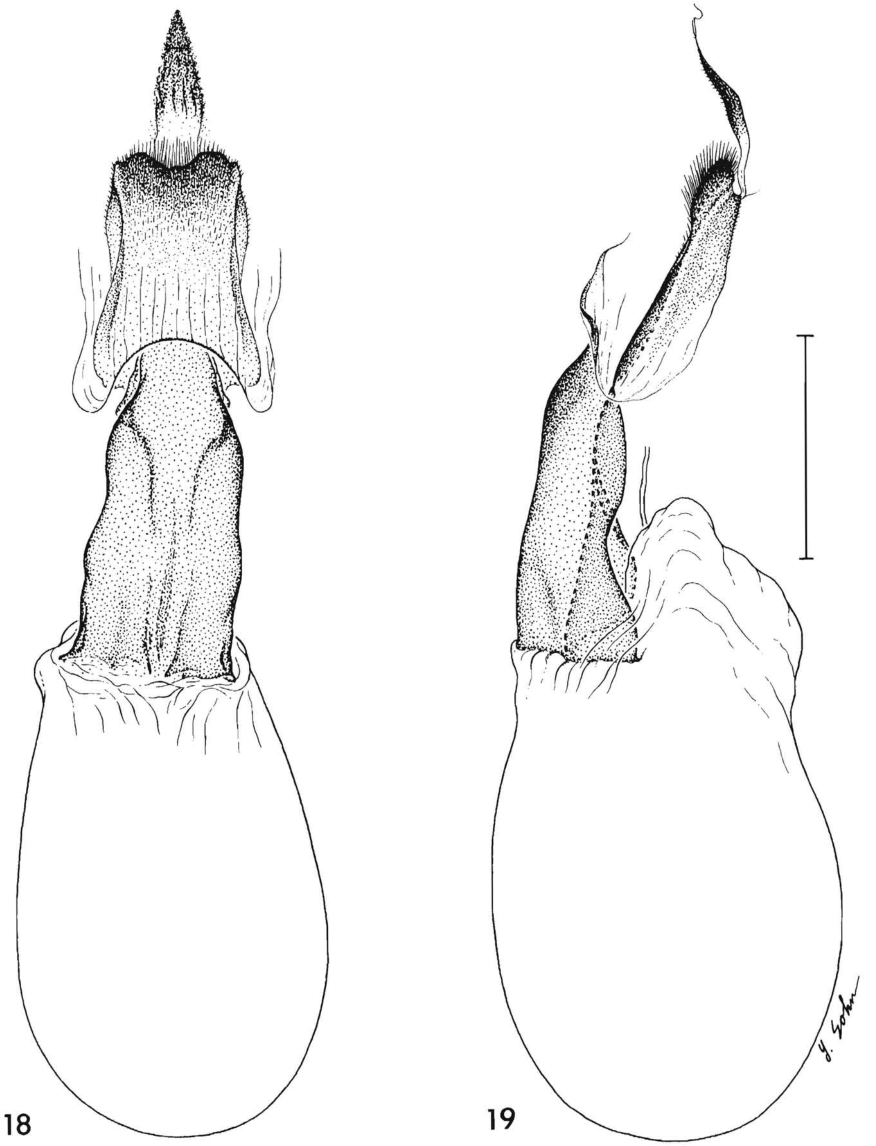
FIGS. 16, 17. Female genitalia of *Atrytone arogos* from Sioux City, Woodbury County, Iowa, USA, 26 June 1938, A. W. Lindsey (X-2745) (USNM). Scale = 1.0 mm. **16,** Sterigma and bursa copulatrix in ventral view. **17,** The same, plus part of the ductus seminalis, in right lateral view.

from central Mexico, through Guatemala, to Honduras; *A. mella,* from southern Mexico, through Central America (Guatemala, Belize, Honduras, Costa Rica, Panama), to Colombia and Peru; *A. sarah* (described below) from southern Colombia, through Ecuador and Peru, to Bolivia; and *A. perfida* (Möschler), from Colombia, Venezuela, Trinidad, Guyana, and French Guiana, through Brazil, to eastern Peru, Paraguay, and northern Argentina.

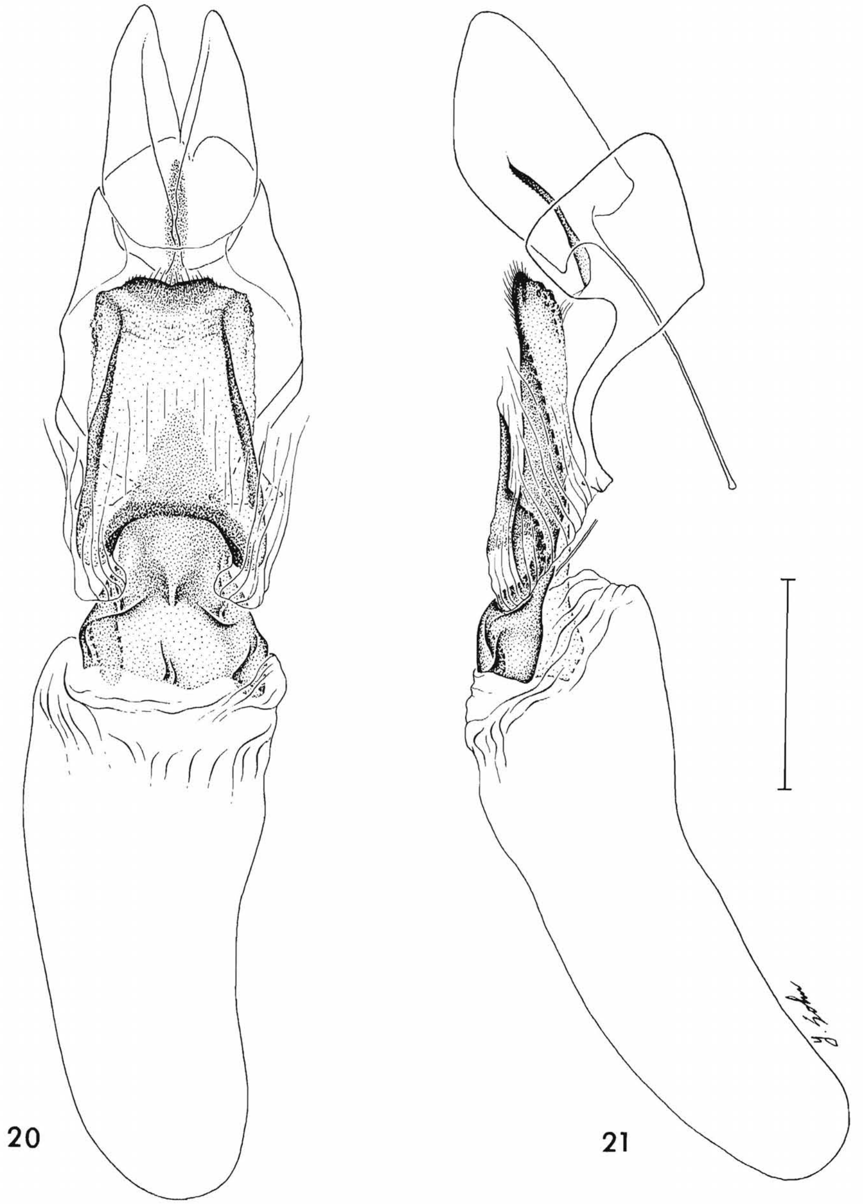
The following comparative description simultaneously characterizes all four species of the *mella* group; *sarah* is phylogenetically closest to *mella*.

***Anatrytone sarah*, new species**
(Figs. 24, 83–86)

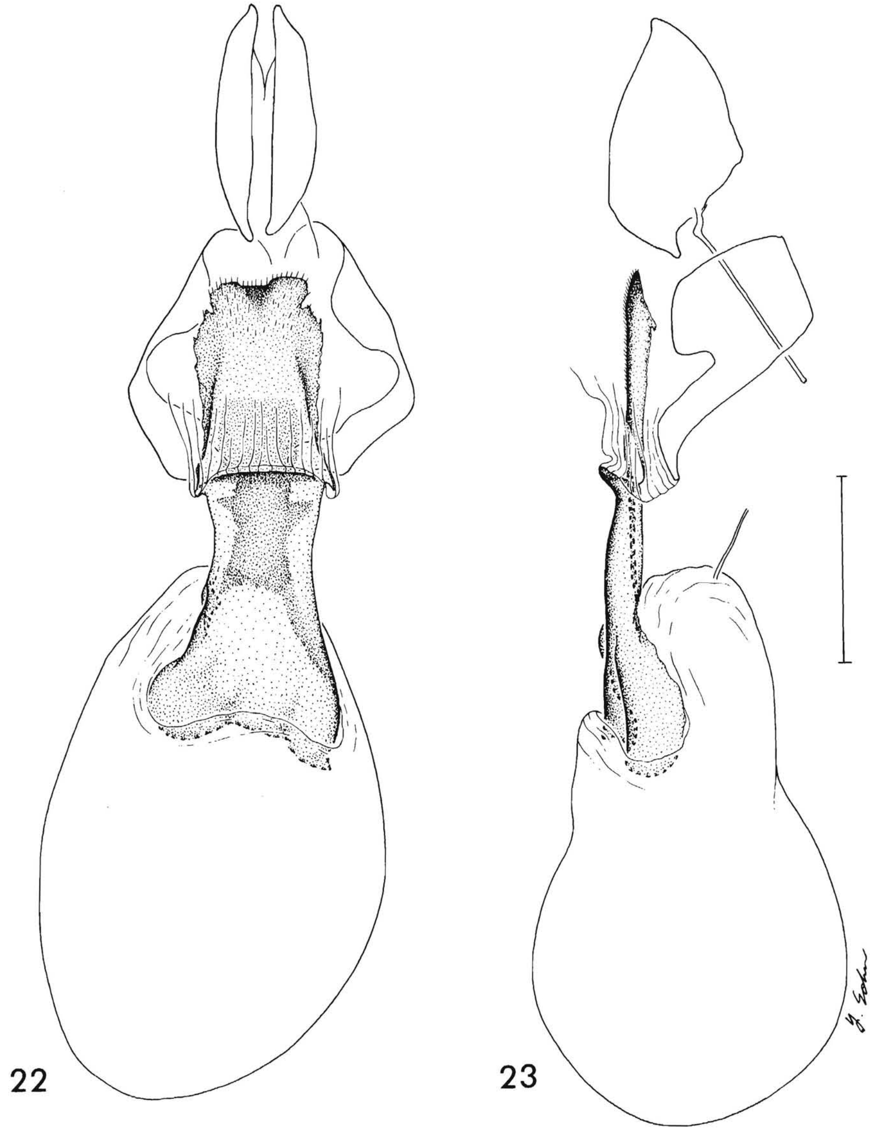
Most readily told by the aedeagus, especially the paired titillators which are longer and distally recurved in *sarah* (Fig. 24) and *mella* (Fig. 25) but shorter and divergent in



FIGS. 18, 19. Female genitalia of *Anatrytone logan* from Austin, Travis County, Texas, USA, 14 May 1966, J. M. Burns (X-2627) (USNM). Scale = 1.0 mm. **18,** Sterigma and bursa copulatrix, plus linear sclerotization in membrane between ovipositor lobes, in ventral view. **19,** The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 20, 21. Female genitalia of *Anatrytone potosiensis* from Cotaxtla Exp. Sta., Cotaxtla, Veracruz, MEXICO, 31 July 1962 (X-2606) (USNM). Scale = 1.0 mm. **20,** Sterigma and bursa copulatrix, plus linear sclerotization in membrane between ovipositor lobes and an indication of the terminal abdominal tergites (including the ovipositor lobes), in ventral view. **21,** The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 22, 23. Female genitalia of *Anatrytone barbara* from Tambopata Reserve, Rio La Torre, 300 m, Madre de Dios, PERU, 2 November 1984, S. S. Nicolay (X-2829) (USNM). Scale = 1.0 mm. **22,** Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the ovipositor lobes) in ventral view. **23,** The same, plus part of the ductus seminalis, in right lateral view.

potosiensis (Figs. 8, 9) and *perfida* (Fig. 26). The titillators are shortest in *perfida*. In *sarah* (Fig. 24) they are abruptly constricted from a broad, knobby base and are bowed farther out than they are in *mella* (Fig. 25) whose basal taper is more even. They are also less flattened in *sarah* than in *mella* but lie more in a horizontal plane. In *sarah*, as in *mella* and most *perfida*, each titillator ends in a single point (Figs. 24–26), instead of in 2 to 4 (usually 3) points, as in *potosiensis* (Figs. 8, 9). (In one of the many males of *perfida* examined, the left titillator ends in 2 points.)

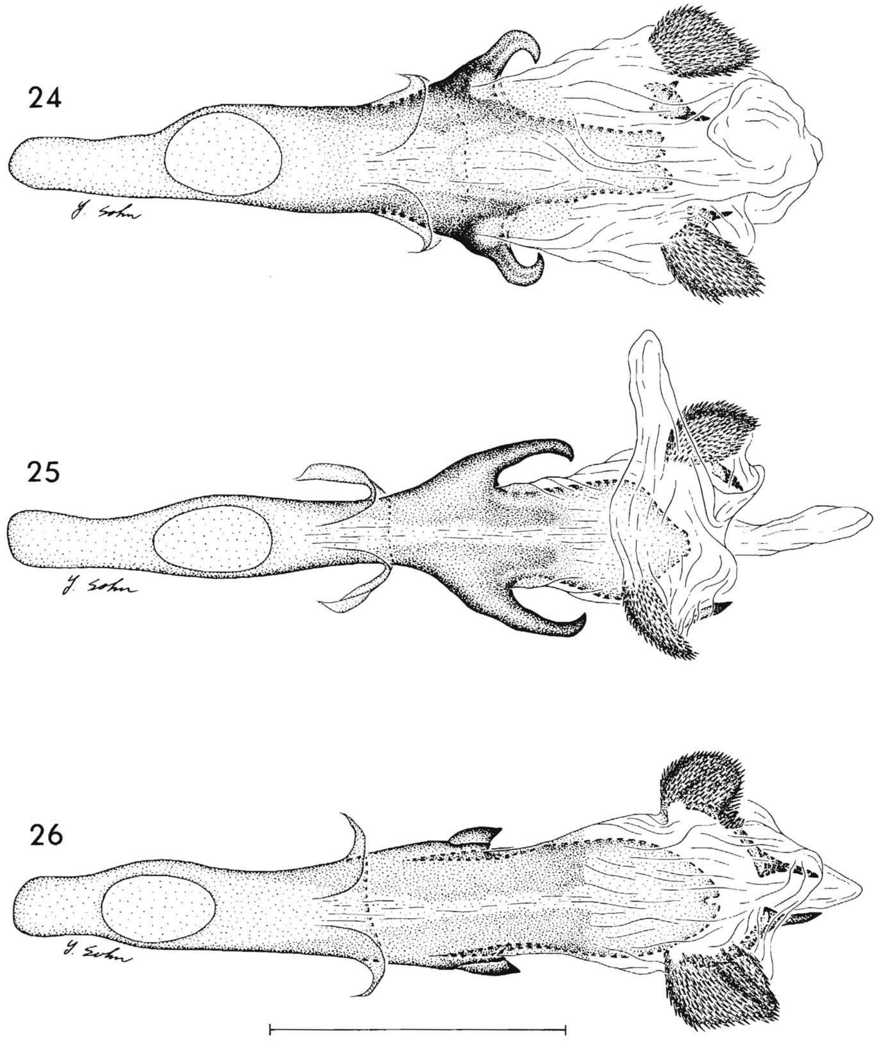
The caudal prolongation of the aedeagal floor is in *sarah* long, generally somewhat narrower than in other members of the *mella* group, continuously tapered from front to back, and distally truncate (Fig. 24); it is also truncate in *potosiensis* but relatively short and broad (Fig. 9). Though long, it is distally rounded in *mella* (Fig. 25) and rounded (Fig. 26) to somewhat truncate in *perfida*—and usually centrally notched in *perfida* (Fig. 26) but not in *mella* (Fig. 25). A lateral view shows it dipping downward sharply in *sarah*, less so in *perfida*, still less in *mella*, and little or not at all (Fig. 8) in *potosiensis*. Despite plenty of individual variation, these characters of the aedeagal floor are good.

Development of both kinds of cornuti, taken together, is intermediate in *sarah*, greatest in *perfida*, least in *mella* and *potosiensis* (in different ways). The paired flexible cornuti ("scouring pads") are large and well sclerotized in *perfida* (Fig. 26), middle-sized and well sclerotized in *sarah* and *mella* (Figs. 24, 25), and small and lightly sclerotized in *potosiensis* (Figs. 8, 9)—to the extent that in one individual they virtually vanish. The paired rigid cornuti are largest in *perfida*, where each has an extra-long base—more or less arcuate in dorsal (Fig. 26) or ventral view—and a long point (which becomes dual on the left side in one of the many *perfida* examined). The rigid cornuti are middle-sized in *sarah*, where each has a respectable base and one or sometimes two usually longish points (the two-point condition can affect the left or the right [Fig. 24] cornutus). The rigid cornuti are also middle-sized in *potosiensis*, where each has a base at least as large as that of *sarah* but usually a shorter point (Fig. 9). They are smallest in *mella*, where they either have smallish to (more often) small, narrow bases and longish to (more often) short points (Fig. 25), or else are drastically reduced to a sliver (such vestigial cornuti can be on the left, on the right, or on both sides).

In ventral view the ventral lip of the ostium bursae forms a caudally directed arch, which is sharper in *sarah* and *mella* than in *potosiensis* (Fig. 20) and *perfida*. Although in all four species this lip curves downward (ventrad), it also curves conspicuously forward along both sides in *sarah* and *mella* but not in *potosiensis* (Figs. 20, 21) and *perfida*. Anterior to the lip region the ductus bursae is more or less lightly and incompletely sclerotized in *mella*, three-quarters to fully sclerotized in *sarah*, and fully sclerotized in *potosiensis* (Figs. 20, 21) and *perfida*. The arch of the ventral lip does not extend as far back in *sarah*, *mella*, and *potosiensis* as it does in *perfida*.

Anatrytone sarah is similar in size to other species of *Anatrytone* (except *barbara* and especially *flavens*, which are small), with the usual sex difference (females larger than males): 9 ♂♂ average 15.5 mm (range 14.9–16.1 mm) in forewing length; 2 ♀♀, 16.5 mm (range 16.4–16.6 mm).

The members of the *mella* group are similar (and, of course, individually variable) in superficial appearance—females so much that I cannot distinguish those of *sarah* (Figs. 85, 86) from those of *mella*, *perfida*, and *potosiensis* (on an average, however, females of *perfida* have the dorsal light areas a little more extensive and the yellow of the broad, ventral light areas brighter and clearer, less darkened with rust). Males of *sarah* (Figs. 83, 84) tend to be more distinctive because of the size and darkness of an irregular dark band in the dorsal forewing running obliquely from the base of the wing mainly through the upper part of the proximal half of space 1b, the proximal end of space 2, the length of the cell, and space 5, or spaces 4 and 5, to the wide dark border along the outer margin. This oblique dark band is variably, and usually less well, expressed in *mella* and especially *perfida* (some *mella* come close) and is completely missing from *potosiensis*. On the dorsal hindwing, males of *sarah* send a narrow, yellow orange ray along vein 1b to the outer margin (Fig. 83). Altogether, males of *sarah* approach the unusual, dorsal look of males of *barbara* of the *logan* group, except that other wing veins in *sarah* are still dark where they cross light areas (Fig. 83).



FIGS. 24–26. Aedeagi, with vesicae everted, in dorsal view, belonging to three species of *Anatrytone* in the *mella* group (compare also Fig. 9). Scale = 1.0 mm. **24,** *Anatrytone sarah* (holotype) from Limoncocha, 240 m, Napo, ECUADOR, 24–27 June 1980, C. V. Covell Jr. (H739) (USNM). **25,** *Anatrytone mella* from Macaracas, Los Santos, PANAMA, 22 December 1984, G. Small (X-2581) (USNM). **26,** *Anatrytone perfida* from Sapucay, PARAGUAY, W. T. Foster (X-2575) (USNM).

Holotype. ♂; ECUADOR, Napo (province), Limoncocha, 240 m, 24–27 June 1980, C. V. Covell Jr.; S. S. Nicolay genitalia dissection H739; USNM.

Paratypes. n = 8 ♂ 2 ♀. BOLIVIA, Santa Cruz (department), Las Juntas, 250 m, J. Steinbach: November 1913, 1 ♂, J. M. Burns genitalia dissection X-2836, CMNH; December 1913, 1 ♀, X-2843, CMNH. COLOMBIA, Amazonas (commissary), Leticia, 20 April 1946,

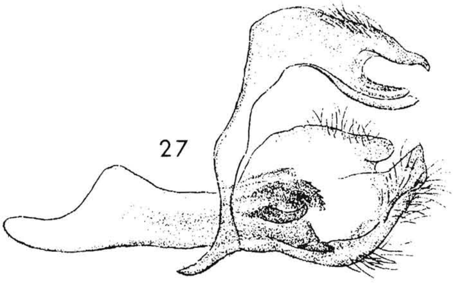


FIG. 27. Godman's figure of the male genitalia of *Anatrytone mella*; complete genitalia (minus left valva and juxta) in left lateral view. Note that, with the left valva removed, Godman's figure shows the inner surface of the right valva, whereas my figures show the outer surface of the left valva.

L. Richter, 1 ♂, E. L. Bell genitalia dissection G1911, AMNH; Puerto Asis, Rio Putumayo, 1 February 1969, S. S. Nicolay, 1 ♂, H484, USNM. ECUADOR, Napo (province): Archidona, 800 m, 13 October 1986, S. S. Nicolay, 1 ♂, H970, USNM; Coca, 350 m, 12 May 1975, Lefebre, 1 ♂, X-3466, collection of O. H. H. Mielke; Pastaza (province), Puyo-Napo Road, km 25, 1100 m, 11 November 1988, D. H. Ahrenholz, 1 ♂, X-3204, collection of S. S. Nicolay. PERU, Loreto (department), 40 km NE Iquitos, 14–20 January 1991, J. Glassberg, 1 ♂, X-3175, USNM; Madre de Dios (department): Puerto Maldonado, 290 m, 14 October 1983, S. S. Nicolay, 1 ♀, X-2607, USNM; Boca Rio La Torre [=Tambopata Reserve], 300 m, 23 November 1983, G. Lamas, 1 ♂, X-2846, MUSM.

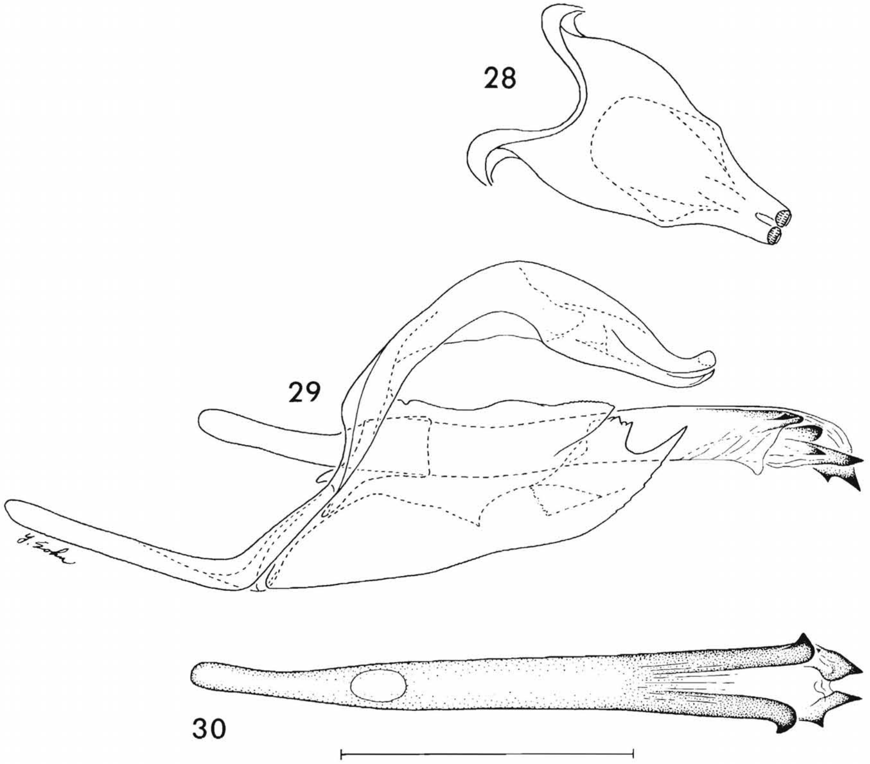
Etymology. The specific name *sarah*, which hails to and from my wife, is a noun in apposition to the generic name *Anatrytone*.

A TWIST OF NOMENCLATURE AND A DASH OF *WALLENGRENIA* (Figs. 27–30)

Besides the one of *sarah*, I have examined the types (also male) of *perfida* Möschler (1878) (ZMHB), *gladolis* Dyar (1914) (USNM), *flavens* Hayward (1940) (IML), *potosiensis* Freeman (1969) (AMNH), and *mazai* Freeman (1969) (AMNH).

When Dyar (1914) described *gladolis* he designated "Cotypes, one male, three females." I have studied all four specimens, which are similarly labelled and conspecific, and have chosen the lone male as lectotype. It bears the following tags, most of which are printed: [1] Georgetown/Br. Guiana, [2] BredSpecimen, [3] HWBMoore/Coll, [4, handwritten] Larva on blades/of sugar cane, [5, red] Type No./18115/ U.S.N.M., [6, handwritten] Atrytone/gladolis/type Dyar, [7] GENITALIA NO./X-2831/J.M.Burns 1990. Although Dyar noted that *gladolis* is "nearest to *A. mella*," his original description (confined to the appearance and spread of the wings) is too brief and superficial to distinguish *gladolis* from *mella*—or from a good many other hesperiines, either. It turns out that *gladolis* Dyar (1914) is a (new) synonym of *perfida* Möschler (1878).

The original figure of the male genitalia of *A. mella* (Godman 1900:



FIGS. 28–30. Male genitalia of holotype of *Hesperia clavus* Erichson from British Guiana (X-2933) (ZMHB), which is a species of *Wallengrenia* similar to, or the same as, *W. otho*. Scale = 1.0 mm. **28,** Tegumen, uncus, and the very tip of the gnathos in dorsal view. **29,** Complete genitalia (minus right valva) in left lateral view. **30,** Aedeagus in dorsal view.

pl. 94, fig. 16 [reprinted in this paper as Fig. 27]) shows the short saccus characteristic of the *mella* group; the long, recurved titillator, evenly tapered at the base (less obvious in this lateral view), characteristic of *mella*; the "scouring-pad" cornuti characteristic of all species of *Anatrytone* except *barbara* and *flavens*; and a valva with the characteristic *Anatrytone* shape, but extra high. Valval height increases out of proportion to valval length in the *mella* group, especially in *mella, sarah,* and *potosiensis* (Fig. 8), and somewhat less consistently in *perfida*.

When Hayward (1948) described the new genus *Mellana,* he took as its type (and sole species) *Atrytone mella* Godman (1900), which he considered the same as *Atrytone gladolis* Dyar (1914). Since Hayward cited a specimen from northern Argentina (Misiones), his type species must really be *perfida* Möschler (1878) (= *gladolis* Dyar [1914]) instead of *mella*; but that makes no difference. Both are congeneric with *Anatrytone logan* (Edwards), and *Anatrytone* Dyar (1905) has priority over *Mellana* Hayward (1948).

Evans (1955:354, 355) muddled his much expanded treatment of Hayward's (1948, 1950b) monotypic *Mellana* by calling *mella* Godman (1900) a synonym of *clavus* Erichson (1848)—which thus, in Evans's eyes, became the type of *Mellana*—and by listing *gladolis* Dyar (1914), *barbara* Williams & Bell (1931), and *flavens* Hayward (1940) as additional synonyms of *clavus*. I have shown that *gladolis* is a synonym of *perfida*, which is a species separate from *mella* but close to it, that *barbara* and *flavens* are very distinct from both of them and rather different from each other, and that all four go in *Anatrytone*. Having borrowed (from ZMHB) the holotype of *Hesperia clavus* Erichson (1848)—a male—and examined its genitalia (Figs. 28–30), I can flatly state that it is a species of *Wallengrenia*!

Wallengrenia clavus (Erichson), new combination, is what Evans (1955 plus associated "Addenda and Corrigenda") called *W. otho curassavica* (Snellen). The name *clavus*, being older, supplants the name *curassavica*. The biologic entity *clavus* closely resembles *otho* Smith (1797), differing chiefly in the direction of the terminal tooth on the right (the longer) distal division of the aedeagus: that tooth points up and to the right in *clavus*, up and to the rear in *otho* (compare Figs. 29, 30 with figs. 11–14, 19–22 in Burns 1985). The type of *clavus* comes from Guyana. In a crude transect—12 more tails of *Wallengrenia* males from Mexico to Brazil—the right aedeagal tooth points up and to the right in the six males from Panama, Colombia, Guyana, and French Guiana, but not in those from farther north or south. Some features of the pair of terminal, dependent, two-toothed cornuti (dubbed "flags" in Burns 1985) also appear to vary geographically. Whether *clavus* is a synonym of *otho*, a subspecies of *otho*, or a separate species is a problem beyond the scope of this paper.

After blindly synonymizing *barbara* with three other species of *Anatrytone* and *Wallengrenia clavus*, Evans (1955:359) went on to describe new species *Mellana villa*, which Mielke (1973) pegged as a synonym of *M. barbara* (Williams & Bell)! Mielke also observed that *M. barbara* was not synonymous with *M. clavus* (Erichson).

Note that *Atrytone*, *Anatrytone*, and *Quasimellana* (the new genus, described below, for most of what was in *Mellana*) all lack a stigma on the forewing of the male whereas *Wallengrenia* bears a bold stigma.

Summary of *Atrytone* and *Anatrytone*

The following capsule of my treatment of *Atrytone* and *Anatrytone* gives the number of male and female genitalia examined at each level—

140 dissections in all. I list neither subspecies nor synonyms of *Atrytone arogos* and *Anatrytone logan* because I did not investigate these familiar nearctic skippers at that low level. Such information is readily available in checklists (Miller & Brown 1981, 1983). Repeating it here would amount to empty endorsement of what may be faulty or undocumented opinion—the kind of deed that has left much of our taxonomy a shambles.

Atrytone Scudder, 1872, 10 ♂ 15 ♀, n = 25
    arogos (Boisduval & Leconte, [1834]), 10 ♂ 15 ♀

Anatrytone Dyar, 1905, 82 ♂ 33 ♀, n = 115
= *Mellana* Hayward, 1948, new synonym
  the *logan* group, 31 ♂ 14 ♀
    the *logan* subgroup, 14 ♂ 10 ♀
      logan (Edwards, 1863), 8 ♂ 8 ♀
      mazai (Freeman, 1969), new combination, 6 ♂ 2 ♀
    the *barbara* subgroup, 17 ♂ 4 ♀
      barbara (Williams & Bell, 1931), new combination, 15 ♂ 4 ♀
      = *villa* (Evans, 1955)
      flavens (Hayward, 1940), new combination, 2 ♂
  the *mella* group, 51 ♂ 19 ♀
      mella (Godman, 1900), new combination, 14 ♂ 11 ♀
      sarah Burns, new species, 9 ♂ 2 ♀
      potosiensis (Freeman, 1969), new combination, 6 ♂ 1 ♀
      perfida (Möschler, 1878), new combination, 22 ♂ 5 ♀
      = *gladolis* (Dyar, 1914), new synonym

Major Generic Characters in the Smallest Genitalic Structures

What remains after subtracting species of *Anatrytone* (and *Wallengrenia clavus*) from *Mellana* as treated by Evans (1955) is an unnamed and difficult neotropical genus at least thrice the size of *Anatrytone* and far more diverse. Ranging from the extreme southern United States (southern Texas; perhaps also southern Arizona—see Bailowitz & Brock 1991) to Peru, Bolivia, Paraguay, and northern Argentina, new genus *Quasimellana* (described below) is broadly sympatric with *Anatrytone*. Both occur from sea level to moderate elevations. Despite some similarities in superficial appearance, which cause confusion, *Quasimellana* and *Anatrytone* are not closely related.

We have seen that the genitalia of *Anatrytone* are basically conservative (in both sexes) and hence invaluable for defining that genus. In gross view, those of *Quasimellana* are signally variable, especially in males (females of a quarter of the species are not yet known): the large middorsal structures (tegumen/uncus plus underlying gnathos) and the

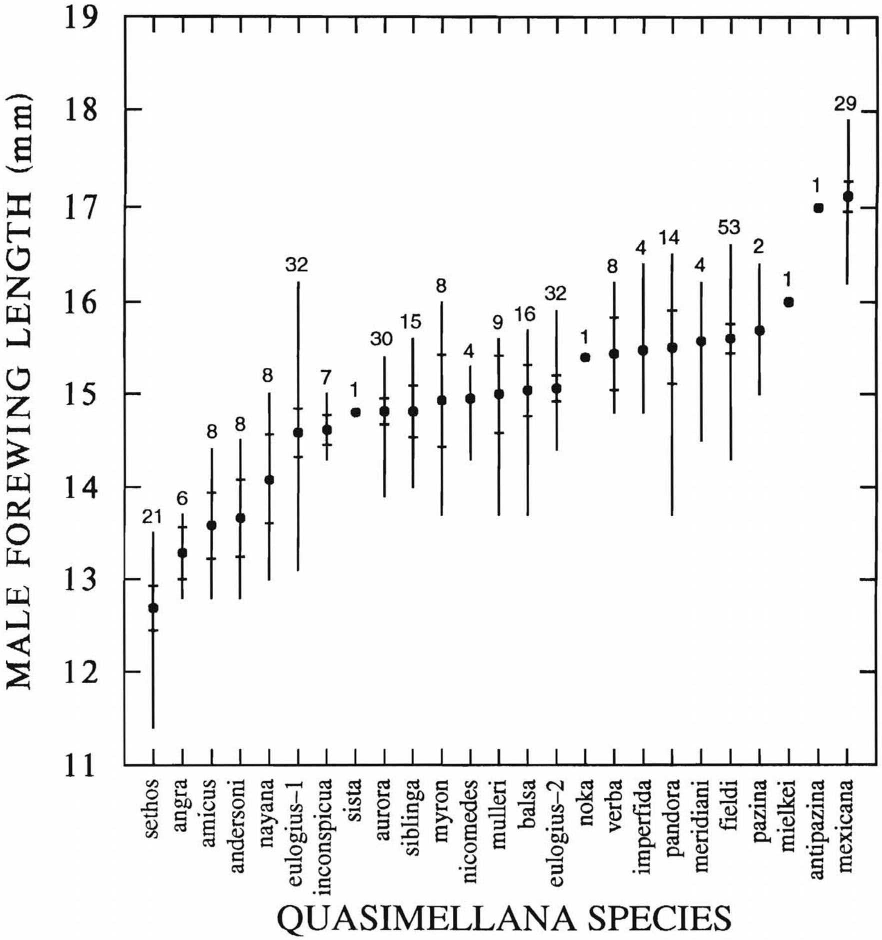
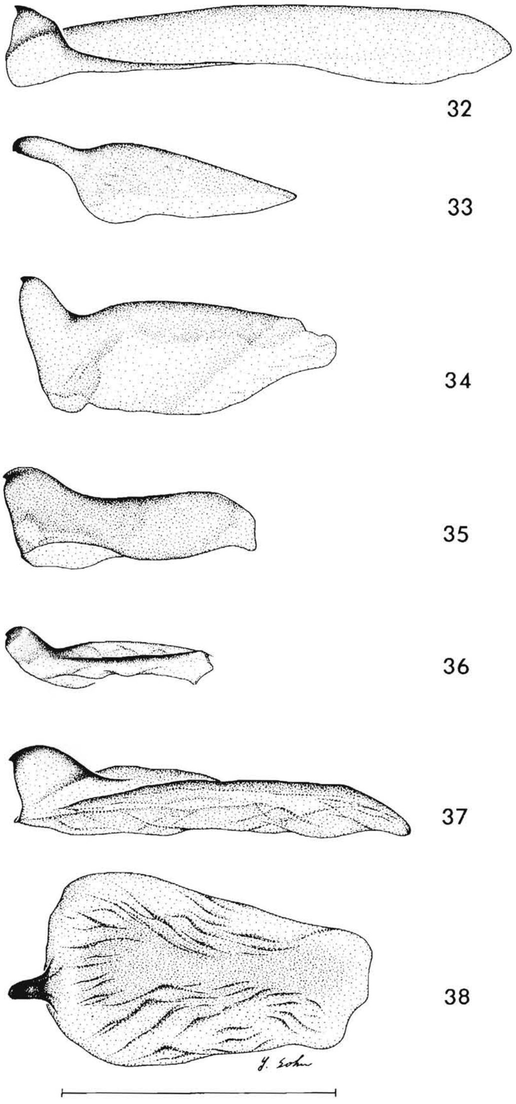


FIG. 31. Size (male forewing length) in species of *Quasimellana* from smallest to largest. Vertical lines show ranges; dots, means (or single observations); crossbars, plus and minus twice the standard error of the mean (when the sample size exceeds five). Sample sizes appear above the range lines. There are two geographic subsamples of the widespread and relatively common *Q. eulogius*: *eulogius*-1 from Mexico and *eulogius*-2 from Honduras, Nicaragua, Costa Rica, and Panama.

large, paired lateral structures (valvae) assume too many forms to permit generalizing across the whole genus. But what do characterize *Quasimellana* are two relatively small and obscure genitalic structures currently lacking the "respect and attention" (Burns 1987:184) they deserve: the cornutus and the juxta.

The shape of the cornutus alone is diagnostic. Though it does vary within—and more perceptibly between—species, the variation is so



FIGS. 32–38. Cornuti of six species of *Quasimellana* showing variations on an essential theme. Scale = 0.5 mm. **32,** *Q. eulogius* from Ciudad de Valles, San Luis Potosí, MEXICO, 13 October 1976, E. C. Knudson (X-2587) (USNM). **33,** *Q. mexicana* (X-2586) shown fully in Figs. 40, 41 (qv for specimen data). **34,** *Q. fieldi* (X-2571) whose juxta appears in Fig. 39 (qv for specimen data). **35,** *Q. nicomedes* from Cacatu, Antonina, 20 m, Paraná, BRAZIL, 25 April 1973, Mielke (X-2366) (MacNeill collection). **36,** *Q. sethos* from Paraíso, Canal Zone, PANAMA, 27 April 1982, S. S. Nicolay (X-2595) (USNM). **37, 38,** *Q. mulleri* (paratype) from Guerrero, MEXICO, August, R. Müller (X-2669) (AMNH).

TABLE 1. Number of antennal nudum segments in species of *Quasimellana*.

Species groups and species	Mean	Number of nudum segments						n
		11	12	13	14	15	16	
eulogius group								
mexicana	13.3			19	8			27
eulogius	13.4	1	6	56	39	5	1	108
siblinga	14.3			1	9	6		16
balsa	13.4		1	9	6	1		17
mulleri	12.9		1	9				10
sethos group								
aurora	13.7			9	12	2		23
nayana	14.4			1	3	4		8
pazina						2		2
antipazina						1		1
sista						1		1
andersoni	14.8				1	4		5
sethos	14.0			4	16	1	1	22
myron	12.9		1	10				11
verba	13.5			4	4			8
inconspicua	13.4		1	3	4			8
angra	14.2			2	4	4		10
nicomedes group								
amicus	13.2			8	2			10
fieldi	14.2		1	3	42	17	1	64
nicomedes	15.2				1	3	2	6
imperfida	14.8				1	4		5
mielkei							2	2
meridiani	15.5					2	2	4
pandora	15.5					6	5	11

constrained that a single, simple generic theme stands out (Figs. 32–38). Since the sclerotized cornutus sits in the membranous vesica which, except during copulation, rests collapsed and folded within the sclerotized aedeagus, the vesica must be everted for a really good look at the cornutus (Figs. 41, 43, 45, 47, 49, 50, 52, 53, 55, 57, 59, 60, 62, 65, 67).

The shape of the juxta (Fig. 39) is likewise diagnostic; but so, too, is its location. An apparent support for the aedeagus, the juxta lies ventral and lateral to it at about the level of the anterior ends of the paired valvae and the adjacent vinculum to which they articulate. Typically, in a lateral view of male genitalia, the juxta is largely to entirely hidden behind the vinculum and the front end of a valva. That is where it is in *Atrytone* (Fig. 2), *Anatrytone* (Figs. 5, 8, 11, 14), and *Wallengrenia* (Fig. 29); in many other genera thought to be related to these (i.e., in the *Hesperia* subgroup of the M or *Hesperia* group of Evans 1955), such as *Hesperia* itself (Burns 1987, fig. 2), *Atalopedes* (Burns 1989,

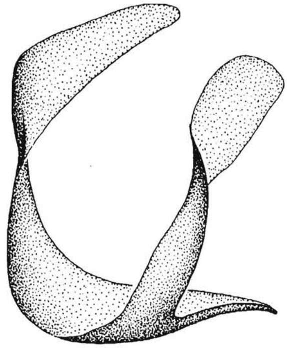


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FIG. 39. Juxta, in left anterodorsolateral view, of *Quasimellana fieldi* from 15.4 mi (24.8 km) S Ciudad de Valles, San Luis Potosí, MEXICO, 22 August 1967, G. F. Hevel (X-2571) (USNM).

figs. 25, 27, 29, 31, 33), *Polites* (Burns 1994, fig. 14), *Poanes* (Burns 1992, figs. 2, 5), *Paratrytone* (Burns 1992, fig. 20), and the like; and in a great many other skippers, as well. However, in *Quasimellana* the juxta is so far forward that most of it shows in lateral view (Figs. 41, 43, 45, 47, 52, 55, 57, 59, 62, 65, 67).

Since the location of the juxta is crucial, I regret to say that it can rarely be determined from published figures of skipper genitalia. In most of them, the juxta does not even appear (see Fig. 27, which exemplifies the many genitalic figures in Godman & Salvin 1879–1901). When it does, it almost always accompanies the aedeagus in an exploded view of the genitalia, displaced from its true position and from its proper relation to other parts. The common practice of dissociating major structures such as the valvae or the aedeagus when dissecting male genitalia, often destroys the juxta. Evans's mode of quick dissection and dissociation routinely did away with it (Figs. 49, 50, 53, 60).

Quasimellana, new genus

(Figs. 31–82, 87–112)

Size. Male forewing length ranges from 11.4 to 17.9 mm; but, in most species, mean male wing length falls between 14 and 16 mm (Fig. 31). The relatively few females available always average larger than conspecific males.

Nudum. Ranging from 11 to 16 segments, the nudum usually numbers 13 to 15 segments (though often to 16 segments in the *nicomedes* group), evenly split between the body of the club and the apiculus (Table 1).

Stigma. Males do not have a stigma.

Male genitalia. The sole (or only sizable) rigid cornutus consists of a simple body with a head-and-neck that ends in a tiny hook (Figs. 32–38, 41, 43, 45, 47, 49, 50, 52, 53, 55, 57, 59, 60, 62, 65, 67). The entire structure is well sclerotized and conspicuous.

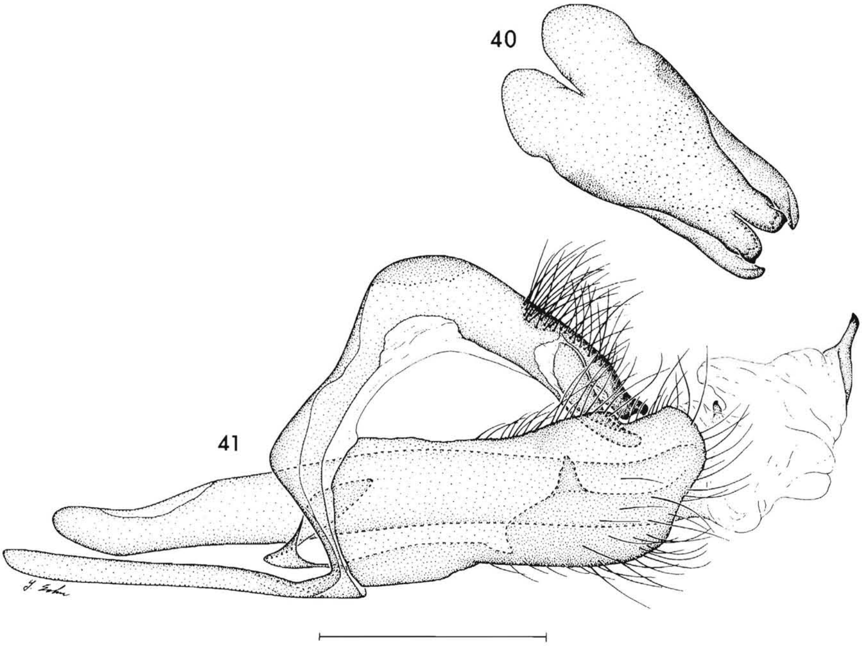
The juxta resembles a **U** whose paired, lateral, upright arms twist once into more or less expanded and posteriorly trending upper ends while the base of the **U** gives off a long, midventral, posteriorly tapering triangle (Fig. 39). The juxta sits unusually far forward, largely exposed in lateral view (Figs. 41, 43, 45, 47, 52, 55, 57, 59, 62, 65, 67).

Female genitalia. The posterior margin of the lamella postvaginalis gives rise midventrally to a single, posteriorly directed, bristly projection (Figs. 68–82). This central projection may be only slightly developed (Fig. 76) or remarkably wide (Fig. 74), but usually it is narrow and long (Figs. 68–73, 75, 77, 81, 82) to very long (Figs. 78–80).

Type species. *Atrytone mexicana* Bell (1942b:461, fig. 5). Figs. 33, 40, 41 (male genitalia); 68, 69 (female genitalia); 87, 88 (adult male); and 89, 90 (adult female).

Individually rather plain, the male genitalia are so interspecifically variable that they seem elaborate in *Quasimellana* as a whole. The tegumen/uncus varies from narrow to wide. The distal end of the uncus varies from about as thick as, to much thicker than, the distal end of the gnathos; from decidedly longer to decidedly shorter than the gnathos; from close above the gnathos to far above it; from undivided to well divided; the uncal divisions, from closely parallel to widely divergent—and then, in one case, bent sharply upward, besides. The distal end of the valva may have zero, one, or two projections, each ranging from broadly rounded to sharply pointed and extending primarily dorsad or caudad (sometimes mediad, as well). The inner side of the valva may develop a triangular middle process, a more oblong dorsal process, both of these, or neither. The aedeagus is a simple tube (devoid of titillators and terminal teeth or prongs) about as long as the total intact genitalia (i.e., saccus plus valvae), but its vesica varies from long, narrow, and fingerlike to shorter and less regular, with protruding, armlike pouches; the diagnostic cornutus, situated near or at the distal end of the everted vesica, may or may not be accompanied by a tiny, secondary, apparently vestigial cornutus near the proximal end of the vesica. The diagnostic cornutus itself varies from short to long and from narrow to wide; in the shape, height, point of attachment, and angle of the head-and-neck on the body; and the body varies from convex to concave, as well as in certain minor decorations. The saccus is usually much shorter than the valva but may approach it or even exceed it in length. The juxta varies in just how far forward it sits, in the height of the twist in each arm, and in details of shape.

Each species account begins (after any synonymy) with two or three kinds of crucial information in condensed form: (1) mention of the holotype, its sex, and its location (abbreviated, for example, "HT♂-USNM") whenever I have seen and studied that specimen and its genitalia; (2) the spatial distribution (based on material examined), arranged geographically by country (and, in the United States, Mexico, Brazil, and Argentina also by state, territory, or province), plus a few important additions from the literature; and (3) the numbers of males and females examined, followed (in parentheses) by the number of genitalia compared in each sex. Whenever I have studied the holotype

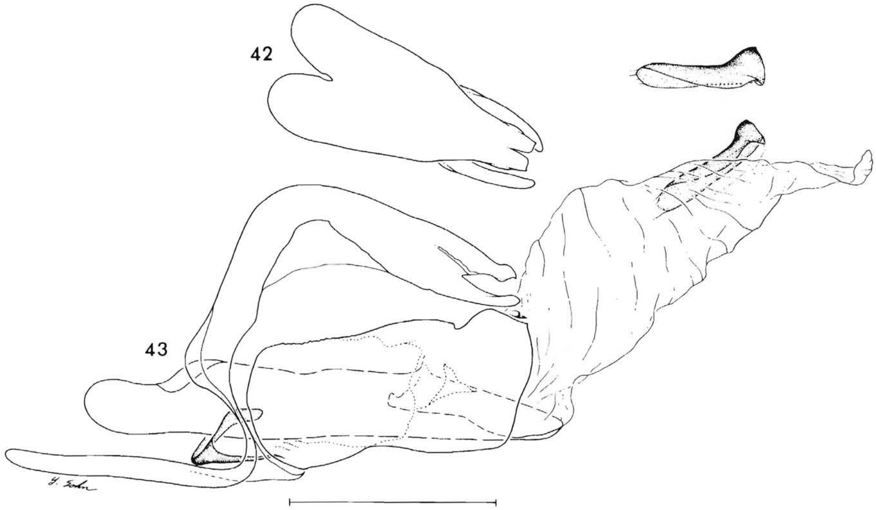


FIGS. 40, 41. Male genitalia of *Quasimellana mexicana* from San Luis Potosí, San Luis Potosí, MEXICO, 3 August 1941, A. H. Moeck (X-2586) (USNM). Scale = 1.0 mm. **40,** Tegumen, uncus, and gnathos in dorsal view. **41,** Complete genitalia (minus right valva), with vesica everted, in left lateral view.

of a synonym, hyphenated abbreviations as in (1) end the entry in the synonymy.

I have examined the genitalia of the types of two species (besides *Wallengrenia clavus*) put in *Mellana* by Evans (1955) but belonging neither in *Quasimellana* nor in *Anatrytone*: *gala* Godman (1900) (USNM), from Mexico, which Evans questioningly listed as a synonym of *monica* Plötz (1886), from southern Brazil (Santa Catarina); and *rivula* Mabille (1891) (ZMHB), which Evans treated as a species with two subspecies—*rivula,* from northern Brazil (Amazonas), and *amicus* Bell (1942), from Ecuador (although *rivula* is not a species of *Quasimellana, amicus* is).

Though I amassed some 450 specimens in my study of *Quasimellana,* only 12 out of 24 species are represented by more than 10 specimens, but 7 of those are represented by more than 20; another 7 species are known from 6 or fewer specimens, and 3 of these (including 2 that Evans described back in 1955), from just 1. In light of these figures, the large (essentially neotropical) range of the genus, and the superficial similarities among various differentiates, additional species doubtless



FIGS. 42, 43. Male genitalia of paratype of *Quasimellana siblinga* from El Vado-San Sebastian, 5500–6500 ft (1675–1980 m), ca 16° 53′ N, 96° 53′ W, Oaxaca, MEXICO, 22 June 1992, J. Kemner (X-3592) (USNM). Scale = 1.0 mm. **42,** Tegumen, uncus, and gnathos in dorsal view. **43,** Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view (plus primary cornutus in profile).

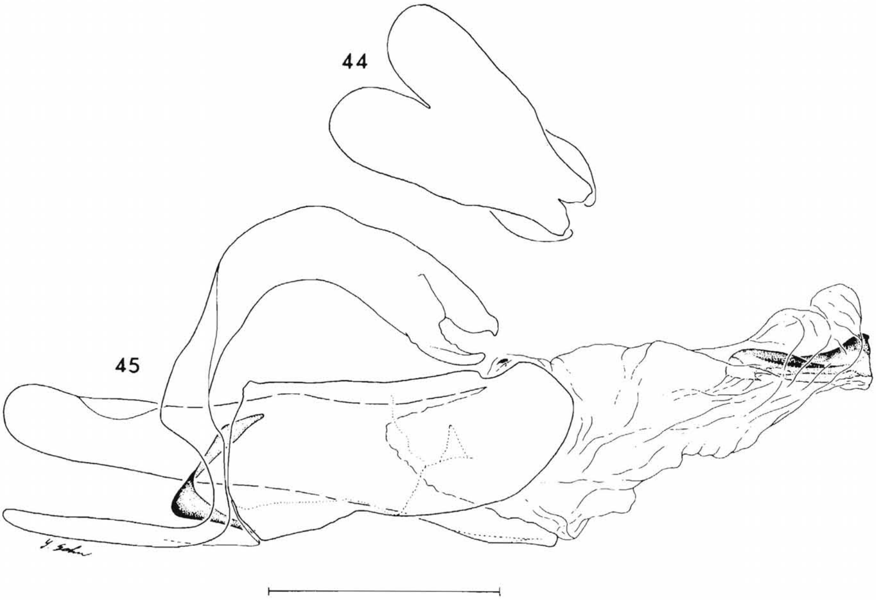
await discovery; and for most described species, knowledge of geographic distribution leaves much to be desired.

THE SPECIES GROUPS AND SPECIES OF *QUASIMELLANA*

The *eulogius* Group

(Figs. 31–33, 37, 38, 40–45, 68–73, 87–92)

Male genitalia. *Juxta*: The juxta is posterior in location (Figs. 41, 43, 45), as it is in *nayana*, *aurora*, and *andersoni* of the *sethos* group (Figs. 47, 55). The level of the twist in each lateral arm of the juxta is low (Figs. 41, 43, 45), as it is in the *sethos* group (Figs. 47, 52, 55, 57, 59). *Cornutus*: Except in *mexicana* (Figs. 33, 41), the head-and-neck of the cornutus is short, wide, and upright (Fig. 37) to backswept (Figs. 32, 43, 45). Its position on the body of the cornutus varies from central (Figs. 33, 41) to left of center (Fig. 38) to left (Figs. 32, 43, 45). The body of the cornutus is narrow except in *mulleri* (Figs. 37, 38). The tiny, secondary, vestigial cornutus is present (Figs. 41, 43, 45), except in two examined individuals of *mulleri* and one of *siblinga*, as it usually is in the *sethos* group (Figs. 47, 49, 52, 55, 57, 60). *Vesica*: The everted vesica is relatively short (Figs. 41, 43, 45). *Valva*: On its inner surface, the valva always has a middle process, which is relatively large and long (Figs. 41, 43, 45), but never the dorsal process that marks the *sethos* group (Figs. 49, 50, 52, 53, 55, 57, 59, 60). In lateral view the dorsodistal end of the valva is simple and more or less broadly rounded (Figs. 41, 43, 45), without prominent sharp points or projections. *Uncus*: The distal end of the uncus is deeply divided, with the resultant prongs more or less close together and parallel (Figs. 40, 42, 44). In lateral view, the distal end of the uncus is only a little thicker than the distal end of the gnathos



FIGS. 44, 45. Male genitalia of *Quasimellana balsa* from 23 mi (37 km) S Ixtapan de la Sal, Guerrero, MEXICO, 16 August 1981, J. A. Chemsak (X-2803) (UCB). Scale = 1.0 mm. **44,** Tegumen, uncus, and gnathos in dorsal view. **45,** Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

(Figs. 41, 43, 45), as it is in the *sethos* group (Figs. 47, 49, 52, 55, 57, 59) plus *amicus* of the *nicomedes* group.

Female genitalia. The anterior apophyses are long (Figs. 68, 69, 72, 73) except in *balsa* (Figs. 70, 71), where they are intermediate to short (the female of *siblinga* is unknown). The corpus bursae is relatively long and narrow (Figs. 68–73).

General features. Sexual dimorphism is strong (Figs. 87–90), except in *mulleri*. Males are always extensively yellowish-orange and blackish-brown dorsally, with dark veins. The species are medium to large in size (Fig. 31).

Distribution. Although the *eulogius* group (with 5 species) extends from the United States (south Texas) to Brazil and Paraguay, it is mainly North American.

Quasimellana mexicana (Bell, 1942b:461, fig. 5), new combination

(Figs. 31, 33, 40, 41, 68, 69, 87–90)

HT♂-USNM. Mexico (San Luis Potosí, Veracruz, Nayarit, Guerrero, Oaxaca), Guatemala, Belize. 29 ♂ 8 ♀ (16 ♂ 4 ♀).

The largest species of *Quasimellana* (Fig. 31), *mexicana* has a narrow cornutus with a distinctive, long, narrow head-and-neck obliquely stretched far in front of the body (Figs. 33, 41). The saccus is relatively long for *Quasimellana* (even for *mexicana*, however, the saccus of the individual in Fig. 41 is unusually long). The sclerotized lateral lobes of the lamella postvaginalis (on either side of the midventral, posteriorly directed, bristly projection) do not extend as far caudad as they do in most species of *Quasimellana*, while the ductus bursae is unusually plain (compare Figs. 68, 69 with Figs. 70–82).

Quasimellana eulogius (Plötz, 1883:64), new combination (Figs. 31, 32, 72)

= *mellona* (Godman, 1900:493, pl. 94, figs. 17–19).
= *heberia* (Dyar, 1914:5), lectotype ♂ (J. M. Burns genitalia dissection X-2832) here designated from 3 cotypes (2 ♂ 1 ♀ bred from larvae on blades of sugarcane, Georgetown, British Guiana, H. W. B. Moore, type no. 18116) in USNM.
= *agnesae* (Bell, 1959:13, figs. 8, 21), new synonym, HT♂-AMNH.
= *oaxaca* (Freeman, 1979:10, figs. 20, 21, 29 [valva upside down]), new synonym, HT♂-AME.

United States (south Texas—Cameron and Hidalgo counties), Mexico (Nuevo León, San Luis Potosí, Sinaloa, Veracruz, Puebla, Guerrero, Oaxaca, Chiapas, Yucatán, Quintana Roo), Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Guyana, Brazil (Pará, Espírito Santo); Evans (1955) also records Bolivia and Paraguay. 80 ♂ 30 ♀ (49 ♂ 29 ♀).

For *Quasimellana*, *eulogius* is unusually common and widespread—the seeming "weed species" of the genus. The large size and latitudinal and altitudinal diversity of my *eulogius* sample may explain why it showed the most individual variation (reflected, for example, in Fig. 31 and Table 1). But then again, it may include more than one species; and some of the above synonyms—particularly *heberia* and *agnesae*—may need resurrection.

Godman (1907) promptly sank his *mellona* Godman (1900) to *eulogius* Plötz (1883). In describing *agnesae* (from two males taken 6 and 9 December 1939 in Acapulco, Guerrero, Mexico), Bell (1959:13) called it "a small species of *Mellana*, with different genitalia from those of its nearest relatives." I have examined the holotype and paratype and Bell's slides of their genitalia, which look just like those of *eulogius*. Although the small size (forewing length 12.2 and 12.7 mm) and greater extent of yellow orange coloring do differ from ordinary *eulogius* (Fig. 31), I have measured an equally dwarf (12.6 mm) but normal looking *eulogius* male from Guatemala and have seen normal sized but equally yellow orange *eulogius* males from Sinaloa, Mexico, and Brownsville, Texas. At least for now, I conservatively view the specimens of *agnesae* as light runts of *eulogius*.

See *siblinga* for characterization of the male genitalia of *eulogius* (which are well shown in lateral view—including the extra long, narrow cornutus [Fig. 32]—in Godman 1900: pl. 94, fig. 19).

The female genitalia (Fig. 72) depart from those of other known *Quasimellana* females because the ductus bursae is extremely short, and its main sclerotization (in ventral view) is a narrow band around it; the midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is usually fairly long and narrow, without any laterally expanding sclerotization at its base; and the sclerotized lateral lobes that flank this projection are relatively narrow. (The female genitalia assigned to a paratype of *Mellana tecla* Steinhauser and to undetermined females of *Mellana* in figs. 82, 88, and 89 of Steinhauser 1974 all come from *eulogius*; even a delicate, female character state that I broadly ascribe to the *eulogius* group—long anterior apophyses—shows in these photographs.)

At present, I can cleanly pull the following species from a possible *eulogius* complex.

***Quasimellana siblinga*, new species** (Figs. 31, 42, 43, 91, 92)

HT♂-USNM. Mexico (Sonora, Sinaloa, Oaxaca). 16 ♂ (9 ♂).

Superficially and genitalically reminiscent of *eulogius* and *balsa*. Primary cornutus (Fig. 43) similarly linear and narrow, about as long as in *balsa* (Fig. 45)—therefore much shorter than in *eulogius* (Fig. 32)—but body of cornutus dorsally convex and without the longitudinal twist of both *eulogius* (Fig. 32) and *balsa* (Fig. 45). Secondary, vestigial cornutus (Fig. 43) smaller than in *eulogius* (completely gone in one individual). In lateral view, dorsodistal end of valva somewhat truncate dorsally (Fig. 43) and so less rounded than in *eulogius* and *balsa* (Fig. 45). Ventrodistal corner of valva (Fig. 43) not cut away as in *eulogius*. Tegumen, uncus, and gnathos (as well as distal end of aedeagus) (Figs. 42, 43) much less massive than in *balsa* (Figs. 44, 45), and uncus prongs (Fig. 42) less widely notched than in *balsa* (Fig. 44)—all about as in *eulogius*; but each uncus prong proximally with a ventrolateral swelling (Figs. 42, 43)—not present in *eulogius*—large enough to show in dorsal view (Fig. 42). Gnathos slightly longer than uncus (Figs. 42, 43). Medium sized species, close to fellow groupies other than *mexicana* (Fig. 31): mean male forewing length and SE = 14.81 ± 0.14 mm, range 14.0–15.6 mm, n = 15. Usually 14 or 15 nudum segments; on average (14.3), about one segment more than in fellow groupies (Table 1).

Holotype. ♂; MEXICO, OAXACA, El Vado-San Sebastian, ca 16° 53′ N, 96° 53′ W, 5500–6500 ft (1675–1980 m), 22 June 1992, J. Kemner; USNM.

Paratypes. n = 15 ♂, all from MEXICO. OAXACA (all collected by J. Kemner and housed in USNM): same data, 6 ♂, J. M. Burns genitalia dissections X-3590, X-3591, X-3592; same data except 27 June 1992, 2 ♂; 3–13 mi (5–21 km) N Sola de Vega and road to Grutas de San Sebastian, 5500–6500 ft (1675–1980 m), 6 July 1991, 1 ♂; same data except 6500 ft (1980 m), 1 ♂, J. M. Burns genitalia dissection X-3241; road to Grutas de San Sebastian, 6500 ft (1980 m), 10 July 1991, 2 ♂, H. A. Freeman genitalia dissections H-1197, H-1202; road to Grutas de San Sebastian, ca 16° 37′ N, 96° 57′ W, 5500–6500 ft (1675–1980 m), 10 July 1991, 1 ♂, J. Kemner & Romack, J. M. Burns genitalia dissection X-3589. SINALOA: Loberas Summit, 5 mi (8 km) NE Potrerillos, 1820 m, parkland forest, 19 August 1973; 1 ♂, L. D. & J. Y. Miller, S. R. Steinhauser genitalia dissection SRS-2691, AME. SONORA: 13 mi (21 km) E El Novillo, 11 August 1985, 1 ♂, J. P. Brock, S. R. Steinhauser genitalia dissection SRS-1851, AME.

Etymology. *Quasimellana siblinga* is a sibling species.

Quasimellana balsa (Bell, 1942b:460, fig. 4), new combination (Figs. 31, 44, 45, 70, 71)

= *balsa freemani* (Steinhauser, 1974:20, figs. 53–56, 85, 86), new synonym, HT♂-AME.

HT♂-AMNH. Mexico (Sonora, Jalisco, Colima, Michoacán, Guerrero); Steinhauser (1974, 1975) reports this species from El Salvador. 17 ♂ 4 ♀ (14 ♂ 4 ♀).

See *siblinga* for definition of the male.

Much as in *mexicana* (Figs. 68, 69), the sclerotized lateral lobes of the lamella postvaginalis (on either side of the midventral, posteriorly directed, bristly projection) do not extend as far caudad (Figs. 70, 71) as they do in most species of *Quasimellana*; but the ductus bursae is remarkably short and oval (in ventral view [Fig. 70]), with an ostium (also somewhat oval) that opens far back at the base of the midventral, bristly projection, which is shorter and wider than it is in *mexicana* (see also Steinhauser 1974:fig. 86).

The subspecies *freemani* is not helpful. *Mellana balsa freemani* was described from six males and three females all from one locality (Santa Tecla) in El Salvador (Steinhauser 1974). When this short series was compared with the still shorter type series of *balsa*, amounting to four males from Guerrero, Mexico, it was said that "*freemani* males differ from typical *balsa* mainly in size and color" (Steinhauser 1974:22), the male genitalia being "essentially identical." In every large sample of a *Quasimellana* species (and sometimes even in small ones) I have seen too much variation in color and pattern to give weight to the two color differences offered. Though real and noteworthy, the larger size of El Salvador specimens does not warrant a formal name. By my measurements the type series of *balsa* is small, averaging 14.3 mm in forewing length (ranging from 13.7 to 14.6 mm); but my total Mexico sample of *balsa* (n = 16), which includes those small types, is nearly a millimeter larger, averaging 15.04 mm (ranging from 13.7 to 15.7 mm) (Fig. 31). The El Salvador sample picks up where the Mexico sample leaves off and adds about another millimeter to the mean: according to Steinhauser (1974:22), the six *freemani* males average 16.2 mm (ranging from 15.8 to 16.5 mm). Elsewhere in *Quasimellana*, with enough *eulogius* to take good geographic subsamples, the forewings of 32 males from Honduras, Nicaragua, Costa Rica, and Panama averaged about half a millimeter more than those of 32 males from Mexico (Fig. 31). In *Autochton cellus*, wing length rose strikingly from central Mexico to southern Mexico to Guatemala and El Salvador

(Burns 1984:10 and table 1). Skipper populations of a single species often increase in average wing length from north to south in the northern hemisphere (see tables and text in Burns 1964, 1984 for examples from *Erynnis* and *Wallengrenia*).

Quasimellana mulleri (Bell, 1942b:462, fig. 6), new combination (Figs. 31, 37, 38, 73)

HT♂-USNM. Mexico (Tamaulipas, Durango, Jalisco, Colima, Guerrero). 9 ♂ 5 ♀ (7 ♂ 3 ♀).

The body of the cornutus is wide, with numerous peripheral wrinkles (Figs. 37, 38); and the rounded dorsodistal end of the valva tends to develop a modest point anterodorsally. Overall the female genitalia (Fig. 73) look most like those of *mexicana* (Figs. 68, 69); but the lateral lobes of the lamella postvaginalis extend well back as they do in most species of *Quasimellana*, while the midventral, posteriorly directed, bristly projection is about as delicate as it is in *andersoni* (Fig. 75), *myron* (Fig. 77), *verba*, *inconspicua*, and *angra* of the *sethos* group.

Freeman (1967) argued that *mulleri*, which Evans (1955) questioningly called a synonym of *eulogius*, is really a distinct species.

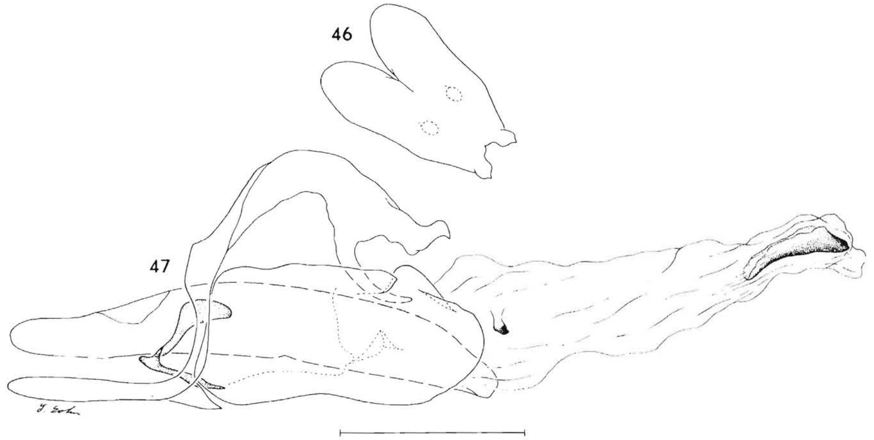
The *sethos* Group (Figs. 31, 36, 46–60, 74–77, 93–108)

Male genitalia. *Juxta*: The juxta may be posterior (Figs. 47, 55) or anterior (Figs. 52, 57, 59) in location. The level of the twist in each lateral arm of the juxta is low (Figs. 47, 52, 55, 57, 59), as it is in the *eulogius* group (Figs. 41, 43, 45). *Cornutus*: The head-and-neck of the cornutus is relatively long and/or narrow (Figs. 36, 47, 49, 50, 52, 55, 57, 59, 60), it projects obliquely forward from the body of the cornutus (Figs. 36, 47, 49, 50, 52, 55, 59, 60), and its "dewlap" is finely crenulate (Figs. 47, 49, 50, 52, 55, 59, 60). (Among other species of *Quasimellana*, only *amicus* has a crenulate "dewlap.") The body of the cornutus is dorsally flattish to concave (at some angles, concavity gives a "swaybacked" look—Figs. 36, 49, 52, 55, 59). The tiny, secondary, vestigial cornutus is present (Figs. 47, 49, 52, 55, 57, 60), as it usually is in the *eulogius* group, except in the two known individuals of *pazina* (Fig. 50), the one of *sista* (Fig. 53), one of the examined males of *verba*, nearly half the examined males of *inconspicua* (Fig. 59), and most examined males of *myron*. *Vesica*: The everted vesica is relatively long (Figs. 47, 49, 50, 52, 53, 55, 57, 59, 60). *Valva*: On its inner surface, the valva has at least a rudimentary, but usually a well developed, dorsal process, which is unique among species of *Quasimellana* (Figs. 49, 50, 52, 53, 55, 57, 59, 60 [in these last two species, the dorsal process is short and extends mostly mediad, so it hardly shows in lateral view]). (The only males of the *sethos* group really lacking a dorsal process are two of the eight *nayana* examined, one of which appears in Fig. 47.) Although the distal end of the valva varies greatly, its basic pattern apparently is a pair of projections, one dorsal and the other more or less midcaudal. *Uncus*: The distal end of the uncus may be very well divided (Figs. 46, 48, 51) or undivided (Figs. 54, 56, 58). (Among other species of *Quasimellana*, only *amicus* has an undivided uncus.) In lateral view, the distal end of the uncus is only a little thicker than the distal end of the gnathos (Figs. 47, 49, 52, 55, 57, 59), as it is in the *eulogius* group (Figs. 41, 43, 45) and in *amicus* of the *nicomedes* group.

Female genitalia. The anterior apophyses are short (Figs. 74, 75) except in *sethos* (Fig. 76), where they are intermediate (females of several species are unknown). The corpus bursae is relatively long and narrow (Figs. 74–77).

General features. Sexual dimorphism is weak to strong. The species are small to large in size (Fig. 31).

Distribution. Extending from Mexico to Bolivia and Brazil, the *sethos* group (with 12 species) is equally North and South American.



FIGS. 46, 47. Male genitalia of *Quasimellana nayana* from Santo Domingo, 15 mi (24 km) SE Simojovel, Chiapas, MEXICO, 8–15 July 1958, J. A. Chemsak (X-2789) (USNM). Scale = 1.0 mm. **46,** Tegumen and uncus in dorsal view. **47,** Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

The *nayana* Subgroup within the *sethos* Group (Figs. 31, 46, 47, 74)

Male genitalia. *Juxta*: The juxta is posterior in location (Fig. 47). *Cornutus*: The head-and-neck arises from the right side of the body of the cornutus. *Uncus*: The distal end of the uncus is very well divided, and the resultant uncus prongs are widely separated from each other (with a **U**-shaped gap) and somewhat divergent (Fig. 46). *Gnathos*: In lateral view, the gnathos is uniquely far below the uncus and uniquely short relative to the uncus (Fig. 47).

Female genitalia. The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is hypertrophied and the rounded lobes of the lamella postvaginalis that flank it are atrophied (Fig. 74) so that the usual size relationships between these parts (Figs. 68–73, 75–82) are reversed.

General features. Sexual dimorphism is strong. The species are medium sized (Fig. 31).

Distribution. The *nayana* subgroup (with 2 species) ranges from southern Mexico to Venezuela.

In a three-paper flurry, Bell (1941, 1942a, 1942b) described eight new species of what is now *Quasimellana*, seven of which are valid (*ricana* is a synonym of *meridiani* Hayward 1934). Bell put all of them in genus *Atrytone* except one: *aurora* went in *Zariaspes*, which is nowhere near *Atrytone*. Ironically, Bell (1942b:460–465) described *aurora* right after *balsa*, *mexicana*, and *mulleri*, with figures of male genitalia detailed enough to show the same (i.e., *Quasimellana*) kind of cornutus in all four species. Although *aurora* diverged from the other three (which are in the *eulogius* group) in the form of the tegumen, uncus, and gnathos, as well as in the form of the valva, it rather resembled *nayana*, one of the *Atrytone* species Bell had described the year before. Evans (1955) misdetermined his only male of *aurora* as *nayana* and left *aurora* in *Zariaspes*, from which I am finally freeing it.

Both *aurora* and *nayana* came from southwestern Mexico. Steinhauser (1974) described them again from El Salvador as *Mellana tecla* and *M. tamana*.

Quasimellana aurora (Bell, 1942b:464, fig. 7), new combination (Figs. 31, 74)

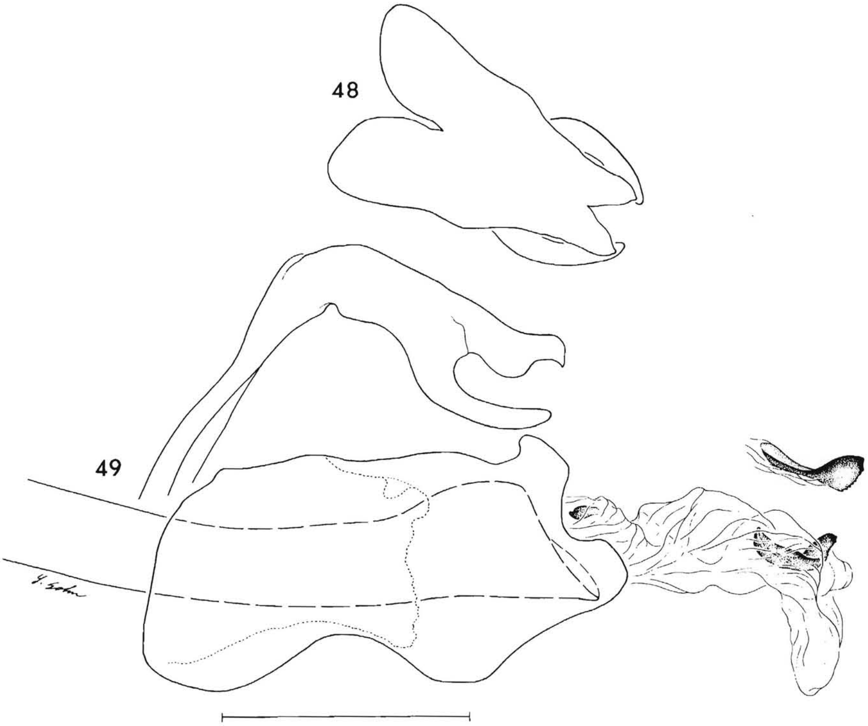
= *tecla* (Steinhauser, 1974:15, figs. 41, 42, 81), new synonym, HT♂-AME.

HT♂-AMNH. Mexico (Sinaloa, Jalisco, Colima, Guerrero, Oaxaca, Chiapas), El Salvador. 30 ♂ 2 ♀ (16 ♂ 2 ♀).

In dorsal view, the tegumen/uncus is narrower and the uncus prongs are closer together in *aurora* than in *nayana* (Fig. 46), while, in lateral view, the uncus prongs are nearly straight (i.e., almost in line with the rest of the tegumen/uncus) in *aurora*, rather than bent sharply upward as they are in *nayana* (Fig. 47). The valva of *aurora*, in lateral view, has short, blunt, but relatively narrow projections both dorsally and midcaudally, with the dorsal projection usually inclined a bit anterodorsally. Both valval projections in *nayana* are broader and more bluntly rounded (the midcaudal projection so much so, that it sometimes melts into a totally rounded caudal end, as in Fig. 47). The triangular middle process on the inner side of the valva is smaller in *aurora* than it is in *nayana* (Fig. 47). These two species are superficially very similar, the males with dorsal light areas that are more extensive, and usually more orange, than in most other species of *Quasimellana*; but, on an average, the light areas are slightly more extensive in *aurora* than in *nayana* (compare the *aurora* and *nayana* males in figs. 41, 42 and figs. 49, 50, respectively, in Steinhauser 1974:30). Two males of *aurora* from Colima, Mexico, are so extensively light, and their orange is so yellow, that they suggest some species of *Anatrytone*, as well as *Quasimellana imperfida*. Although both species are medium sized, *aurora* is a little larger than *nayana* (Fig. 31).

Genitalia can be deceitful even in published figures. In the lateral views accompanying Bell's original descriptions (Bell 1941:fig. 2, 1942b:fig. 7), the uncus prongs look straight not only in *aurora* (where they should) but also in *nayana* (where they should bend sharply upward). The uncal bend does not show in Bell's genitalic slide of the *nayana* holotype because the tegumen, uncus, and gnathos are mounted at an odd angle. The valva of *aurora* is poorly drawn in Bell (1942b:fig. 7) but well photographed in Steinhauser (1974:fig. 81). Evans's (1955:pl. 79, fig. M.25.1) caricature of the male genitalia of what he calls *nayana* actually depicts *aurora*; and Steinhauser's (1974:figs. 43, 44, 82) photos of a *tecla* (= *aurora*) female, and her genitalia, really relate to *eulogius*.

To match mates can be tricky, especially in strongly dimorphic species. I know from comparing series of *Quasimellana* females that the taxonomically important, midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis may vary greatly in size and shape among conspecific individuals. It certainly varies among the three females I have seen in the *nayana* subgroup (whose genitalia—with their ultrawide, midventral, bristly projection and small lateral lobes [Fig. 74]—are immediately distinct). Though all three females may belong to the same species, I am tentatively referring the two with shorter bristly projections (Fig. 74) to *aurora* and the one with the bristly projection twice as long (about as in Steinhauser 1974:fig. 84) to *nayana*. Even so, a large measure of individual variation remains since the bristly projection is considerably shorter and wider in the unfigured female of *aurora* than it is in the figured female (Fig. 74), and distally truncate, instead of rounded.



FIGS. 48, 49. Male genitalia of holotype of *Quasimellana noka* (what remains of Evans's dissection), locality unknown, (X-3457) (BMNH). Scale = 1.0 mm. **48,** Tegumen, uncus, and gnathos in dorsal view. **49,** Tegumen, uncus, gnathos, upper vinculum, left valva, and distal end of aedeagus, with vesica everted and cornuti stippled, in left lateral view (plus primary cornutus in profile).

Quasimellana nayana (Bell, 1941:1, fig. 2), new combination (Figs. 31, 46, 47)

= *tamana* (Steinhauser, 1974:18, figs. 49, 50, 83, 84), new synonym, HT♂-AME.

HT♂-AMNH. Mexico (Nayarit, Chiapas), Guatemala, El Salvador, Venezuela. 8 ♂ 1 ♀ (8 ♂ 1 ♀).

See *aurora*.

Ungrouped Species within the *sethos* Group (Figs. 31, 36, 48–57, 75, 76, 93–104)

This artificial assemblage of 6 species includes an obvious sister pair: *pazina* and *antipazina*.

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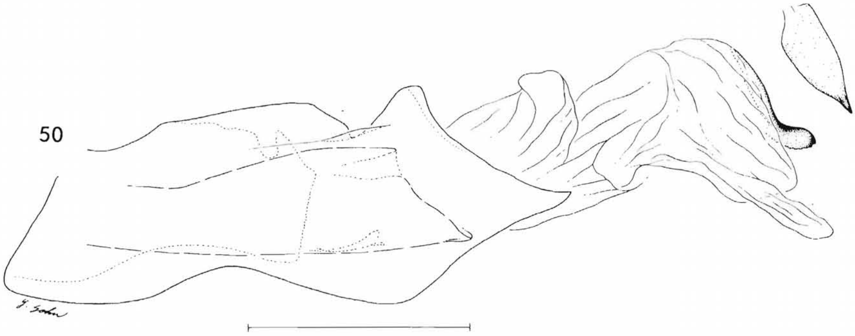


FIG. 50. Male genitalia of holotype of *Quasimellana pazina* (what remains of Evans's dissection) from Yungas and La Paz, 1000 m, BOLIVIA, 1902 (X-3460) (BMNH). Scale = 1.0 mm. Most of left valva and distal end of aedeagus, with vesica everted and cornutus stippled, in left lateral view (plus cornutus in dorsal view).

Quasimellana noka (Evans, 1955:357, pl. 79, fig. M.25.10), new combination
(Figs. 31, 48, 49, 93, 94)

HT♂-BMNH. No locality. 1 ♂ (1 ♂).

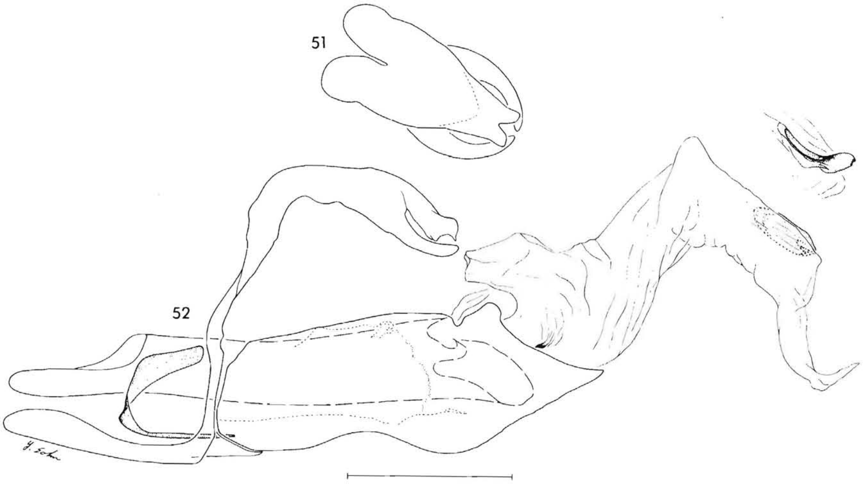
I can safely claim that this genitalically peculiar species, known only from a dataless type, comes from somewhere in the neotropics. The valva of *noka* is unique: two narrow, rounded, posterodorsal and midcaudal projections extend not just dorsad and caudad but, at the same time, strongly mediad (Fig. 49). The valva lacks a triangular middle process on its inner side. Although the uncus is well divided (Fig. 48), the prongs are neither widely separated nor somewhat divergent as they are in the *nayana* subgroup (Fig. 46). Instead, they are much as in *pazina* and *antipazina* (Fig. 51), with a **V**-shaped (not **U**-shaped) intervening gap and just a hint of divergence. Since Evans's dissection wrecked the juxta, I cannot say whether it is posterior or anterior in location. Dorsally the light areas of the wings are neither extensive and orangy, as in *aurora* (Steinhauser 1974:fig. 41), *nayana* (Steinhauser 1974:fig. 49), *sista* (Fig. 99), and *andersoni* (Fig. 101), nor reduced and pale yellow, as in *inconspicua* and *angra* (Fig. 107). The result is an "average look" (Fig. 93), with yellow orange spots—the spotting less developed than in *pazina* (Fig. 95) but much as in *myron* and *verba* (Fig. 105). Ventrally a dirty, dull orangish shade runs over the hindwing and along the costa and across the apex of the forewing (Fig. 94).

Quasimellana pazina (Evans, 1955:357, pl. 79, fig. M.25.9), new combination
(Figs. 31, 50, 95, 96)

HT♂-BMNH. Bolivia. 2 ♂ (2 ♂).

See *antipazina*.

Evans described *pazina* from a single male. Light areas (which are dorsally yellow orange to orange and ventrally yellower) are much more extensive in the second known male of *pazina* than they are in the first (the type, shown in Figs. 95, 96)—so much so,



FIGS. 51, 52. Male genitalia of holotype of *Quasimellana antipazina* from La Estrella, 1500 m, Cartago, COSTA RICA, 20 May 1979, G. B. Small (X-2592) (USNM). Scale = 1.0 mm. **51,** Tegumen, uncus, and gnathos in dorsal view. **52,** Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view (plus primary cornutus in profile).

that the second male will not key to *pazina* in Evans (1955). Dissection of the new male reveals that the juxta is anterior in location and confirms the fact that the uncus is divided. Evans (1955:pl. 79, fig. M.25.9) clearly showed a divided uncus in his trio of original genitalia figures; but the tegumen, uncus, gnathos, and vinculum of his dissected holotype have since been lost.

***Quasimellana antipazina*, new species**
(Figs. 31, 51, 52, 97, 98)

HT♂-USNM. Costa Rica. 1 ♂ (1 ♂).

Superficially and dorsally much like *myron* and *verba*, with light areas reduced to discrete orange yellow spots (Fig. 97); ventral overscaling (narrowly along costa of forewing, broadly across apex of forewing, and all over the hindwing) not pale, cold, dull greenish as in those species but warm, yellowish brown (Fig 98). Light dashes on dorsal hindwing distal to cell reduced to only two, in spaces 3 and 4 (Fig. 97)—usually more in *myron* and *verba* (and other species). Much larger than *myron* and *verba*: lone male (forewing 17.0 mm) nearly attaining mean male forewing length of *mexicana*, the giant of *Quasimellana*, and exceeding the larger (16.4 mm) of two known males of *pazina* (Fig. 31). As in *pazina*, nudum of 15 segments (Table 1) and apiculus exceptionally long for *Quasimellana* (but *pazina* with better developed light areas dorsally, especially on hindwing [Fig. 95], and *pazina* bright yellow to orange yellow ventrally [Fig. 96], instead of yellowish brown). Genitalia (Figs. 51, 52) very like those of *pazina* (Fig. 50)—including juxta anterior in location—but divided uncus narrower, with each prong less massive in dorsal view, less elevated distally in lateral view, and proximally lacking ventrolateral swelling large enough to show in dorsal view; valva with dorsodistal projection (which extends dorsad and mediad) narrower (though with extended, sharp, midcaudal projection just as in *pazina* [compare Figs. 52 and 50]); and tiny, secondary, vestigial cornutus present.

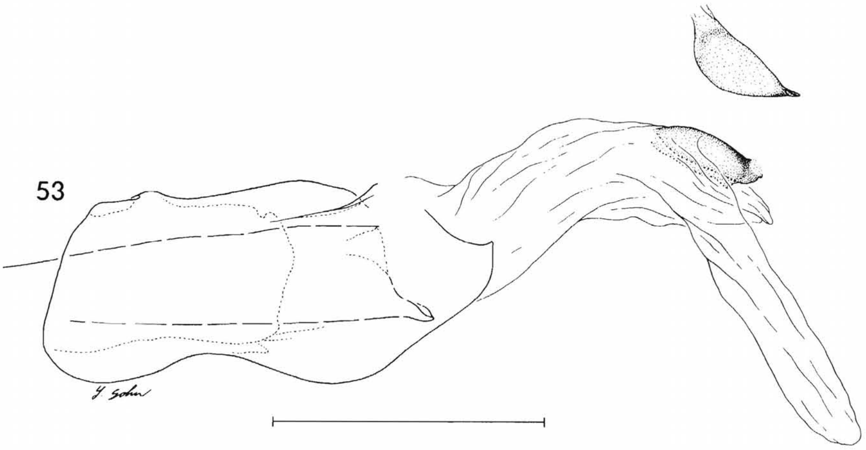


FIG. 53. Male genitalia of holotype of *Quasimellana sista* (what remains of Evans's dissection) from VENEZUELA (X-3459) (BMNH). Scale = 1.0 mm. Most of left valva and distal end of aedeagus, with vesica everted and broken cornutus stippled, in left lateral view (plus broken cornutus in dorsal view).

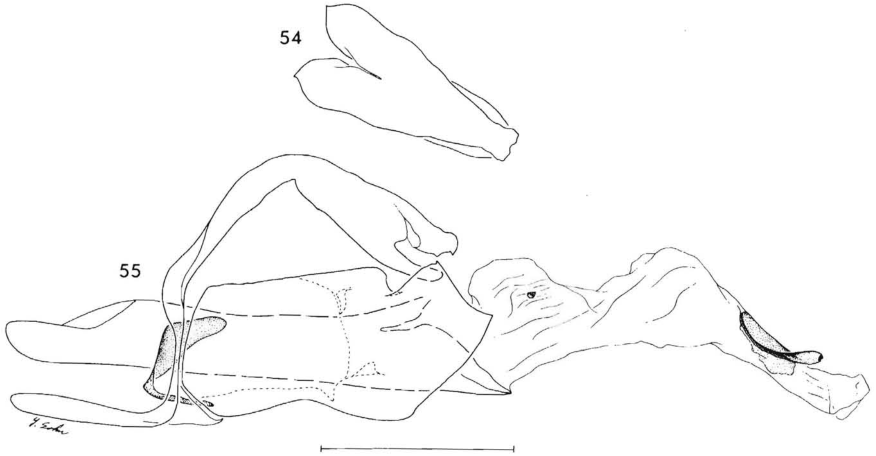
Holotype. ♂; COSTA RICA, CARTAGO, La Estrella, 1500 m, 20 May 1979, G. B. Small; J. M. Burns genitalia dissection X-2592; USNM.

Etymology. *Quasimellana antipazina* is the sister species and counterpart of *Q. pazina* in the opposite hemisphere (northern instead of southern).

Quasimellana sista (Evans, 1955:356, pl. 79, fig. M.25.5), new combination (Figs. 31, 53, 99, 100)

HT♂-BMNH. Venezuela. 1 ♂ (1 ♂).

Placing this species (or determining its sista) is extra difficult because the holotype is still the only specimen, Evans (1955:pl. 79, fig. M.25.5) provided just two of his usual three genitalic views (omitting the ventral view of the tegumen, uncus, gnathos, and distal end of the aedeagus), most of Evans's dissection of the genitalia is now missing, and the parts that remain (valva, aedeagus, cornutus) are broken (Fig. 53). Both the everted vesica and what there is of the cornutus clearly indicate the *sethos* group. For finer placement it would help to know whether the juxta is posterior or anterior, and the uncus, divided or undivided. Though the (incomplete) valva looks most like that of *andersoni* (Fig. 55), there are significant differences: the sharp, midcaudal projection points dorsad instead of caudad, the ventrodistal corner of the valva curves gently instead of angling sharply, and the triangular middle process on the inner side has disappeared (Fig. 53). Finally, *sista* lacks the tiny, secondary cornutus; and its big cornutus lacks the ventrally protruding sclerotization of *andersoni* (Fig. 55). Superficially, with extensive light areas and orange coloring, *sista* looks a lot like *andersoni, pazina, aurora,* and *nayana* (and it may be sympatric with *nayana*, since both occur in Venezuela—but no further locality data exist for *sista*). However, the orange in space 1b of the dorsal forewing essentially stays in the lower half of that space in *sista* (Fig. 99) while spreading the full height of that space in the other four species (Figs. 95, 101 and Steinhauser 1974:figs. 41, 49).



FIGS. 54, 55. Male genitalia of paratype of *Quasimellana andersoni* from Dos Amates, Veracruz, MEXICO, 15 January 1972, (X-3004) (Anderson collection). Scale = 1.0 mm. **54**, Tegumen, uncus, and gnathos in dorsal view. **55**, Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

Quasimellana andersoni, new species

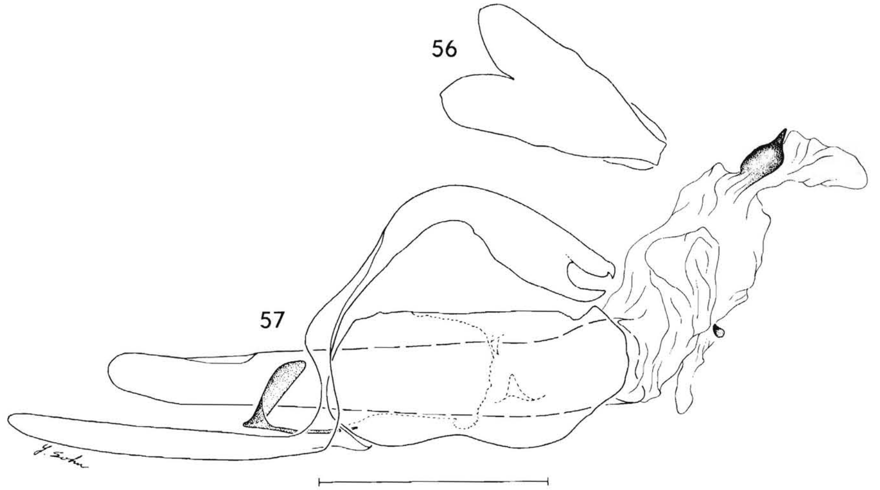
(Figs. 31, 54, 55, 75, 101–104)

HT♂-USNM. Mexico (Veracruz, Chiapas), Costa Rica. 8 ♂ 2 ♀ (8 ♂ 2 ♀).

Superficially very like *aurora* and especially *nayana* of *nayana* subgroup, with extensive, orange, light areas dorsally and ventrally in male and strong sexual dimorphism (Figs. 101–104). Near *nayana* in size, probably a little smaller on average (Fig. 31), so one of the smallest species of *Quasimellana*: mean male forewing length and SE = 13.66 ± 0.21 mm, range 12.8–14.5 mm, n = 8; but number of nudum segments (mean 14.8) maximum for *sethos* group (Table 1). Despite posterior juxta (Fig. 55), male genitalia highly distinct from *nayana* subgroup: tegumen/uncus long and narrow, with uncus undivided (Fig. 54); valva (Fig. 55) perhaps most like *sista* (qv) (Fig. 53; Evans 1955:pl. 79, fig. M.25.5), but also somewhat remindful of *myron*, *verba*, *pazina* (Fig. 50), and *antipazina* (Fig. 52) except for very short, unextended, sharp, midcaudal projection; body of cornutus with at least some ventrally protruding sclerotization (Fig. 55) and dorsally more concave than in other species of *Quasimellana*. Midventral, posteriorly directed, bristly projection from posterior margin of lamella postvaginalis, delicate (Fig. 75), about as in *myron* subgroup (Fig. 77) and *mulleri* of *eulogius* group (Fig. 73); outline of ostium bursae flask-shaped in ventral view (Fig. 75); anterior ductus bursae abruptly constricted to half the posterior width, in dorsal and ventral view (Fig. 75).

Holotype. ♂; MEXICO, VERACRUZ, Tapalapa, September 1971; J. M. Burns genitalia dissection X-3003; USNM.

Paratypes. n = 7 ♂ 2 ♀. MEXICO, VERACRUZ: Dos Amates, 15 January 1972, 1 ♂, J. M. Burns genitalia dissection X-3004, collection of R. A. Anderson; Catemaco, December 1963, 3 ♂, T. Escalante, H. A. Freeman genitalia dissection H-257, J. M. Burns genitalia dissections X-3644, X-3645, AMNH; same data except October 1965, 1 ♂, S. R. Steinhauser genitalia dissection SRS-2702, AME. MEXICO, CHIAPAS, Santa Rosa, Comitán, September 1963, 1 ♂ 2 ♀, T. Escalante, H. A. Freeman genitalia dissection H-64, J. M. Burns genitalia dissections X-3642, X-3643, AMNH. COSTA RICA, HEREDIA, 3.8 km N Santa Clara, 5 September 1987, 1 ♂, G. & A. Austin, S. R. Steinhauser genitalia dissection SRS-2957, collection of G. T. Austin.



FIGS. 56, 57. Male genitalia of *Quasimellana sethos* from Paraíso, Canal Zone, PANAMA, 27 April 1982, S. S. Nicolay (X-2596) (USNM). Scale = 1.0 mm. **56,** Tegumen, uncus, and gnathos in dorsal view. **57,** Complete genitalia (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

Etymology. I am pleased to name this species for Richard A. Anderson who generously and patiently provided large numbers of *Quasimellana* from his collection.

Quasimellana sethos (Mabille, 1889:173, fig. 2), new combination (Figs. 31, 36, 56, 57, 76)

Panama, Colombia, Ecuador; Evans (1955) also records a total of three males from Nicaragua and Venezuela. 21 ♂ 3 ♀ (6 ♂ 2 ♀).

This, the smallest species of *Quasimellana* (Fig. 31), is what Godman (1900) called *Atrytone helva* and Evans (1955), *Mellana helva*. Godman (1900:494), on examining the female type of *Pamphila helva* Möschler (1876) from Surinam and the male type of *P. sethos* Mabille (1889) from Chiriquí (western Panama), erroneously judged them conspecific and applied the older name. Godman (1900:pl. 94, figs. 25–29) figured, in color, "the type of *P. sethos*, a male, from Chiriqui, and a female from Coatepec [Veracruz, Mexico], agreeing with the type of *P. helva*," and, in black and white, the male genitalia. The genitalic figure represents this species best (even a *Quasimellana*-style cornutus shows). With orange yellow spots, the figured female looks much like the male; but she has well developed subapical spots on the forewing in spaces 6, 7, and 8, where the male has only a small point in space 6. The trouble is that this species of *Quasimellana* (like many others) exhibits strong sexual dimorphism in which the spots of the female are white instead of yellow to orange, and are less well expressed than those of the male. I have carefully studied the original descriptions of *Pamphila helva* (Möschler 1876), described from a male as well as a female, and *P. sethos* (Mabille 1889), described from a single male. Each description includes critical verbal detail plus a good black and white figure of the adult. Without question, *sethos* is the species long designated as *helva*; and *helva* is not a species of *Quasimellana*.

The saccus of *sethos* is exceptionally long for *Quasimellana*—from slightly shorter to slightly longer (Fig. 57) than the valva. In lateral outline the valva (Fig. 57) is the simplest of the *sethos* group—about as plain as those of the *eulogius* group (Figs. 41, 43, 45). The body of the cornutus is peripherally wrinkled (Fig. 36)—but much less densely than in *mulleri* (Figs. 37, 38) of the *eulogius* group. The juxta is anterior and the uncus undivided (Figs. 56, 57), a combination of character states that relates to the upcoming *myron* subgroup of four species (qv). The midventral, caudally directed projection from the posterior margin of the lamella postvaginalis is just a suggestion of its usual self (Fig. 76). Dorsally, in color and pattern, the dimorphic sexes of the diminutive *sethos* resemble those of the larger *myron* and *verba*, except that *sethos* males express a slender spot in space 4 usually missing from *myron*/*verba*. Ventrally, in fresh specimens of *sethos*, a slight greenish cast—over orange yellow in males and over brownish yellow in females—somewhat suggests the dull but more pronounced ventral greenish often visible in the *myron* subgroup.

The *myron* Subgroup within the *sethos* Group (Figs. 31, 58–60, 77, 105–108)

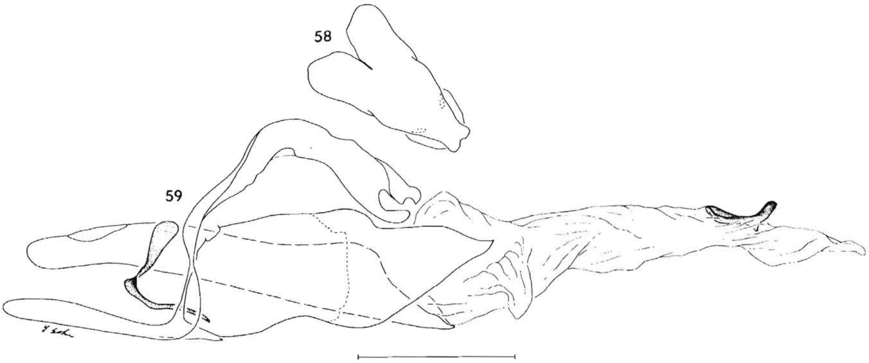
Male genitalia. *Juxta*: The juxta is anterior in location (Fig. 59). *Valva*: The valva has at least a long, sharp midcaudal projection that points caudad, and often a little mediad (Figs. 59, 60). *Uncus*: The distal end of the uncus is undivided, though usually a bit bilobed (Fig. 58).

Female genitalia. The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is delicate (Fig. 77), about as in *andersoni* (Fig. 75) and *mulleri* (Fig. 73). The posterior part of the sclerotized ductus bursae usually extends farther caudad, bringing the ostium bursae closer to the midventral, bristly projection (Fig. 77). The anterior part of the sclerotized ductus bursae has a central, longitudinal, unsclerotized zone (Fig. 77).

General features. Male spotting varies from average to much reduced, with many males dark enough that the sexual dimorphism typical of *Quasimellana*, though present, is not striking. Ventral overscaling in both sexes often gives a pale, dull greenish cast. The species are medium sized to small (Fig. 31).

Distribution. The *myron* subgroup (with 4 species) ranges from Mexico to Bolivia and Brazil.

Evans (1955) treated three of the four taxa in this subgroup (*myron*, *verba*, and *inconspicua*) as subspecies of *myron*, describing the fourth (*angra*) as a separate species. Though all four are closely related, male genitalia show conclusively that two pairs of sister taxa are involved: *myron* and *verba*, on the one hand, and *inconspicua* and *angra*, on the other. The distal end of the valva in *myron* and *verba* has a major dorsal projection—totally lacking in *inconspicua* and *angra* (Figs. 59, 60)—which extends dorsad and mediad so that the valva as a whole resembles that of *pazina* and *antipazina* (Figs. 50, 52). Also, the dorsal process on the inner surface of the valva is long and conspicuous (as in most members of the *sethos* group) in *myron* and *verba* but short and inconspicuous in *inconspicua* and *angra* (Figs. 59, 60). Female genitalia support this grouping, though less showily: the posterior part of the ductus bursae is much longer than the anterior part in *myron* and *verba* (Fig. 77) but only a little longer in *inconspicua* and *angra*.



FIGS. 58, 59. Male genitalia of *Quasimellana inconspicua* from Puyo, 1000 m, Pastaza, ECUADOR, 19 October 1989, S. S. Nicolay (X-2826) (USNM). Scale = 1.0 mm. **58,** Tegumen, uncus, and gnathos in dorsal view. **59,** Complete genitalia (minus right valva), with vesica everted and juxta and cornutus stippled, in left lateral view.

(I will say nothing further about females within the *myron* subgroup because sound interspecific differences in genitalia and external appearance are not evident among the few specimens at hand.)

Although males of *myron* and *verba* are not difficult to recognize as a unit, they are hard to separate from each other. Evans (1955) described *verba* (from Costa Rica, Colombia, Ecuador, and Guyana) as a southern subspecies of *myron* (from Mexico, Nicaragua, and Costa Rica). But distinguishing characters neither hold completely nor neatly divide geographically. All things considered, these skippers look more like overlapping species than subspecies. A quick and easy alternative would be a single, too variable, species, at least as dissatisfying as *eulogius* (and unfortunately, for supplemental analysis, far rarer in collections). The *myron*/*verba* complex now appears to range from central Mexico to southern Brazil.

By contrast, *inconspicua* and *angra* are strictly South American, with *inconspicua* western (Ecuador to Bolivia) and *angra* to the east. Though their genitalia look the same and their wings look similarly dark, they differ enough in color, pattern, and size (Fig. 31) to warrant specific rank. Since Evans's (1955:358) lists of specimens examined include an *inconspicua* male from "Chanchamayo," Peru, and an *angra* male from "Perene," Peru, since both names refer to the same general collecting area, and since both skippers live at low elevation (even the western *inconspicua* is known only from 250–1000 m), *inconspicua* and *angra* may well be in contact or sympatric.

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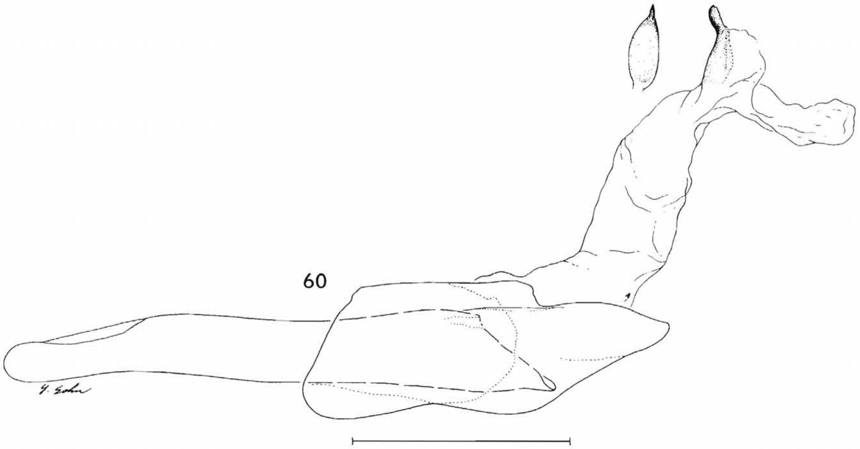


FIG. 60. Male genitalia of holotype of *Quasimellana angra* (what remains of Evans's dissection) from Pará, BRAZIL, H. W. Bates (X-3461) (BMNH). Scale = 1.0 mm. Left valva and aedeagus, with vesica everted and cornuti stippled, in left lateral view (plus primary cornutus in dorsal view).

Quasimellana myron (Godman, 1900:493, pl. 94, figs. 20–24), new combination
(Figs. 31, 77)

Mexico (San Luis Potosí, Veracruz, Guerrero, Oaxaca, Quintana Roo), Guatemala, Honduras, Nicaragua, Costa Rica, Panama. 16 ♂ 5 ♀ (9 ♂ 4 ♀).

The dorsodistal projection of the valva is broader and distally rounder than it is in *verba*, and the valva has no middle process on its inner surface (see Evans 1955:pl. 79, fig. M.25.12 *myron*). The secondary, vestigial cornutus is usually absent (present in two males from Oaxaca, Mexico, but smaller than it is in *verba*). Male spot development in *myron* and *verba* is generally about average to somewhat reduced (Figs. 105, 106); but, in the specimens at hand (as in any appreciable series of *Quasimellana*), it varies considerably. Evans's (1955) observation that the yellow dorsal markings of the male are paler in *myron* and darker in *verba* appears valid but ever so subtle. I find the yellow spot in space 2 of the dorsal forewing more helpful: it tends to be rectangular (often squarish), with its inner edge more or less vertical, in males of *myron* but more nearly triangular (and wider), with its inner edge oblique, in males of *verba* (Fig. 105).

Quasimellana verba (Evans, 1955:358, pl. 79, fig. M.25.12), new combination
(Figs. 31, 105, 106)

HT♂-BMNH. Mexico (San Luis Potosí, Yucatán), Panama, Colombia, Venezuela, Ecuador, Brazil (São Paulo). 12 ♂ 3 ♀ (12 ♂ 1 ♀).

The dorsodistal projection of the valva is narrower and distally more pointed than it is in *myron*, and the valva usually has a middle process on its inner surface (see Godman 1900:pl. 94, fig. 22 and Evans 1955:pl. 79, fig. M.25.12 *verba*)—but that process is small in three males from Mexico and Panama and absent in two males from Ecuador and Brazil. The secondary, vestigial cornutus is usually present (absent in the male from

Brazil). See *myron* for slight average differences between *myron* and *verba* in the external appearance of males.

Quasimellana inconspicua (Hayward, 1950a:465, fig. 5), new combination
(Figs. 31, 58, 59)

HT♂-IML. Ecuador, Peru, Bolivia. 8 ♂ 2 ♀ (8 ♂ 1 ♀).

Spotting is so reduced in males of both *inconspicua* and *angra* that they look mostly dark. Their dorsal forewing bears a total of three small yellow spots in the lower part of space 1b and in spaces 2 and 3. Even though *inconspicua* is the larger species, averaging more than a millimeter longer than *angra* in wing length (Fig. 31), its spots are smaller and relatively diffuse—much less sharply defined than they are in *angra* (Fig. 107). Moreover, in *inconspicua* the yellow of these spots is a little paler; and the spot in space 3 is slightly distad of the spot in space 2, whereas in *angra* the spot in space 3 slightly overlaps the spot in space 2 (Fig. 107). Ventrally, males of *inconspicua* are darker and vaguely greenish brown when fresh, whereas *angra* males are lighter and somewhat yellowish brown. For whatever it may be worth with such small numbers, I note that the secondary, vestigial cornutus is absent in nearly half the dissected males of *inconspicua* (Fig. 59) but present in all four dissected males of *angra* (Fig. 60).

Specimens of *inconspicua* have been misdetermined as *pandora*, a superficially similar species or subspecies of *Quasimellana* in the *nicomedes* group and a very close sister of *meridiani*. See *meridiani* for a discussion of external differences between *inconspicua* and *pandora*.

Quasimellana angra (Evans, 1955:358, pl. 79, fig. M.25.13), new combination
(Figs. 31, 60, 107, 108)

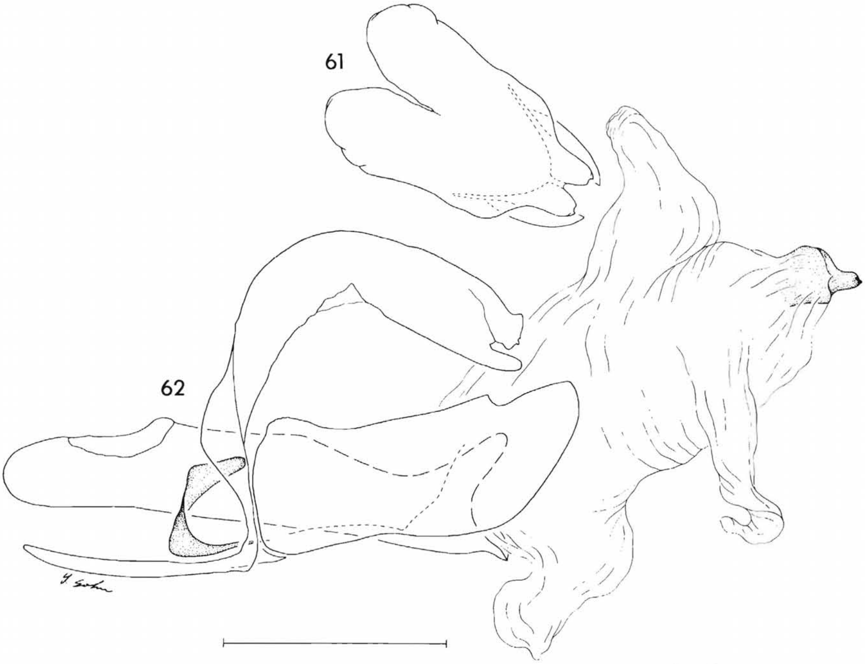
HT♂-BMNH. French Guiana, Brazil (Pará, Maranhão, Pernambuco, Bahia, Minas Gerais, Rondônia); Evans (1955) also lists one male each from Venezuela, Ecuador, and Peru. 6 ♂ 4 ♀ (4 ♂ 2 ♀).

See *inconspicua*.

This is the second smallest species of *Quasimellana*, exceeding only *sethos* (Fig. 31).

The *nicomedes* Group
(Figs. 31, 34, 35, 39, 61–67, 78–82, 109–112)

Male genitalia. *Juxta*: As in some members of the *sethos* group, the juxta is anterior in location (Figs. 62, 65, 67); but the level of the twist in each lateral arm of the juxta is high (Figs. 39, 62, 65, 67), not low as it is in all other species of *Quasimellana* (Figs. 41, 43, 45, 47, 52, 55, 57, 59). *Cornutus*: The head-and-neck of the cornutus is short; it rises almost vertically from the body of the cornutus (Figs. 34, 35, 62, 65, 67). No member of the *nicomedes* group has the tiny, secondary, vestigial cornutus that usually occurs in other species of *Quasimellana*. *Vesica*: The everted vesica is relatively short, fat, and irregular (Figs. 62, 65, 67). *Valva*: The valva has neither a middle process nor a dorsal process on its inner surface (Figs. 62, 65, 67) (one or both processes are present in other species of *Quasimellana*). Distally the valva terminates in one or two dorsally directed, sharp points (Figs. 65, 67), except in *fieldi* (Fig. 62). *Uncus*: In lateral view, the distal end of the uncus is much thicker than the distal end of the gnathos (Figs. 62, 65, 67), except in *amicus* where (as in all other species of *Quasimellana*) the uncus is only a little thicker than the gnathos. Again, in lateral view, the uncus is usually (but not always) a little shorter than the gnathos (Figs. 62, 65, 67), except in *amicus*. *Tegumen*: In dorsal view the tegumen generally tapers more abruptly to the uncus (Figs. 61, 63, 64, 66) than it does in other species.



FIGS. 61, 62. Male genitalia of *Quasimellana fieldi* from San Salvador, EL SALVADOR, 29 December 1953, M. Salazar (X-2589) (USNM). Scale = 1.0 mm. **61,** Tegumen, uncus, and gnathos in dorsal view. **62,** Complete genitalia (minus right valva), with vesica everted and juxta and cornutus stippled, in left lateral view.

Female genitalia. The ductus bursae extends caudad ventrally but not laterally to form a unique scoop beneath the ostium bursae (Figs. 78–82). At its anterior end the sclerotized ductus bursae is longitudinally grooved and more or less expanded (Figs. 78–82). The anterior apophyses are neither long (as in the *eulogius* group) nor short (as in the *sethos* group). The only species outside of the *nicomedes* group with anterior apophyses of intermediate length are *sethos* and (in some individuals) *balsa*. The corpus bursae is relatively short and fat (Figs. 78–82), though less so in *fieldi*.

General features. Sexual dimorphism runs the gamut from nonexistent (*amicus*), through weak (*nicomedes, meridiani,* and presumably *pandora*), to strong (*imperfida, mielkei,* and *fieldi*); color pattern, from mostly dark (*meridiani* and especially *pandora*), through roughly half-and-half (*amicus* and *nicomedes*), to mostly light (in the predominantly yellow orange males of *fieldi, mielkei,* and especially *imperfida*). The species are small to medium in size (Fig. 31).

Distribution. Although the *nicomedes* group (with 7 species) extends from Mexico to Argentina, it is mainly South American.

Quasimellana amicus (Bell, 1942a:2, fig. 3), new combination (Figs. 31, 78)

HT♂-AMNH. Ecuador. 8 ♂ 4 ♀ (5 ♂ 3 ♀).

Superficially this smallish species (Fig. 31) seems out of place in *Quasimellana* because females look just like males, the discal spotband (yellow orange) runs boldly and continuously (cut by dark veins) up the forewing from space 1b to space 6 (or rarely 7) without the usual break in space 5 (distal to the upper half of the cell), and the ventral hindwing flaunts a dark border (interrupted by yellow in space 1c). This is the sole member of the *nicomedes* group in which the uncus is undivided and (in lateral view) only a little thicker than the gnathos. The long, low valva ends distally in a single, dorsally (and medially) directed, sharp point. The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is exceptionally delicate and long (extending far caudad of the paired, sclerotized, lateral lobes that flank it); its base is not quite hidden, in ventral view, by the posterior edge of the ventral scoop of the ductus bursae; and the longitudinally grooved, anterior end of the sclerotized ductus bursae is diagonal, slanting sharply forward (at about 45°) from right to left (Fig. 78).

Quasimellana fieldi (Bell, 1942a:2, fig. 4), new combination (Figs. 31, 34, 39, 61, 62)

= *montezuma* (Freeman, 1969:41, pl. 13, figs. 5–8; pl. 15, fig. 10), new synonym, HT♂-AMNH.

HT♂-USNM. Mexico (San Luis Potosí), Guatemala, El Salvador, Nicaragua; Evans (1955) gives Costa Rica. 54 ♂ 13 ♀ (10 ♂ 3 ♀).

The only North American species of the *nicomedes* group, *fieldi* superficially resembles members of the *eulogius* group (especially *mexicana*, *eulogius*, and *balsa*) inhabiting the same general region. The long, low valva comes dorsodistally to a blunt or vaguely pointed end (Fig. 62)—not a sharp point as in *amicus*. The uncus prongs (in dorsal view) are short, parallel, and more or less rounded at their distal ends (Fig. 61). The body of the cornutus is large and mostly flat (Figs. 34, 62). The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is medium in length (extending a little caudad of the paired, sclerotized, lateral lobes that flank it) and about as wide as it is in *mielkei* (Fig. 81) or *meridiani* (Fig. 82) to considerably wider. The longitudinally grooved, anterior end of the sclerotized ductus bursae is diagonal, much as it is in *amicus* (Fig. 78), but it slants forward from right to left even more steeply than in that species. (See Steinhauser 1974:fig. 87 for a photograph of the female genitalia of *fieldi* in ventral view.)

When Freeman (1969) described *montezuma* (which is synonymous with *fieldi*), he grouped it with what he called its "nearest relatives"—*nayana* and *mulleri*—in a "*nayana* complex," based only on a few similarities in external appearance. In reality, these three species are not even close, each belonging in a different one of the three species groups of *Quasimellana*.

Quasimellana nicomedes (Mabille, 1883:LXX), new combination (Figs. 31, 35, 79, 80)

= *monica* (Plötz, 1886:98), new synonym, HT♀-ZMHB.

HT♂-ZMHB. Brazil (Paraná, Santa Catarina); Evans (1955) gives localities to the north in the neighboring states of São Paulo and Rio de Janeiro. 4 ♂ 4 ♀ (3 ♂ 3 ♀).

In the modest sexual dimorphism of *nicomedes*, the female expresses spots almost as well as the male, and her spots are a malelike yellow orange (not whitish and semihyaline on the forewing as they are in most species of *Quasimellana*). The long, low valva comes dorsodistally either to a single, sharp, dorsally directed point, as in *amicus*, or to two such points, as in *imperfida*, *mielkei* (Fig. 65), *pandora* (Fig. 67), and *meridiani*—but in *nicomedes* the points are a little closer together, and the distal point is higher than the proximal point instead of the other way around. The uncus prongs (in dorsal view) are very short, barely divergent, and truncate at their distal ends. The body of the cornutus is narrow and highly convex (Fig. 35). The midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis (Figs. 79, 80) is delicate and long, extending somewhat caudad of the paired, sclerotized, lateral lobes that flank it—but not as far as in *amicus* (Fig. 78).

Quasimellana imperfida, new species
(Figs. 31, 63)

HT♂-USNM. Brazil (Mato Grosso, Goiás), Bolivia; Evans (1955) also lists Colombia and Paraguay under the name *Mellana perfida*. 4 ♂ 2 ♀ (4 ♂ 2 ♀).

I have scrutinized the type (♂-ZMHB), its genitalia (X-3763), and the original description of *perfida* Möschler (1878:221) and found that it is a species of *Anatrytone* and that what everyone is currently calling *Mellana perfida* is an undescribed species of *Quasimellana*.

See *mielkei*. Size similar to *mielkei*, maybe a little smaller (Fig. 31): mean male forewing length 15.4 mm, range 14.8–16.2 mm, n = 4; mean female forewing length 16.8 mm, range 16.5–17.0 mm, n = 2. Nudum 14 or, usually, 15 segments (Table 1).

Externally, the light males of *imperfida* suggest males of *Anatrytone*—especially *A. perfida* or some combination of that species and *A. logan*. *Quasimellana imperfida* is a close sister to *mielkei* (qv); and these two are related, on the one hand, to the sisters *meridiani*/*pandora* and, on the other, to *nicomedes* (qv). The tegumen, uncus, and gnathos of *imperfida* (Fig. 63) are about as in *nicomedes*, while the cornutus is about as in *meridiani* and *pandora* (Fig. 67), i.e., with the body slightly less narrow and rather less highly convex (flatter) than in *nicomedes*. In lateral view the valva is not quite as low as in *fieldi* (Fig. 62) and especially *nicomedes* and *amicus*; in this regard, it is much like that of *meridiani* and *pandora* (Fig. 67) but longer. The female genitalia of *imperfida* are similar to those of *meridiani* (Fig. 82) and presumably *pandora*.

Holotype. ♂; BRAZIL, MATO GROSSO, Colegio Buriti, Chap. Guimarães, 700 m, 26 May 1969, S. S. Nicolay; S. S. Nicolay genitalia dissection H435 (left valva missing); USNM.

Paratypes. n = 3 ♂ 2 ♀. BRAZIL: MATO GROSSO: Nivac, 1 ♂, J. M. Burns genitalia dissection X-3462, collection of O. H. H. Mielke; Buriti, Chapada dos Guimarães, 600 m, 27 June 1972, 1 ♀, Mielke & Brown, X-3463, specimen number DZ 3519 in UFPR; Cáceres, 7–9 February 1985, 1 ♂, C. Elias, X-3116, DZ 3513 in UFPR; GOIÁS, Goiás Velho, 25 February 1979, 1 ♀, Gifford, X-3464, DZ 3521 in UFPR. BOLIVIA, Chiquitas, 1 ♂, X-3764, ZMHB.

Etymology. *Quasimellana imperfida* simply is *not perfida*. Ever since Evans (1955), it has been going under the name *Mellana perfida*; but *perfida* is really a superficially similar looking species of *Anatrytone* (see p. 286).

Quasimellana mielkei, new species
(Figs. 31, 64, 65, 81, 109–112)

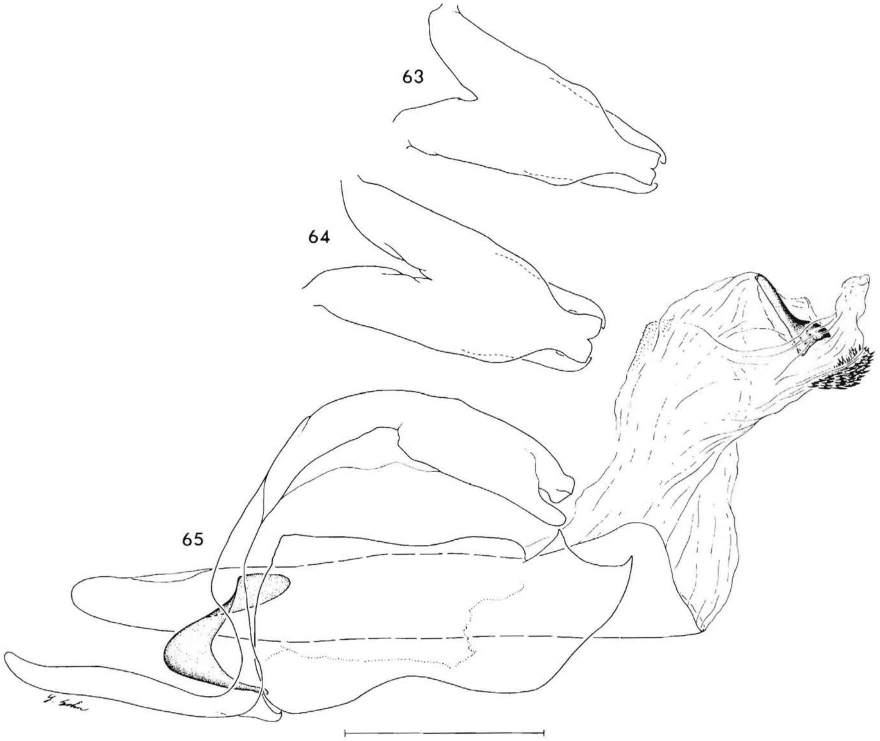
HT♂-UFPR. Brazil (Minas Gerais). 1 ♂ 1 ♀ (1 ♂ 1 ♀).

Close sister to *imperfida*. Sexual dimorphism strong (Figs. 109, 111), as in *imperfida* and *fieldi*. Wings fuller than in *imperfida*. Facies much as in *imperfida*, but dorsally, in male, extensive light areas of wings more orange (*imperfida* yellower), and transition between broad, light areas and narrow, dark, outer borders less hard and sharp; dorsally, in female, semihyaline spot in cell of forewing double (Fig. 111) instead of single as in *imperfida* (with so little material, this difference perhaps nothing more than individual variation); ventrally, in both sexes, dark ground color evident through thin, light overscaling (Figs. 110, 112)—wings ventrally not almost all bright yellow as in *imperfida*. Genitalia in both sexes (Figs. 64, 65, 81) like those of *imperfida* (including small, flexible, well sclerotized, conspicuous, and coarsely spinulose scouring-pad cornutus in male [Fig. 65], not present in other species of *Quasimellana*) except uncus slightly wider in dorsal view (compare Figs. 64 and 63), aedeagus somewhat stouter, and ductus bursae slightly wider in ventral or dorsal view. Size similar to *imperfida*, maybe a little larger (Fig. 31): forewing length of male 16.0 mm; of female 17.0 mm. Nudum long—16 segments in both specimens.

Holotype. ♂; BRAZIL, MINAS GERAIS, Diamantino, November 1977, Sakakibare; J. M. Burns genitalia dissection X-3119; specimen number DZ 3515 in UFPR.

Paratype. ♀; same data; X-3120; DZ 3514 in UFPR.

Etymology. I am delighted to name this species for Olaf H. H. Mielke who has enormously increased our knowledge of neotropical skippers and has generously lent much helpful material.



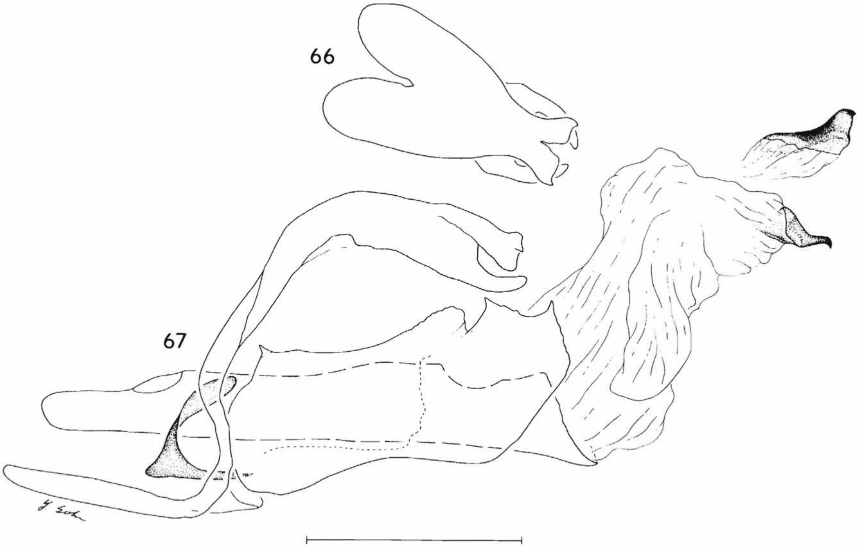
FIGS. 63–65. Male genitalia of paratype of *Quasimellana imperfida* from Cáceres, Mato Grosso, BRAZIL, 7–9 February 1985, C. Elias (X-3116) (UFPR) and of holotype of *Q. mielkei* from Diamantino, Minas Gerais, BRAZIL, November 1977, Sakakibare (X-3119) (UFPR). Scale = 1.0 mm. **63,** Tegumen, uncus, and gnathos of *imperfida* in dorsal view. **64,** Tegumen, uncus, and gnathos of *mielkei* in dorsal view. **65,** Complete genitalia of *mielkei* (minus right valva), with vesica everted and juxta and cornuti stippled, in left lateral view.

Quasimellana meridiani (Hayward, 1934:117, pl. 5, fig. 16), new combination
(Figs. 31, 82)

= *ricana* (Bell, 1941:1, fig. 1), HT♂-AMNH.

Brazil (Paraná), Paraguay, Argentina (Misiones). 4 ♂ 1 ♀ (3 ♂ 1 ♀).

Though genitalically close to the sisters *imperfida* and *mielkei*, sisters *meridiani* and *pandora* depart widely from them superficially: wings are relatively elongate and narrow (much as in various species of *Panoquina*), and are mostly blackish brown above. Males of *meridiani* are dorsally darkened enough to resemble females of *imperfida*, while males of *pandora*—their forewings usually with small yellow orange spots only in spaces 1b, 2, and 3—are so dark that they look like males of *inconspicua* of the *sethos* group. (However, spots in *pandora* are more orange than they are in *inconspicua*; the spot in space 3 is more distad of the spot in space 2 in *pandora* than it is in *inconspicua*; and the spot in



FIGS. 66, 67. Male genitalia of *Quasimellana pandora* from Rio Xingu Camp, 52° 22′ W, 3° 39′ S (first jungle stream trail 1, malaise trap day and night collection), ca 60 km S Altamira, Pará, BRAZIL, 2–8 October 1986, P. Spangler and O. Flint (X-2673) (USNM). Scale = 1.0 mm. **66,** Tegumen, uncus, and gnathos in dorsal view. **67,** Complete genitalia (minus right valva), with vesica everted and juxta and cornutus stippled, in left lateral view (plus cornutus in profile).

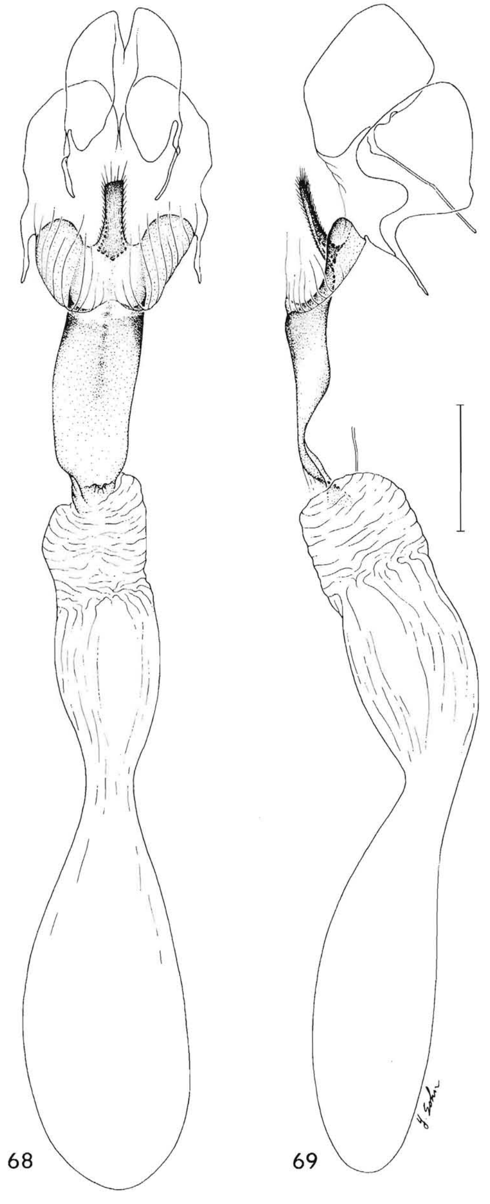
space 1b is, in *pandora,* often a sort of **V** on its side, spanning the height of space 1b, instead of a mere dot or bar, always limited to the lower part of that space, as it is in *inconspicua.* Moreover, males of *meridiani* and *pandora* average about a millimeter longer in the forewing than do males of *inconspicua* [Fig. 31]). Spotting in the female of *meridiani* is reduced from that in the male, but the spots are still a pale yellow orange; the female of *pandora* is unknown (spots in the female of *inconspicua* are whitish). Ventrally males of *meridiani* are mostly yellow but duller than in *imperfida,* and males of *pandora* are duller still (especially in Ecuador). The uncus prongs of *meridiani* and *pandora* are higher and wider than they are in other members of the *nicomedes* group: in left lateral view, the rounded, ventral lobe of the left prong projects exceptionally far downward (Fig. 67); in dorsal view, the prongs are truncate but distinctly divergent, usually with a good, triangular notch between them (Fig. 66). The valva (Fig. 67) is about as in *imperfida* and *mielkei* (Fig. 65) but shorter. The female genitalia (Fig. 82) are similar to those of *imperfida* and *mielkei* (Fig. 81), but the midventral, posteriorly directed, bristly projection from the posterior margin of the lamella postvaginalis is a little heavier and wider, at least in *meridiani* (the female of *pandora* is unknown).

Quasimellana pandora (Hayward, 1940:867, fig. 20), new combination (Figs. 31, 66, 67)

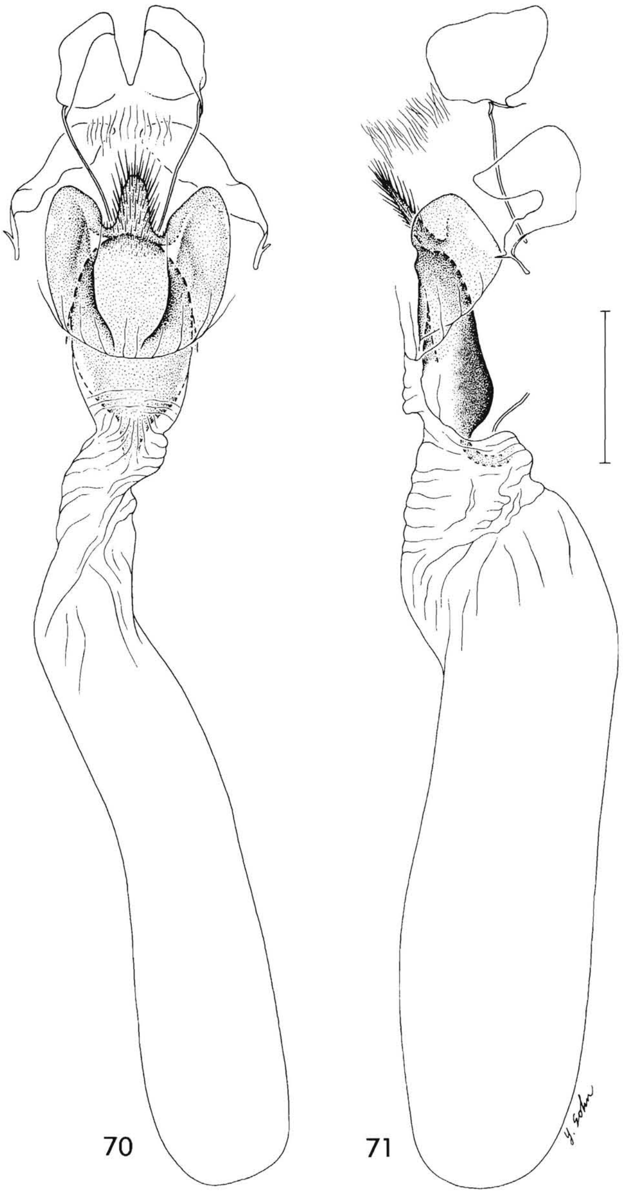
HT♂-IML. Ecuador, Peru, Bolivia, French Guiana, Brazil (Pará, Distrito Federal); Evans (1955) also lists Guyana. 14 ♂ (13 ♂).

See *meridiani.*

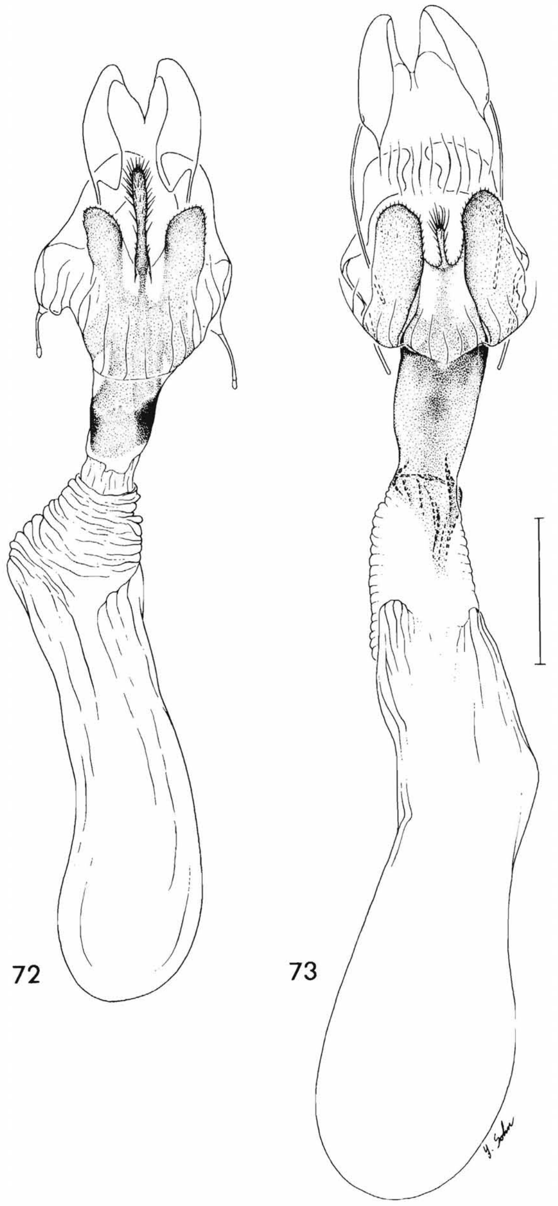
Evans (1955) may have been correct in treating *meridiani* and *pandora* as subspecies. More material is needed to resolve this matter.



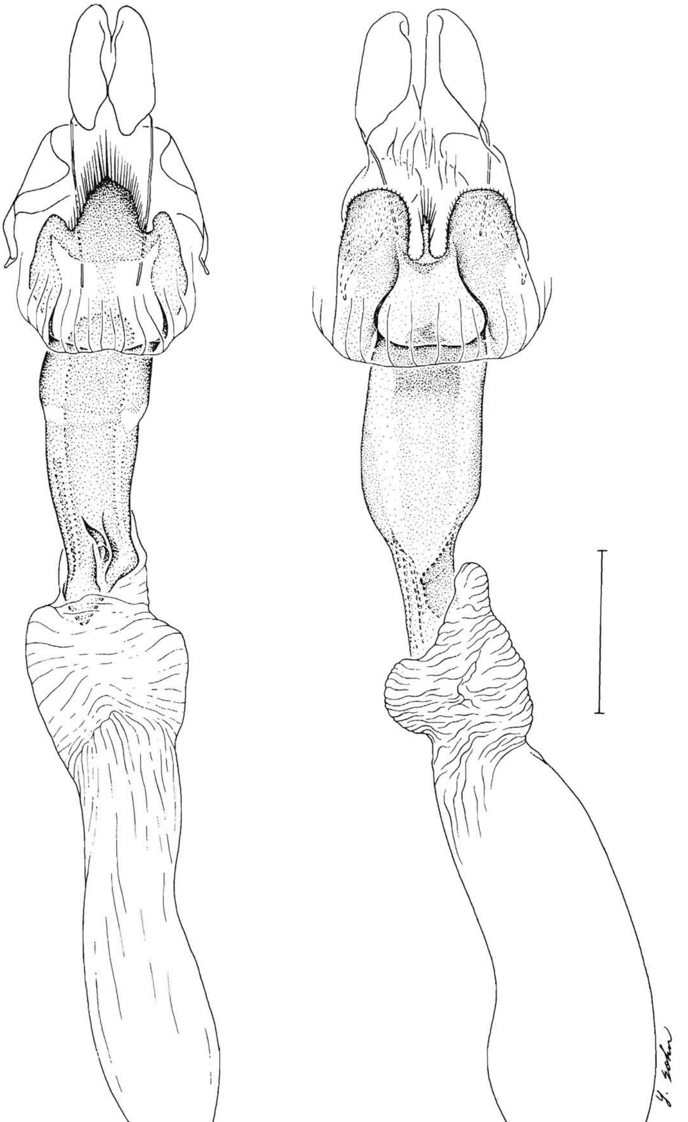
FIGS. 68, 69. Female genitalia of *Quasimellana mexicana* from Rio Metlec, Fortín de las Flores, Veracruz, MEXICO, 2 October 1975, J. Powell and J. Chemsak (X-2809) (UCB). Scale = 1.0 mm. **68,** Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. **69,** The same, plus part of the ductus seminalis, in right lateral view.



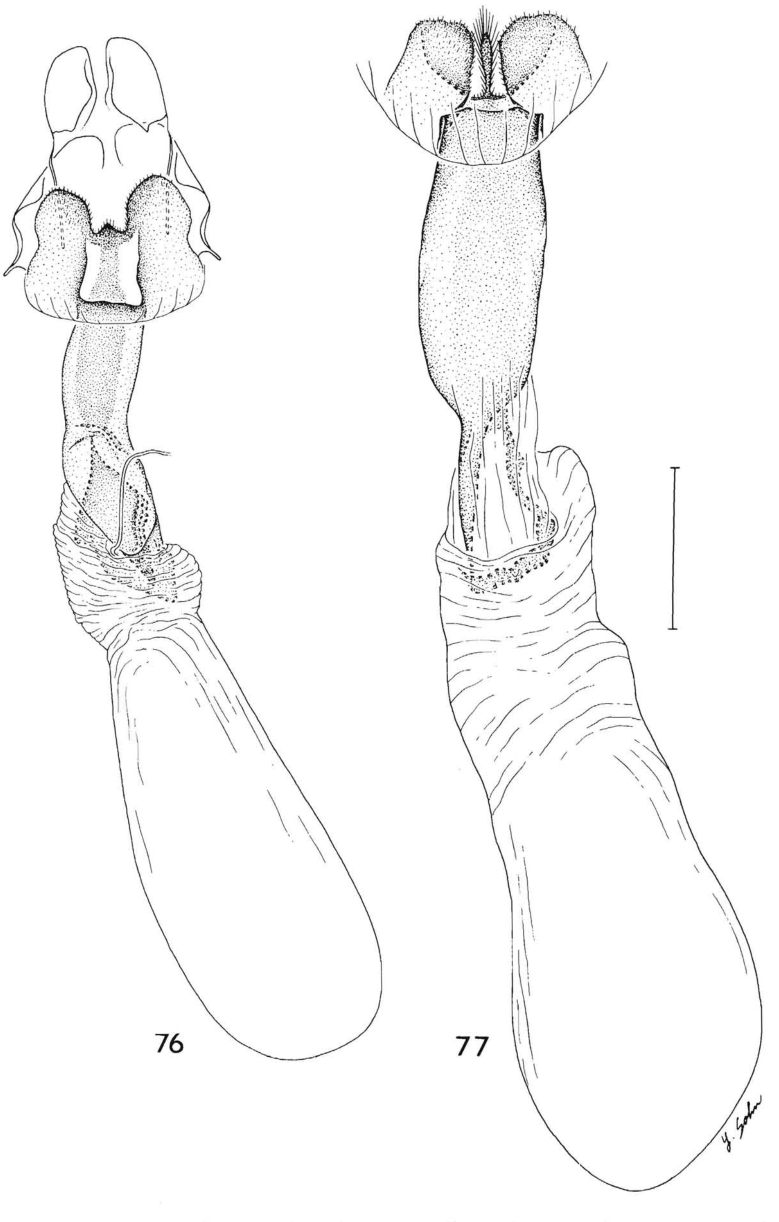
FIGS. 70, 71. Female genitalia of *Quasimellana balsa* from Rte. 16, km 242–254, Sonora, MEXICO, 1 September 1991, J. P. Brock (X-3656) (USNM). Scale = 1.0 mm. **70,** Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. **71,** The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 72, 73. Female genitalia of *Quasimellana* showing the sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. Scale = 1.0 mm. **72,** *Q. eulogius* from Cayuga, GUATEMALA, September (X-3062) (USNM). **73,** *Q. mulleri* from Victoria, Tamaulipas, MEXICO, 16 August 1962, Stallings, Turner (X-3648) (AMNH).



FIGS. 74, 75. Female genitalia of *Quasimellana* showing the sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. Scale = 1.0 mm. **74,** *Q. aurora* from Las Juntas Verano, 1000 ft (305 m), Hwy. 200 below Puerto Vallarta, Jalisco, MEXICO, 8 August 1989, J. Kemner (X-2823) (USNM). **75,** *Q. andersoni* (paratype) from Santa Rosa, Comitán, Chiapas, MEXICO, September 1963, T. Escalante (X-3643) (AMNH).



FIGS. 76, 77. Female genitalia of *Quasimellana* showing the sterigma and bursa copulatrix in ventral view. Scale = 1.0 mm. **76,** *Q. sethos,* with an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) and the ductus seminalis, from Howard Air Force Base, Canal Area, PANAMA, 3 February 1985, R. A. Anderson (X-3006) (USNM). **77,** *Q. myron* from Coatepec, Veracruz, MEXICO, (X-2600) (USNM).

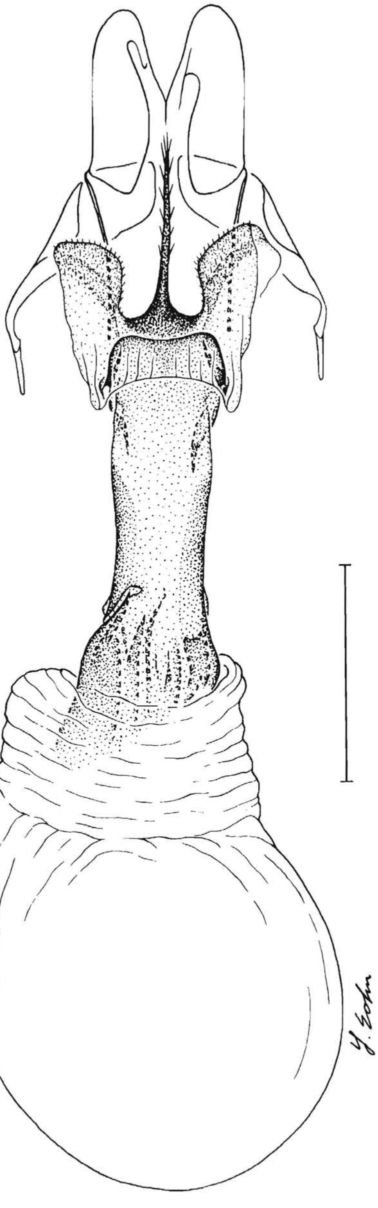


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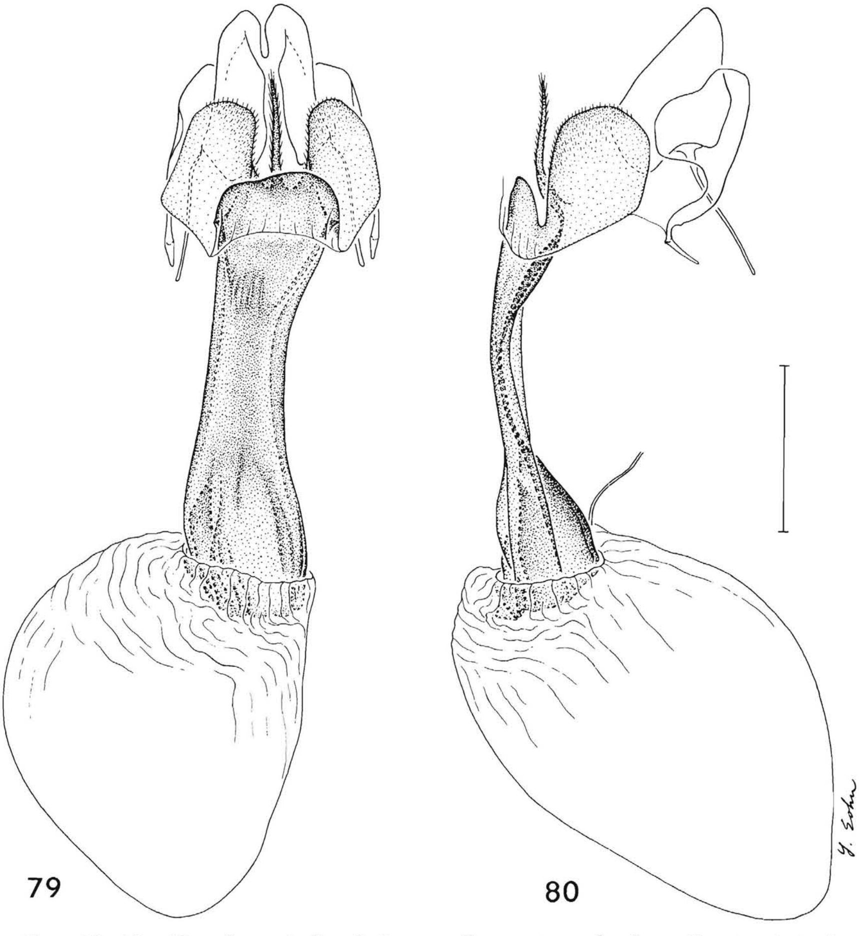
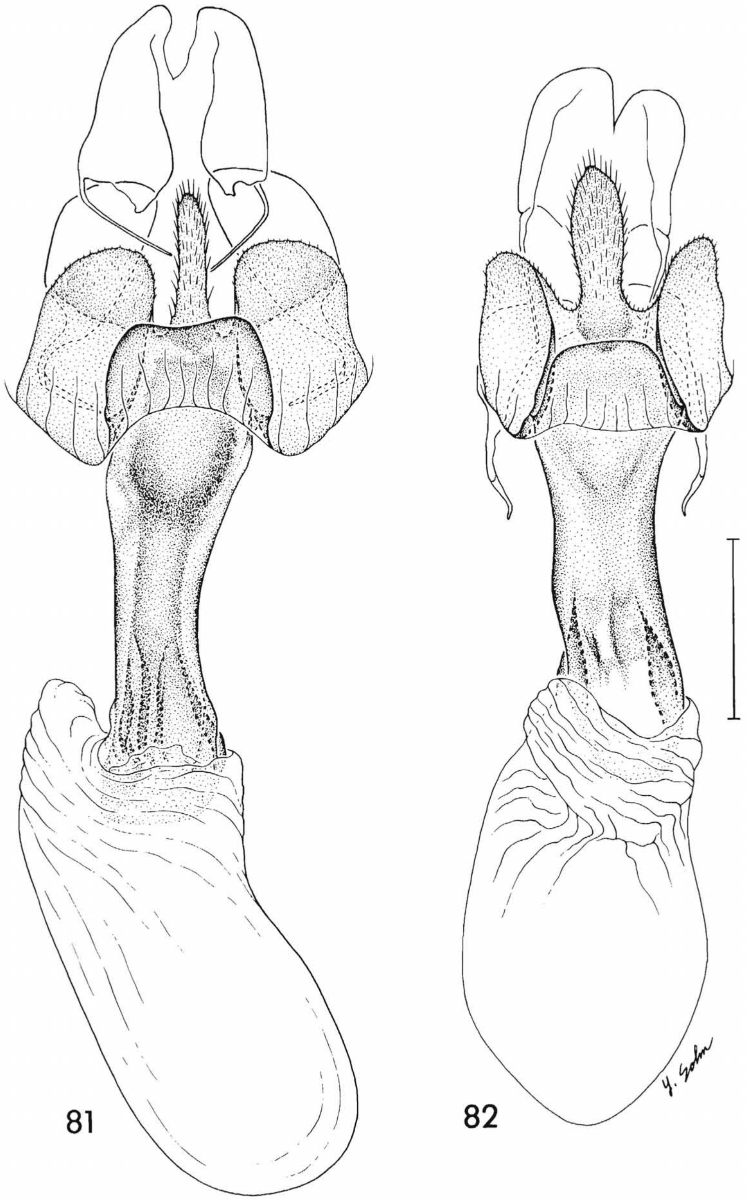
FIG. 78. Female genitalia of *Quasimellana amicus* from Napac, 1000 m, Pichincha, ECUADOR, 23 September 1975, S. S. Nicolay (X-2852) (USNM). Scale = 1.0 mm. Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view.



FIGS. 79, 80. Female genitalia of *Quasimellana nicomedes* from Cacatu, Antonina, 20 m, Paraná, BRAZIL, 25 April 1973, Mielke (X-2367) (MacNeill collection). Scale = 1.0 mm. **79,** Sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. **80,** The same, plus part of the ductus seminalis, in right lateral view.



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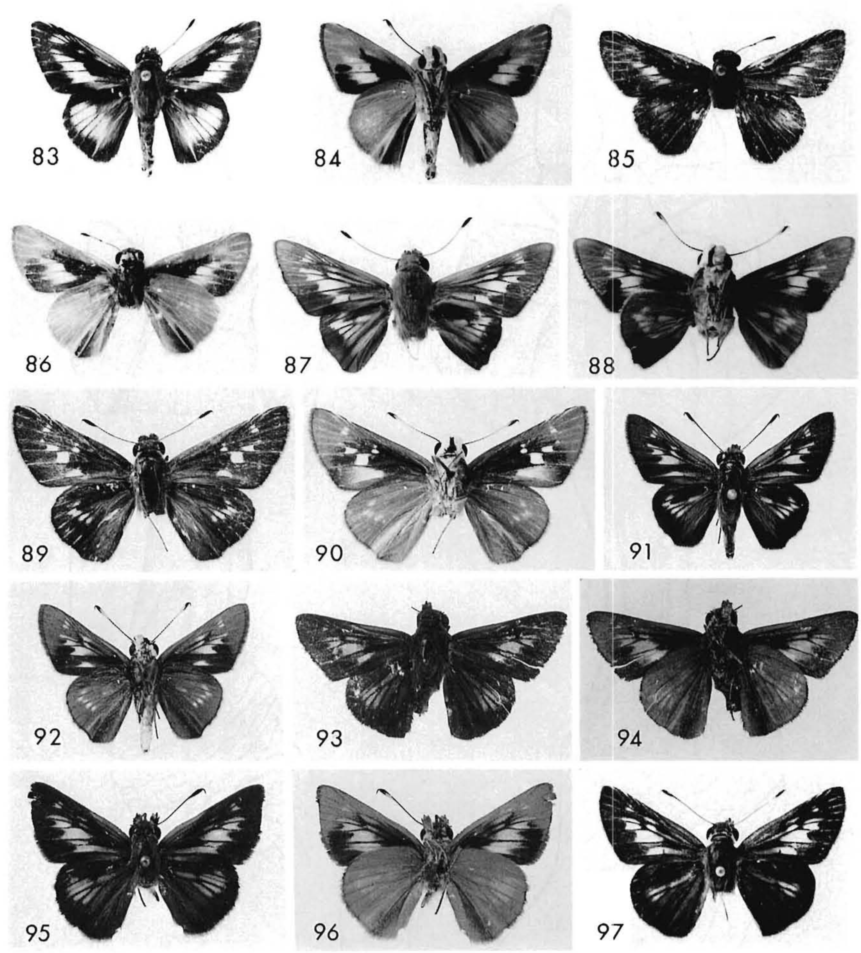
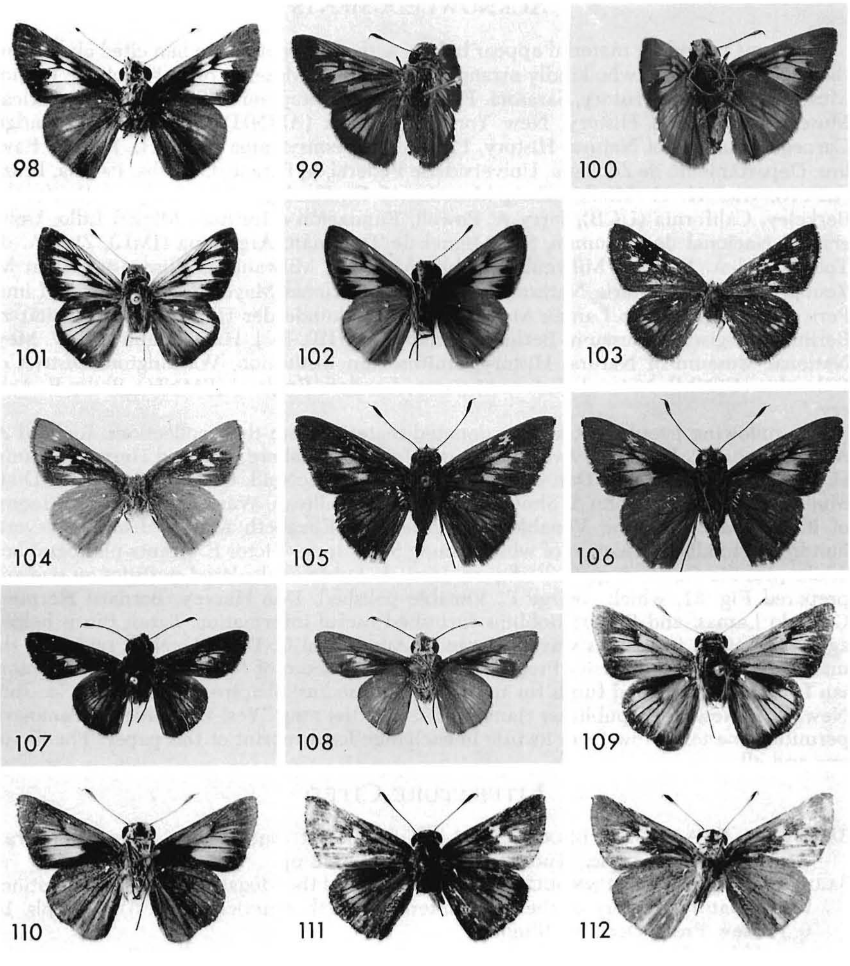
FIGS. 81, 82. Female genitalia of *Quasimellana* showing the sterigma, bursa copulatrix, and an indication of the terminal abdominal tergites (including the anterior and posterior apophyses and the ovipositor lobes) in ventral view. Scale = 1.0 mm. **81,** *Q. mielkei* (paratype) from Diamantino, Minas Gerais, BRAZIL, November 1977, Sakakibare (X-3120) (UFPR). **82,** *Q. meridiani* from Dos de Mayo, Misiones, ARGENTINA, 7 March 1989, Foerster (X-3614) (Mielke collection).



FIGS. 83–97. Mostly holotypes (HT) and paratypes (PT) of *Anatrytone* and *Quasimellana* in dorsal (D) and (&) ventral (V) views (all ×1). **83, 84,** *Anatrytone sarah* ♂, HT, D & V, Limoncocha, 240 m, Napo, ECUADOR (S. S. Nicolay genitalia dissection H739) (USNM). **85, 86,** *A. sarah* ♀, PT, D & V, Puerto Maldonado, 290 m, PERU (X-2607) (USNM). **87, 88,** *Quasimellana mexicana* ♂, HT, D & V, La Gloria, Cardel, Veracruz, MEXICO (W. D. Field genitalia dissection 1820) (USNM). **89, 90,** *Q. mexicana* ♀, D & V, Rio Metlec, Fortín de las Flores, Veracruz, MEXICO (X-2809) (UCB). **91, 92,** *Q. siblinga* ♂, HT, D & V, El Vado-San Sebastian, 1675–1980 m, Oaxaca, MEXICO (USNM). **93, 94,** *Q. noka* ♂, HT, D & V, locality unknown (X-3457) (BMNH). **95, 96,** *Q. pazina* ♂, HT, D & V, Yungas and La Paz, 1000 m, BOLIVIA (X-3460) (BMNH). **97,** *Q. antipazina* ♂, HT, D, La Estrella, 1500 m, Cartago, COSTA RICA (X-2592) (USNM).



FIGS. 98–112. Holotypes (HT) and paratypes (PT) of *Quasimellana* in dorsal (D) and (&) ventral (V) views (all ×1). **98,** *Q. antipazina* ♂, HT, V, La Estrella, 1500 m, Cartago, COSTA RICA (X-2592) (USNM). **99, 100,** *Q. sista* ♂, HT, D & V, VENEZUELA (X-3459) (BMNH). **101, 102,** *Q. andersoni* ♂, HT, D & V, Tapalapa, Veracruz, MEXICO (X-3003) (USNM). **103, 104,** *Q. andersoni* ♀, PT, D & V, Santa Rosa, Comitán, Chiapas, MEXICO (X-3643) (AMNH). **105, 106,** *Q. verba* ♂, HT, D & V, Balzapamba, Bolívar, ECUADOR (X-3458) (BMNH). **107, 108,** *Q. angra* ♂, HT, D & V, Pará, BRAZIL (X-3461) (BMNH). **109, 110,** *Q. mielkei* ♂, HT, D & V, Diamantino, Minas Gerais, BRAZIL (X-3119) (UFPR). **111, 112,** *Q. mielkei* ♀, PT, D & V, Diamantino, Minas Gerais, BRAZIL (X-3120) (UFPR).

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