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GENITALIA, DNA BARCODES, AND LIFE HISTORIES SYNONYMIZE *TELLES* WITH *THRACIDES*—A GENUS IN WHICH *TELLES ARCALAUS* LOOKS OUT OF PLACE (HESPERIIDAE: HESPERIINAE)

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**ABSTRACT.** Independent characters—genitalia (male and female), DNA barcodes, and larval foodplants—show that *Telles arcalaus* (Stoll), despite its exceedingly distinctive facies and small size, belongs in the genus *Thracides*, where it relates closely to *Thracides phidon* (Cramer). Because *phidon* and *arcalaus* are the type species of their respective genera and *Thracides* is the older name, *Telles* is a **synonym** of *Thracides*. Because the only other species in *Telles*, *T. pyrex* Evans, is not a species of *Thracides*, it is **incertae sedis**. Either in Trinidad or in Pará, Brazil, as in Area de Conservación Guanacaste (ACG), Costa Rica, caterpillars of *Thracides phidon* and *Thracides arcalaus*, **new combination**, eat plants in the genera *Heliconia* and *Musa* (Zingiberales), whereas members of the *Thracides nanea* species complex eat *Cyclanthus* and *Asplundia* (Cyclanthaceae). Taxa of the mostly South American *nanea* species complex include *Thracides nida* Evans, **new status** and, in ACG, *T. chiricana* Röber, **new status**. For now, owing to the numbers of cryptic species recently discovered within supposedly well-known species of neotropical hesperiids, the taxa treated here are viewed as morphospecies. DNA barcodes, which have proved so useful in distinguishing among cryptic species, are noteworthy in this study for supporting the union in a single genus of ostensibly unrelated species.

**Additional key words:** morphospecies, secondary sex character, panneotropical, Zingiberales, Cyclanthaceae, “*Telles*” *pyrex* Evans *incertae sedis*.

Ever since Scudder & Burgess (1870), genitalia have been used effectively in distinguishing and describing species of skipper butterflies. But what follows is an example of their utility (still underexploited) in pulling a misclassified species into the proper genus (Burns 1994, 1996).

Because the facies of *Telles arcalaus* (Stoll) is both complex and strange (Figs. 1–4), it was startling when the male genitalia, upon KOH-dissection, looked familiar. Might déjà vu reflect genitalic convergence? No. Direct comparison of the new genitalia dissection (Figs. 16–18) with prior ones (Figs. 19–24) revealed morphologic similarity too pervasive for anything other than close phylogenetic relationship. It was clear that *Telles arcalaus*, a species in the K Group of neotropical hesperiids (Evans 1955), really belongs in *Thracides*, a genus in Evans’s O Group.

Genitalic characters for this move are supported by characters derived from life histories and DNA barcodes: a neighbor-joining tree links *Thracides arcalaus*, **new combination**, with *Thracides phidon* (Cramer); and caterpillars of both species eat *Heliconia latispatha* and *H. irrasa* (Heliconiaceae) in Area de Conservación Guanacaste (ACG) in northwestern Costa Rica.

The disparate characters noted above are illustrated and discussed, along with some others, in a broader context below. But first, consider the rationale for applying certain names to several of the taxa involved.

#### NAMES

Because the type species of *Thracides* 1819 is *phidon* and that of *Telles* 1900 is *arcalaus*, because these two species are congeneric, and because *Thracides* is the

older generic name, *Telles* is a **synonym** of *Thracides*. Over the course of the long, erratic taxonomic history that preceded its segregation in the monotypic genus *Telles*, *arcalaus* was variously placed in five other genera: *Papilio*, *Augiades*, *Hesperia*, *Goniloba*, and *Proteides* (Mielke 2005).

*Telles pyrex* Evans (1955), the only species added to *Telles*, was described from a single Colombian female, caught in 1932. Owing to her sex, Evans did not examine and figure genitalia. Study of the facies and genitalia of another female, taken in eastern Peru in 1992, shows that *pyrex* is not a species of *Telles* (see *pyrex* Postscript). So *pyrex* cannot follow *arcalaus* to *Thracides* and is left, for now, without a generic name, in nomenclatural limbo (***incertae sedis***).

Recent literature (Mielke 2004, 2005) ascribes seven species, exclusive of *arcalaus*, to *Thracides*. However, in light of the 14 cryptic, relatively specialized, neotropic skipper species recently shown to be masquerading as two, common, widespread, and ecologically generalized species, each described in 1775—i.e., *Astraptes fulgerator* (Walch) and *Perichares philetus* (Gmelin) (Hebert *et al.* 2004, Burns *et al.* 2008)—some species of *Thracides* may comprise species complexes. Until more data are available, the taxa noted in this paper should be viewed as morphospecies.

If an ACG morphospecies turns out to be a member of a superspecies or a species complex, its specific name may change. Take the simplest case: both *Thracides arcalaus* and *T. phidon* were originally described from Surinam, which is historically, geographically, and ecologically so far removed from ACG that the populations in ACG may well be specifically distinct from their counterparts in Surinam (and adjacent areas) and need different names. Nevertheless, provided that the original specific name has not been too broadly and uncritically applied, it can be a convenient and helpful (though hopefully temporary) peg on which to hang new biologic data for analysis and discussion.

Not so simple is the third species of *Thracides* reared in ACG, which belongs to a “*nanea* species complex.” Even a provisional name for what is in ACG is debatable. *Thracides nanea* (Hewitson) itself is a skipper of the Amazon drainage (eastern Peru to Pará, Brazil) and Maranhão, Brazil (from which it was described). Two subspecies have been described from extremely limited material: *T. nanea chiricana* Röber (1926) from one male from Chiriqui and *T. nanea nida* Evans (1955) from one male and one female from interior Colombia. Both original descriptions are brief; and, in an important respect, Röber's is incorrect (he states that the male has no stigma when, in fact, it has a good one). *Thracides nanea nida* differs from *T. nanea*

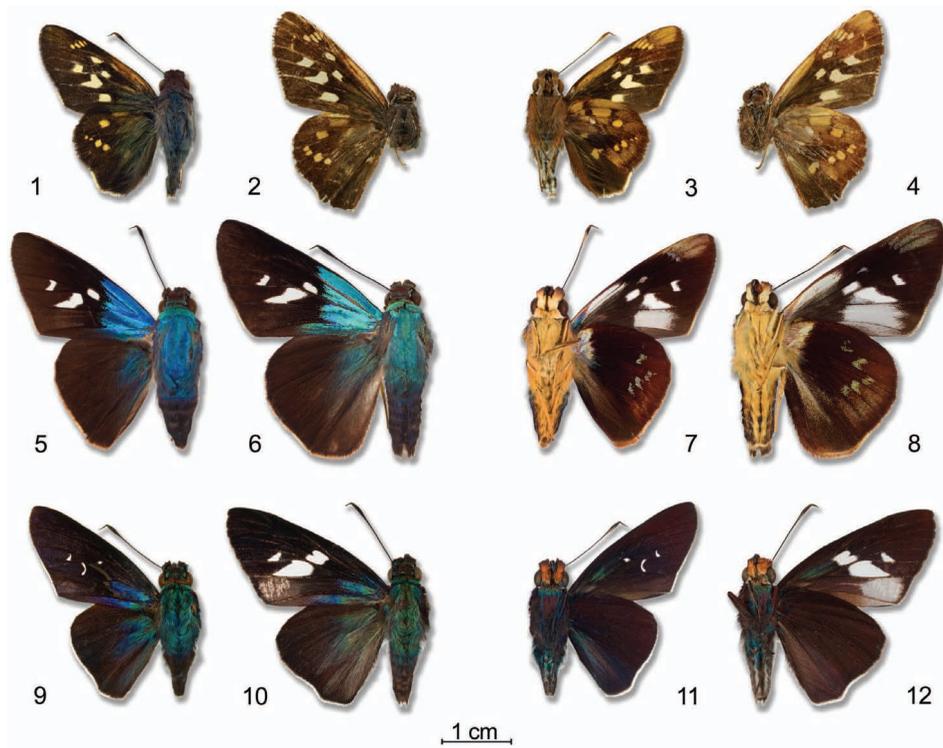
*nanea* primarily in having a white hyaline spot in forewing space 3. Although Röber did not say so, *T. nanea chiricana*, like *T. nanea nanea*, lacks this spot; and Mielke (1989), having examined holotypes, synonymized the former with the latter, without discussion. The seven ACG specimens in the *nanea* complex have this spot (but its expression is so variable that in one male it is reduced to a tiny point, and so it may occasionally vanish). Inasmuch as ACG specimens share this spot with the male holotype of *T. nanea nida*, that name might apply to them.

However, in Evans's dry-dissection of the *nida* holotype's genitalia (glued to a bit of card on the specimen's pin), the valvae are pointed at their distal end. See the valval caricature for *nida* in Evans (1955: pl. 87), which is actually less pointed than are the valvae themselves. Evans also indicates that the valvae of *nanea* are still more pointed than are those of *nida*. The valvae of *T. nanea* and *T. nida*, **new status**, differ significantly from each other and differ sharply from the rounded valvae of ACG males (Fig. 26). Indeed, valvae are rounded in all three of the *Thracides* species in ACG (Figs. 17, 20, 23, 26). Because genitalic form is usually stable within skipper species (but see Burns 2000 for a striking exception), it is safe to assume that neither *T. nanea* nor *T. nida* is conspecific with the ACG population.

Although the latter may represent a fourth taxon in the *nanea* complex, a conservative (but tentative) action extends the name *T. chiricana*, **new status**, to the ACG population, owing to the proximity of Chiriqui (western Panama) to ACG and to the similarity of the skipper fauna and the ecosystems in these two areas. Future studies may show that the shape, in males, of the forewing spot in space 2 (which looks like a parenthesis in the four ACG males but like an Erlenmeyer flask in the male *chiricana* holotype) is more important in discriminating between species than is presence vs. absence of the variably expressed spot in space 3; but that remains to be seen. In the *nanea* complex (and, no doubt, in myriad others), arriving at names that are both apt and stable will require ample samples from many and various localities and further analysis.

#### FACIES (FIGS. 1–15)

**Wings (Figs. 1–12).** Dark wings (ventrally reddish brown) with a structural blue to greenish blue sheen, a few hyaline white forewing spots, and ventrally orange palpi are elements of the prevailing color pattern in *Thracides*. *Thracides chiricana* exemplifies this pattern (Figs. 9–12). Two South American species, *T. panimeron* H. H. Druce and *T. thrasea* (Hewitson), always lack white spots.



FIGS. 1–12. Adults of three species of *Thracides* in dorsal and ventral view: *T. arcalaus* (top row), *T. phidon* (middle row), *T. chiricana* (bottom row); males (columns 1 and 3), females (columns 2 and 4); dorsal (columns 1 and 2), ventral (columns 3 and 4). Voucher codes denote reared specimens from Area de Conservación Guanacaste, Costa Rica. Specimens in USNM. **1, 3**, 07-SRNP-42031. **2, 4**, Cana, 400 m, Darien, Panama, 10 September 1982, leg. G. B. Small (Burns genitalia dissection X-5795). **5, 7**, 03-SRNP-34311. **6, 8**, 04-SRNP-48834. **9, 11**, 05-SRNP-5086. **10, 12**, 03-SRNP-20435.

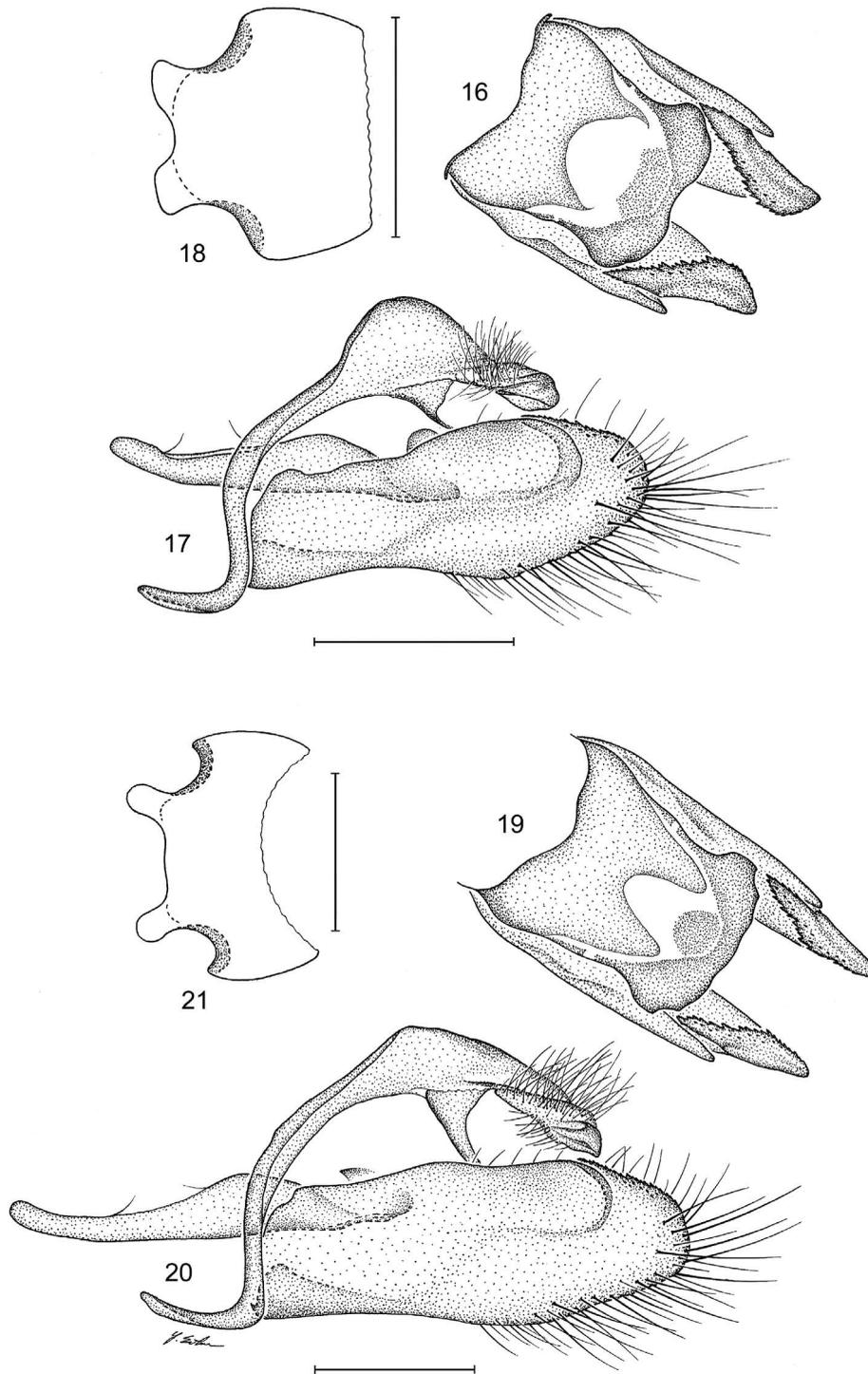
White spots usually include two in the cell; and, in most of the spotted species, one spot is directly above the other. These spots are so much larger in females than in males that they unite (Figs. 10, 12). In sharp contrast, the upper cell spot of *T. arcalaus* and *T. phidon* is not above the lower one but distal to it. The proximal, lower spot in both of these species is medium-sized and expressed to the same degree both dorsally and ventrally (Figs. 1–8). The distal, upper spot is similar in size to the proximal one and is equally expressed on both wing surfaces in *T. arcalaus* (Figs. 1–4). But in *T. phidon*, the distal spot is far smaller than the proximal

one and is usually expressed ventrally (Figs. 7, 8); and when it appears dorsally (in ~60% of 88 individuals examined), it is only a point.

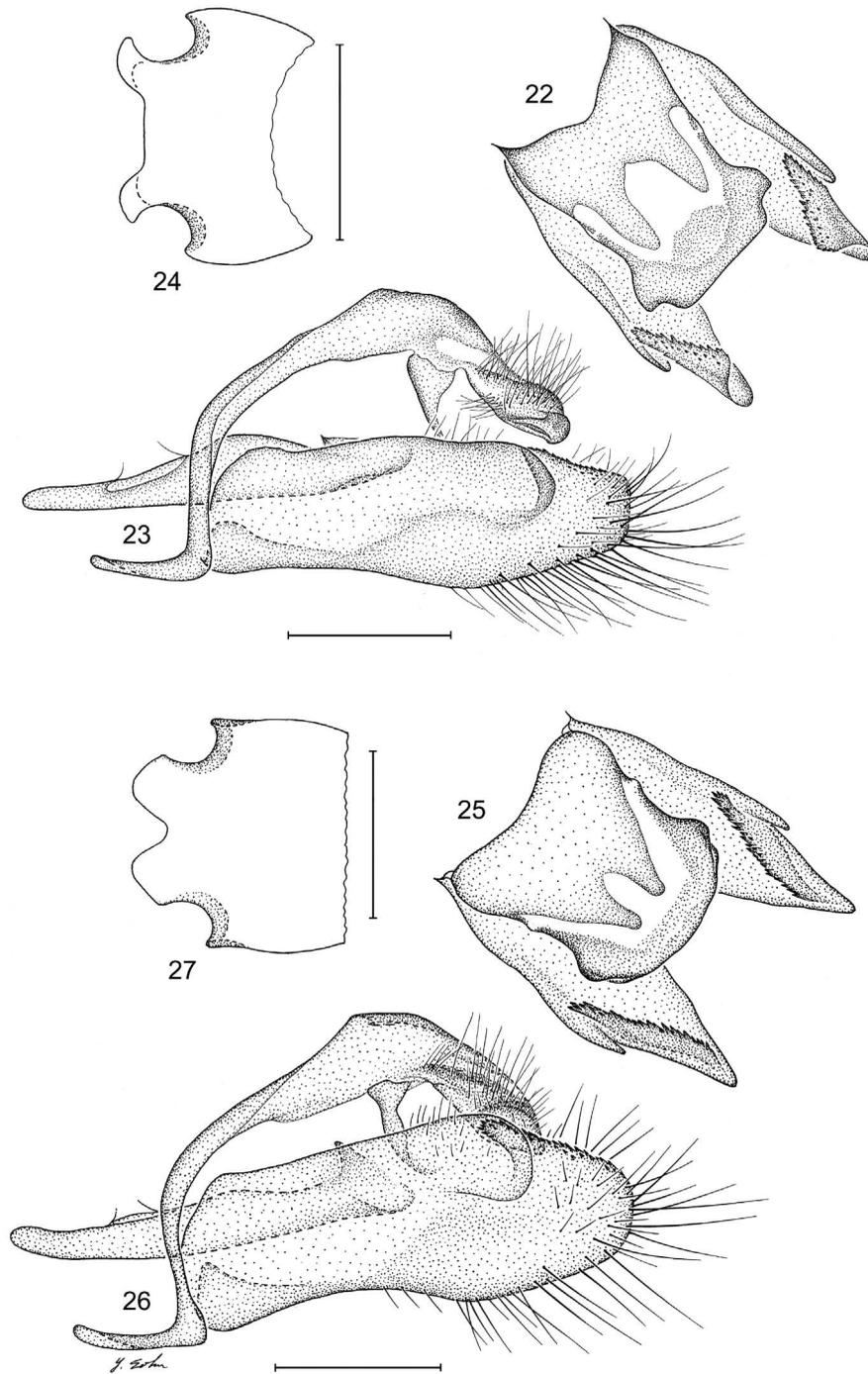
Though bizarre, much of the appearance of *T. arcalaus* (Figs. 1–4) relates to other species of *Thracides* (primarily to *T. phidon* [Figs. 5–8], which, itself, departs appreciably from its congeners). In *T. arcalaus*, the ventral ground color of both pairs of wings, although paler than in other species, is still reddish brown. The pale yellowish hyaline spots of the forewing are white spots in other species. On the ventral forewing, the bright yellow strip along the proximal half of the costa



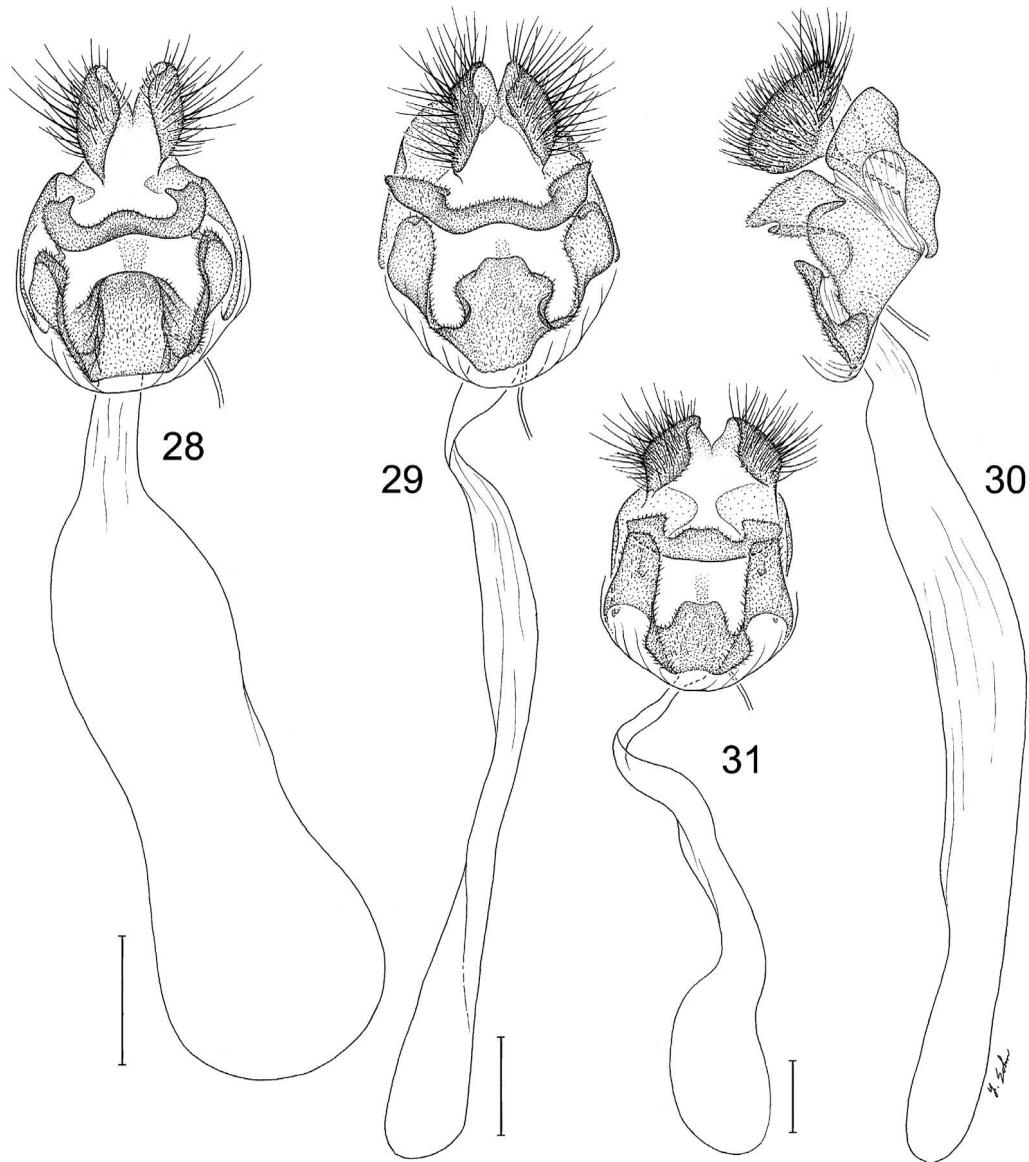
FIGS. 13–15. Stigma, centrally located on the dorsal forewing of the *Thracides* males in Figs. 1, 5, and 9. **13**, *T. arcalaus*, absent. **14**, *T. phidon*, vestigial. **15**, *T. chiricana*, well-developed.



FIGS. 16–21. Male genitalia of *Thracides arcalaus* (above), dissection X-5764, voucher 03-SRNP-8957, and *T. phidon* (below), dissection X-5541, voucher 00-SRNP-2027, from ACG, Costa Rica (specimens in USNM). **16, 19**, Tegumen, uncus, and valvae in dorsal view; scale = 1 mm. **17, 20**, Genitalia in left lateral view; scale = 1 mm. **18, 21**, Juxta in dorsal view; scale = 0.5 mm.



FIGS. 22–27. Male genitalia of *Thracides phidon* (above), dissection X-5546, voucher 00-SRNP-2549, and *T. chiricana* (below), dissection X-6669, voucher 05-SRNP-5087, from ACG, Costa Rica (specimens in USNM). **22, 25**, Tegumen, uncus, and valvae in dorsal view; scale = 1 mm. **23, 26**, Genitalia in left lateral view; scale = 1 mm. **24, 27**, Juxta in dorsal view; scale = 0.5 mm.



FIGS. 28–31. Female genitalia of *Thracides* (specimens in USNM); scale = 1 mm. **28**, *T. arcalaus*, ventral view; Colon (Sta. Rita), 1500 ft [457 m], Panama, 15 February 1991, leg. S. S. Nicolay; dissection X-5794. **29**, **30**, *T. phidon*, ventral and right lateral views; ACG, Costa Rica; dissection X-5544, voucher 00-SRNP-11721. **31**, *T. chiricana*, ventral view; ACG, Costa Rica; dissection X-6670, voucher 03-SRNP-20434.

corresponds to a white strip in *T. phidon*; and the wider, duller yellow patch at the distal end of the costa corresponds to a largely pale lilac patch in *T. phidon*. At the proximal end of this ventral forewing patch, small, yellow subapical spots in spaces 6, 7, 8, and 9 correspond to tiny bluish lilac spots usually visible in more or less unworn specimens of *T. phidon*. Dorsally, in *T. arcalaus*, these yellow subapical spots are conspicuous in spaces 6, 7, and 8 and may even become hyaline. Similarly, on both surfaces of the hindwing of *T. arcalaus*, yellow submarginal spots in spaces 2, 3, 4, 5, 6, and 7 correspond to pale greenish to bluish spots on the ventral hindwing of *T. phidon*, and to those of *T. cilissa* (Hewitson), as well. (In *T. arcalaus*, the spots in spaces 4 and 5 are tiny and not always present.) On the ventral hindwing of *T. arcalaus*, distal to these spots, light yellow overscaling (which is most evident in the upper part of space 1c and in spaces 2 and 3) corresponds to sparser overscaling in the same places in *T. phidon*.

Basically, many spots, much yellow, and the suppression of structural blue, plus a few unique features of the proximal ventral hindwing, are what superficially set *T. arcalaus* far apart from its congeners—that, and its obviously smaller size (Figs. 1–12).

**Stigma (Figs. 13–15).** In *Thracides*, this male secondary sex character of the dorsal forewing varies from all to nothing. When well-developed, as it is in *T. chiricana* (Figs. 9, 15), it is wide and tripartite, extending from near the middle of vein 1 to the origin of vein 3, with parts one and two together spanning space 1b and part three spanning the proximal part of space 2; there, part three runs mostly along the lower edge of the cubital vein; the bottom of part three is medially displaced, and therefore conspicuously offset from part two. The stigma is greatly and variably reduced in *T. phidon* (Figs. 5, 14), in which it is narrow and relatively straight instead of conspicuously staggered; the parts vary not only in length but also in presence (i.e., part two, and especially part three, may be missing; and part three, when present, is always so short that it never even approaches the cubitus). *Thracides arcalaus* (Figs. 1, 13) lacks a stigma.

#### GENITALIA (FIGS. 16–31)

Dissected genitalia that are free instead of mounted can be viewed from every angle, and they can be placed side by side and oriented in parallel. Their liberation is critical for comparing species, especially those with similar to virtually identical genitalia. So is an appreciation of individual variation. The genitalia of two males of *T. phidon* are illustrated (Figs. 19–24) in order to give some sense of intraspecific variation, which must

be taken into account in detecting real interspecific differences in morphology.

**Male genitalia (Figs. 16–27).** The general genitalic theme in *Thracides* involves (1) an uncus that is wide and, at its distal end, undivided; (2) a valva with (in lateral view) a long, low, roughly rectangular body whose dorsal half distally splits to form a distinctive, dorsally dentate division, situated in a slightly more mesial plane; (3) a juxta with a pair of short, rounded, anteriorly to anterolaterally directed lobes; and (4) a penis with a dorsodistal pair of more or less mammate titillators.

In dorsal view (Figs. 16, 19, 22, 25): (1) Where the tegumen joins the uncus is a mid-dorsal, membranous area with a strongly curved anterior margin; and flanking this area are sclerotized, posteriorly directed projections of the tegumen. In *T. arcalaus*, the membranous area is wider, leaving narrow tegumen projections that taper to a sharp point. This area is narrower, leaving wide, bluntly rounded projections in both *T. phidon* and *T. chiricana*; but it is narrower in *T. chiricana* than it is in *T. phidon*. (2) The distal end of the uncus is concave in *T. arcalaus*, more or less straight in *T. phidon*, and straight to convex in *T. chiricana*. (3) The distolateral lobes of the uncus are more protuberant in *T. arcalaus* and *T. phidon* than they are in *T. chiricana*, but are more evenly rounded in *T. arcalaus* and *T. chiricana* than they are in *T. phidon*. (4) The paired anterior lobes of the juxta (Figs. 18, 21, 24, 27) are relatively narrow and far apart in *T. phidon*, wider and closer together in *T. arcalaus*, and widest and closest in *T. chiricana*.

**Female genitalia (Figs. 28–31).** The lamellae antevaginalis and postvaginalis are the two major sclerotized elements. Those of ACG *Thracides* have the following aspect in ventral view: (1) A lamella antevaginalis that is peripherally U-shaped but, at the bottom of the U, expanded into a wide, robust, midventral piece (with a flared base) extending posteriorly, ventral to both the ostium bursae and a membranous area (resembling an inverted U) that joins the anterior edge of (2) a lamella postvaginalis that is about as wide as the lamella antevaginalis, but smaller, and shaped like a very low W, with a pair of small, short, medially pointing lobes at the top of the W.

In the middle of the membranous area that separates the two lamellae, some sclerotization runs from the ostium bursae to (or at least partway to) the lamella postvaginalis. The ductus bursae and corpus bursae are membranous. The connection of the ductus seminalis to the ductus bursae is as far posterior as possible, i.e., at about the level of the ostium bursae.

Obvious interspecific differences are in the shape of

the midventral sclerotized piece that extends posteriorly, beneath the ostium bursae, from the bottom of the U of the lamella antevaginalis. This piece is large and rectangular, with splayed sclerotized sides, in *T. arcalaus* (Fig. 28); large, with a pair of (variably expressed) lateral lobes in *T. phidon* (Fig. 29); and smaller, laterally tapered, and distally a bit concave (altogether suggesting a symmetric volcanic cone) in *T. chiricana* (Fig. 31). The paired, short, medially directed lobes at the top of the lamella postvaginalis W are well-developed in both *T. arcalaus* and *T. phidon* and are moderately developed in *T. chiricana*. (Note that the size and shape of these lobes—and of the W itself—vary with the angle of observation and with the degree to which the lamella postvaginalis is tilted. The lobes appear smaller in Figs. 29 and 31 than they really are.)

#### FOODPLANTS (TABLE 1)

In ACG, *T. phidon* caterpillars have been found feeding primarily on *Heliconia* (Heliconiaceae) and secondarily on an introduced species of *Musa* (Musaceae). (A single record of *T. phidon* on *Pleiostachya leiostachya* [Marantaceae] is suspect because the plant may be misdetermined.) Two of the

TABLE 1. Larval foodplants of three species of *Thracides* in Area de Conservación Guanacaste, northwestern Costa Rica, and number of rearing records for each species of plant.

|                                   |                                    |     |
|-----------------------------------|------------------------------------|-----|
| <b><i>Thracides arcalaus</i></b>  |                                    |     |
| Heliconiaceae                     |                                    |     |
|                                   | <i>Heliconia irrasa</i>            | 3   |
|                                   | <i>Heliconia latispatha</i>        | 2   |
| <b><i>Thracides phidon</i></b>    |                                    |     |
| Heliconiaceae                     |                                    |     |
|                                   | <i>Heliconia irrasa</i>            | 33  |
|                                   | <i>Heliconia latispatha</i>        | 644 |
|                                   | <i>Heliconia longa</i>             | 5   |
|                                   | <i>Heliconia longiflora</i>        | 3   |
|                                   | <i>Heliconia mathiasiae</i>        | 22  |
|                                   | <i>Heliconia metallica</i>         | 16  |
|                                   | <i>Heliconia pogonantha</i>        | 53  |
|                                   | <i>Heliconia tortuosa</i>          | 2   |
|                                   | <i>Heliconia umbrophila</i>        | 10  |
|                                   | <i>Heliconia vaginalis</i>         | 52  |
|                                   | <i>Heliconia wagneriana</i>        | 1   |
| Musaceae                          |                                    |     |
|                                   | <i>Musa acuminata</i> (introduced) | 102 |
| <b><i>Thracides chiricana</i></b> |                                    |     |
| Cyclanthaceae                     |                                    |     |
|                                   | <i>Asplundia microphylla</i>       | 16  |
|                                   | <i>Asplundia utilis</i>            | 20  |
|                                   | <i>Cyclanthus bipartitus</i>       | 5   |

five reared specimens of *T. arcalaus* ate *Heliconia latispatha*, which seems to be by far the most favored foodplant of *T. phidon*; and the other three specimens ate *H. irrasa*, which *T. phidon* also uses. The above plant families are closely related and are grouped in the order Zingiberales. On the other hand, caterpillars of *T. chiricana* have been found mostly on two species of *Asplundia* but also on *Cyclanthus* (both in the unrelated family Cyclanthaceae).

Foodplant selection is geographically conservative. In Pará, Brazil, Moss (1949) found caterpillars of *T. phidon* feeding “on Banana [*Musa*], *Heliconia*, and similar plants,” and of *T. nanea* (in a species complex that includes *T. chiricana*) on *Cyclanthus bipartitus*. In Trinidad, M. J. W. Cock “twice reared [*T. arcalaus*] from larvae collected on *Heliconia hirsuta*,” and F. J. Simmonds reared it once from *H. psittacorum* (Cock 2005).

This particular pattern of foodplant selection involving genera in both the Zingiberales and Cyclanthales is unique among the many lepidopteran species that have been reared to date in ACG (Janzen & Hallwachs 2008).

#### IMMATURES (FIGS. 32–37)

**Caterpillars (Figs. 32–35).** In frontal view, the light brown head of the last instar caterpillar of *T. phidon* presents five big, bold, black spots whose arrangement resembles that of the dots denoting five on dice. The central spot is on the frontoclypeus, and the peripheral spots are at roughly 2, 4, 8, and 10 o'clock. There may be an additional spot, generally less obvious than the others, at 12 o'clock. In frontal view, the head of the last instar caterpillar of *T. chiricana* is similar, but with an obvious sixth black spot at 12 o'clock and a tendency for the peripheral spots to connect to the central spot. Powdery white wax produced by *Thracides* caterpillars can mask the pattern on the head (but not the appearance of the body, which is already pale and almost patternless).

The caterpillar of *T. arcalaus*, which has rarely been found in ACG, must resemble that of *T. phidon* because the parataxonomists who have encountered it have called it *T. phidon* and therefore have seen no reason to take its picture and swell an ample photographic record of a common species.

The spot patterns in Moss's (1949: plate V, figs. 19, 20) frontal views of the heads of caterpillars of *T. phidon* and *T. nanea* from Pará, Brazil, recall those described and illustrated here (Figs. 32, 34). On the other hand, Cock's (2005: fig. 38) dorsolateral view and verbal description of a mature *T. arcalaus* caterpillar indicate a



FIGS. 32–37. Head (frontal view) and entire last-instar caterpillar, plus pupa (dorsal and left lateral views), of *Thracidus* from ACG, Costa Rica. **32, 33**, *T. phidon*, vouchers 01-SRNP-4824, 06-SRNP-21519. **34, 35**, *T. chiricana*, 03-SRNP-20435. **36, 37**, *T. phidon*, 01-SRNP-2400.

much reduced spot pattern (but, since the text also notes that the head is “entirely covered with white waxy powder,” some elements may possibly be obscured).

The arresting head patterns of *T. phidon* and, especially, *T. chiricana* approach the crisper, black on orange patterns of *Neoxeniades luda* (Hewitson) and *N. pluviasilva* Burns (Janzen & Hallwachs 2008) in what is probably the sister genus to *Thracides*.

**Pupa (Figs. 36, 37).** The most striking feature of the light green pupa of *T. phidon* is a single, conical, slender, elongate, pointed “horn” that projects straight

forward from the anterior end of the head. In lateral view (Fig. 37), the downward slope of the dorsal edge of the thorax and head continues into the horn at the same angle. The body of the pupa is long, narrow, and cylindrical, with a uniform diameter. Cock (2005) describes the “frontal spike” of *T. arcalaus* as “strongly curved upwards for distal half.”

In its general form, the pupa is similar to those of the closely related species *N. luda* and *N. pluviasilva* (whose green pupae are patterned, however, with a heavy dorsal and dorsolateral speckling of small brown spots) and to

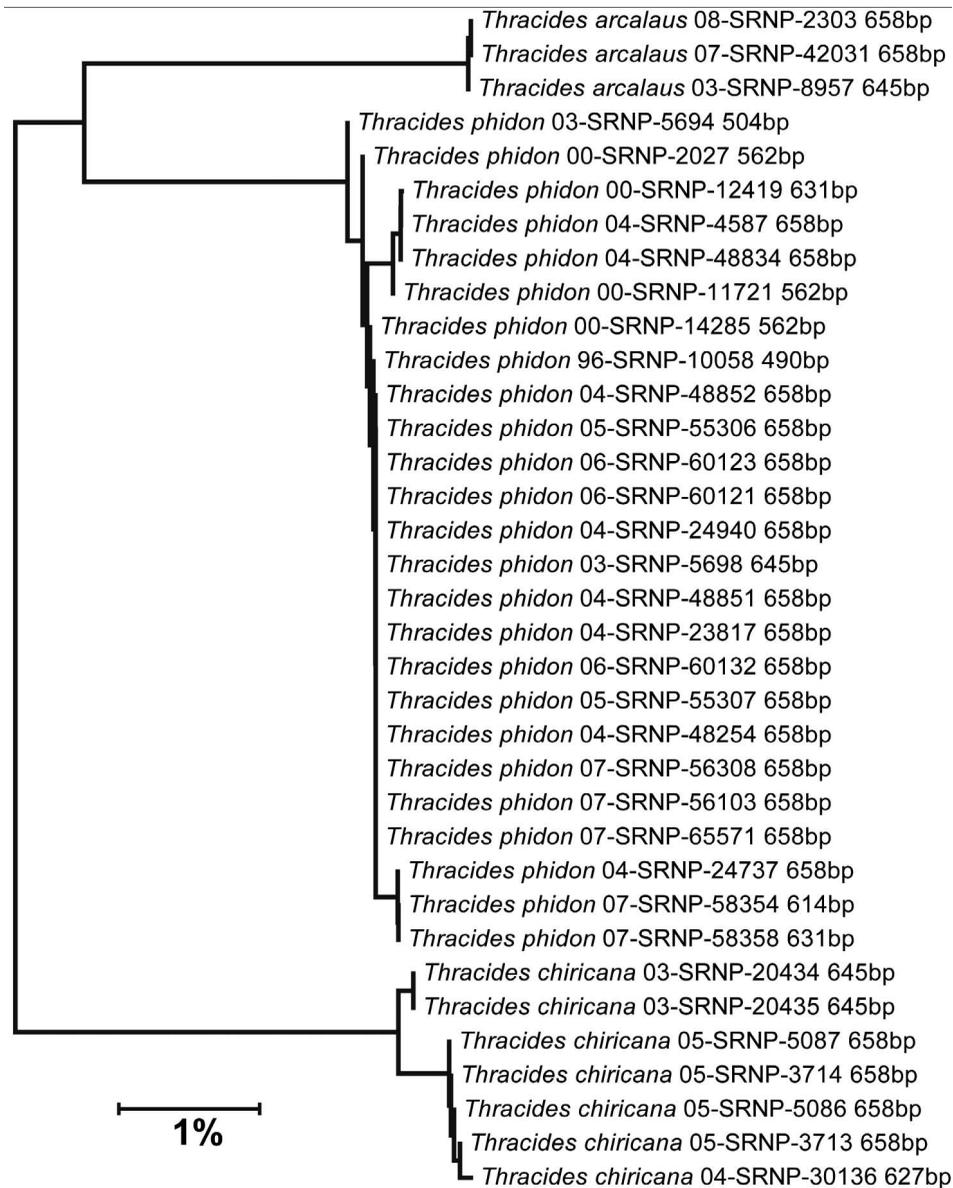


FIG. 38. Neighbor-joining tree based on Kimura two-parameter distances for COI DNA barcodes of three species of *Thracides* reared in ACG, Costa Rica. Species name, voucher code, and sequence length (i.e., number of base pairs, or bp) given for each individual.

those of species in more distantly related genera such as *Saliana*, *Calpodetes*, *Panoquina* (whose thorax is dorsally humped), and *Aroma* (whose horn, although conical, is basally broad, sharply upturned, and bright white; and whose thorax and anterior abdomen are each dorsally humped) (Janzen & Hallwachs 2008).

DNA BARCODES (FIG. 38)

Together, morphologic evidence and foodplant choice indicate that *T. arcalaus* is genetically closer to *T. phidon* than it is to *T. chiricana*; and a genomic fragment as limited as a barcode says the same thing (Fig. 38). The

TABLE 2. GenBank numbers for the individuals in Fig. 38. Numbers beginning with DQ were published in Hajibabaei *et al.* 2006; numbers beginning with FJ are new.

|               |          |
|---------------|----------|
| 03-SNRP-8957  | DQ293590 |
| 03-SNRP-20435 | DQ293593 |
| 03-SNRP-20434 | DQ293594 |
| 04-SNRP-30136 | DQ293595 |
| 03-SNRP-5694  | DQ293596 |
| 03-SNRP-5698  | DQ293597 |
| 00-SNRP-11721 | DQ293598 |
| 00-SNRP-12419 | DQ293599 |
| 00-SNRP-14285 | DQ293600 |
| 00-SNRP-2027  | DQ293601 |
| 96-SNRP-10058 | DQ293602 |
| 05-SNRP-3713  | FJ769051 |
| 05-SNRP-5086  | FJ769052 |
| 05-SNRP-3714  | FJ769053 |
| 05-SNRP-5087  | FJ769054 |
| 06-SNRP-60132 | FJ769055 |
| 06-SNRP-60121 | FJ769056 |
| 06-SNRP-60123 | FJ769057 |
| 05-SNRP-55307 | FJ769058 |
| 05-SNRP-55306 | FJ769059 |
| 04-SNRP-24737 | FJ769060 |
| 04-SNRP-48254 | FJ769061 |
| 04-SNRP-23817 | FJ769062 |
| 04-SNRP-48851 | FJ769063 |
| 04-SNRP-24940 | FJ769064 |
| 04-SNRP-48852 | FJ769065 |
| 04-SNRP-48834 | FJ769066 |
| 04-SNRP-4587  | FJ769067 |
| 07-SNRP-58358 | FJ769068 |
| 07-SNRP-58354 | FJ769069 |
| 07-SNRP-65571 | FJ769070 |
| 07-SNRP-56103 | FJ769071 |
| 07-SNRP-56308 | FJ769072 |
| 08-SNRP-2303  | FJ788099 |
| 07-SNRP-42031 | FJ788100 |

agreement of data as different and independent as these makes a convincing case for the relationship. This is not to say that additional information from DNA sequences of certain nuclear genes is irrelevant, but only that, for some taxonomic purposes, the cheap, fast, short barcode may be all the molecular data required.

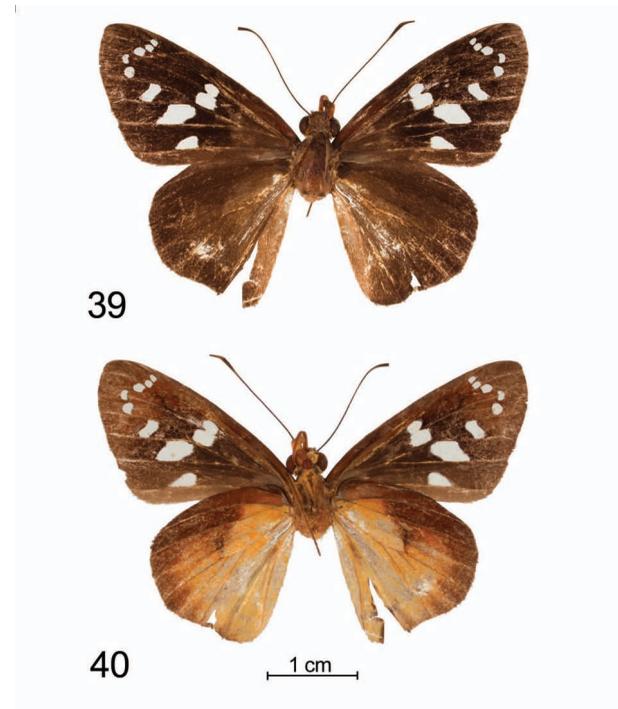
GenBank numbers for all barcoded specimens appear in Table 2.

GEOGRAPHIC DISTRIBUTION

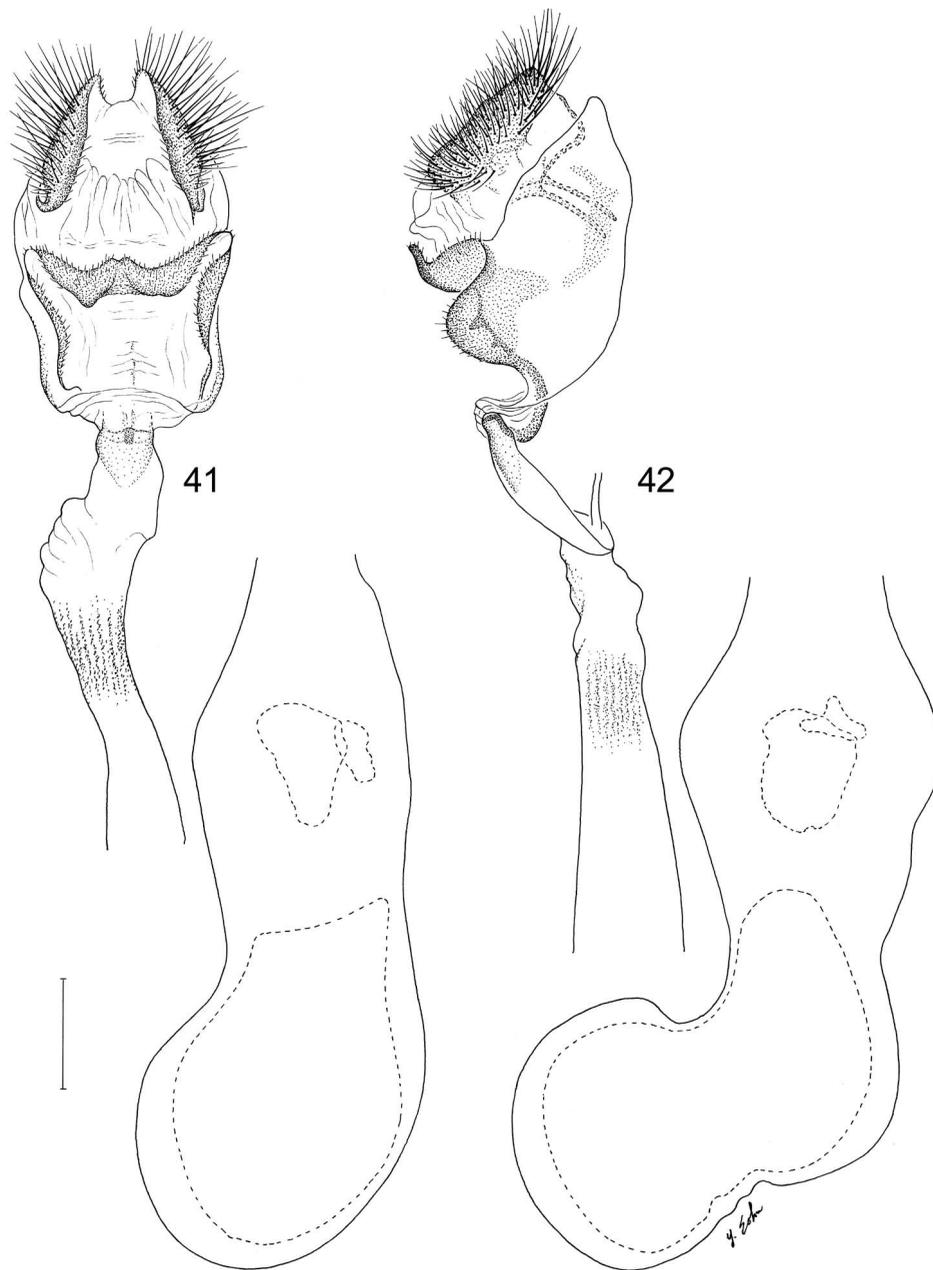
*Thracides* is a panneotropic genus ranging from Mexico to Bolivia, Paraguay, northeastern Argentina, and southern Brazil. Both *T. phidon* and *T. arcalaus* are widespread, spanning all but the southmost extent of the generic range. Each of these taxa probably consists of more than one biologic species. *Thracides chiricana* is rare in collections and of limited and uncertain distribution (known from Costa Rica and Panama). It is the northern taxon in the *nanea* species complex, which is mainly South American (known from Colombia, eastern Peru, and Brazil) (see Names).

PYREX POSTSCRIPT (FIGS. 39–42)

The following illustrations and observations are provided both to warrant the exclusion of *pyrex* from *Thracides* and to aid future efforts in placing this



FIGS. 39, 40. Adult female of *pyrex*. "IX-XI-1992 100 km L [= east of] / PUERTO MALDONADO / PERU. Tello leg.," Mielke collection (Burns genitalia dissection X-6392). **39**, Dorsal view. **40**, Ventral view.



FIGS. 41, 42. Female genitalia (dissection X-6392) of mated *pyrex* in Figs. 39, 40. Long bursa copulatrix shown in two parts; persistent spermatophore(s) indicated; scale = 1 mm. **41**, Ventral view. **42**, Right lateral view.

skipper to genus. The wings of *pyrex* (Figs. 39, 40) are rounder than are those of *Thracides*, and the forewing does not extend as far beyond the hindwing as it does in *Thracides*. In *Thracides* the club of the antenna swells gradually, but conspicuously, and then decreases slightly in thickness before turning sharply backward into a long, delicate apiculus. The nudum segments are somewhat evenly divided between the club and the apiculus (e.g., 7/10 in *T. arcalaus*, 8/10 to 8/11 in *T.*

*phidon*, 8/10 to 9/13 in *T. chiricana*, and 8/10 to 9/12 in the remaining species of *Thracides*). In the lone specimen of *pyrex*, the less damaged antennal club (which lacks one or more terminal segments) is slender throughout, the apiculus is not sharply reflexed, and the nudum (comprising 12+ segments) is entirely on the apiculus.

Genitalia can be just as useful in removing misfits from a polyphyletic genus as they are in bringing truly

congeneric species together. Compare the mostly membranous female genitalia of *pyrex* (Figs. 41, 42) with the much more sclerotized female genitalia of *Thracides* (Figs. 28–31). In *pyrex*, the lamella antevaginalis is anteroventrally membranous and laterally sclerotized in a pair of small plates. As in *Thracides*, the sclerotized lamella postvaginalis is narrow and transverse, spanning the width of the genitalia; but its posterior edge, in *pyrex*, is shaped like a bracket whose posteriorly directed, midventral point is slightly notched. The beginning of the ductus bursae is lightly sclerotized ventrally and ventrolaterally. The connection of the ductus seminalis to the ductus bursae is conspicuously anterior to the ostium bursae. The outer edge of an ovipositor lobe, in lateral view, is straight instead of curved; and the entire structure looks more rectangular than elliptical.

Differences in the shape of the corpus bursae are irrelevant. The corpus bursae is collapsed in reared females (Figs. 29–31) because they are virgin. In wild-caught females (Figs. 28, 41, 42), the corpus bursae is distended because those females have mated and received one or more spermatophores—parts of which persist in the figured *pyrex* female (Figs. 41, 42), despite KOH-dissection.

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