

JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

Volume 50

1996

Number 3

Journal of the Lepidopterists' Society
50(3), 1996, 173–216

GENITALIA AND THE PROPER GENUS: *CODATRACTUS* GETS *MYSIE* AND *UVYDIXA*—IN A COMPACT *CYDA* GROUP—AS WELL AS A *HYSTERECTOMY*, WHILE *CEPHISE* GETS PART OF *POLYTHRIX* (HESPERIIDAE: PYRGINAE)

JOHN M. BURNS

Department of Entomology, National Museum of Natural History, Smithsonian
Institution, Washington, D.C. 20560, USA

ABSTRACT. Many features of genitalic morphology show that Evans's monotypic, neotropical genus *Cephise* contains not only additional tailless species but also several species with long hindwing tails currently misplaced in the unrelated genus *Polythrix*: *Cephise auginulus* (Godman & Salvin), **new combination**, *Cephise callias* (Mabille), **new combination**, and *Cephise guatemalaensis* (Freeman), **new combination**. (Even with their removal, *Polythrix* is still polyphyletic.) There are major problems with the names of various tailed and tailless species of *Cephise*. All species of *Cephise* express a remarkable character state of the palpus (males more fully than females) in which scales at the distal end of the first segment turn sharply outward across the ventral edge of the eye. In Guanacaste, Costa Rica, larvae of both a tailless species (***Cephise nuspesez*, new species**) and a tailed species (*C. auginulus*) eat the same plants: 4 species in the Malpighiaceae and 1 in the Combretaceae. Both tailed and tailless species are widespread, collectively ranging from San Luis Potosí, Mexico, to Bolivia, Paraguay, northern Argentina, and Brazil.

Again, features of genitalic morphology serve in extracting species from disparate genera (*Thorybes*, *Cogia*) (and from synonymy) and uniting them with *Codatractus cyda* (Godman) in a compact species group. Like *cyda*, the added species—*Codatractus mysie* (Dyar), **new combination**, and *Codatractus uvydixa* (Dyar), **new combination**—are tailless; but some species of *Codatractus* are prominently tailed. The three species of the *cyda* group closely replace one another geographically, from southeastern Arizona to northwestern Honduras; their distribution strongly reflects allopatric speciation and reinforces their taxonomic union. In superficial appearance, the geographically intermediate (strictly Mexican) species, *uvydixa*, resembles the southeastern *cyda* in Chiapas, Puebla, and Guerrero, but the northwestern *mysie* in Colima, Jalisco, and Sinaloa. Although all three species are genitalicly extremely close, they differ markedly in size (*mysie*, smallest; *uvydixa*, largest); and *mysie* differs completely from *uvydixa* and *cyda* in the number of segments in the nudum of the antenna—an unusual evolutionary development for closely related species.

Removed from *Codatractus* on morphologic (and also behavioral) grounds, *hyster* (Dyar) is temporarily a species **incertae sedis**.

Additional key words: allopatric speciation, Combretaceae, Malpighiaceae, New World, palpus.

Species in the wrong genus can mask, warp, or wreck potential insights. It takes properly delimited groups to make valid evolutionary patterns.

Closely related species often replace one another geographically. This evolutionary pattern has been so thoroughly documented that now, when species thought to be closely related on morphologic grounds turn out to be closely allopatric, the distribution can be viewed as independent evidence for their close relationship. I adopt such a semicircular view later in this paper.

Congeneric species tend to have essentially similar copulatory parts. Again, this evolutionary pattern has been sufficiently well supported that one can fairly reverse it by pulling genitally similar species together and saying they are related.

With a primary interest in nearctic skippers, I have lately been emphasizing genitalic morphology in changing the limits of many much-used, much-studied, long-stable, and supposedly well-defined genera (Burns 1987, 1989, 1990, 1992, 1994a, 1994b). My revisions have variously involved generic lumping, generic splitting, and especially the shifting of species from one genus to another (or to temporary limbo, when they screamed for release without telling me where they should go). I have pursued the genera in question throughout their geographic ranges, which has usually led from the nearctic to the neotropics (but occasionally to the palearctic). Though the genera treated so far (*Hesperia*, *Atalopedes*, *Polites* [incorporating both *Poanopsis* and *Yvretta*], *Atrytone*, *Anatrytone* [assuming its own identity], *Paratrytone*, *Poanes*, *Ochlodes*, *Quasimellana* [superseding *Mellana*], and *Amblyscirtes*) are all hesperiine, hesperiines have no monopoly on the taxonomic mess.

The pyrgine genus *Codattractus* (which enters the United States in southern Texas, New Mexico, and Arizona, and extends to northern Argentina) first intrigued me because it included both prominently tailed (e.g., Figs. 89, 90) and totally tailless (e.g., Figs. 85–88) species. Morphologic comparison of these species, with particular attention to genitalia, shows that all but one really do belong in a single genus. It follows that striking differences in wingshape can evolve with relative ease.

Variations on the tailed-and-tailless pattern appear in other pyrgine genera such as *Thessia*, which Steinhauser (1989) proposed for two species (with peculiar, and notably similar, male and female genitalia) that Evans (1952) stuck in *Urbanus* and *Achalarus*: *Thessia athesis* (Hewitson) has hindwings with short but definite tails whereas *T. jalapus* (Plötz) has hindwings with slight lobes. *Thessia* ranges from the United States (southern Texas) to Colombia and Venezuela, plus Tobago (Evans 1952).

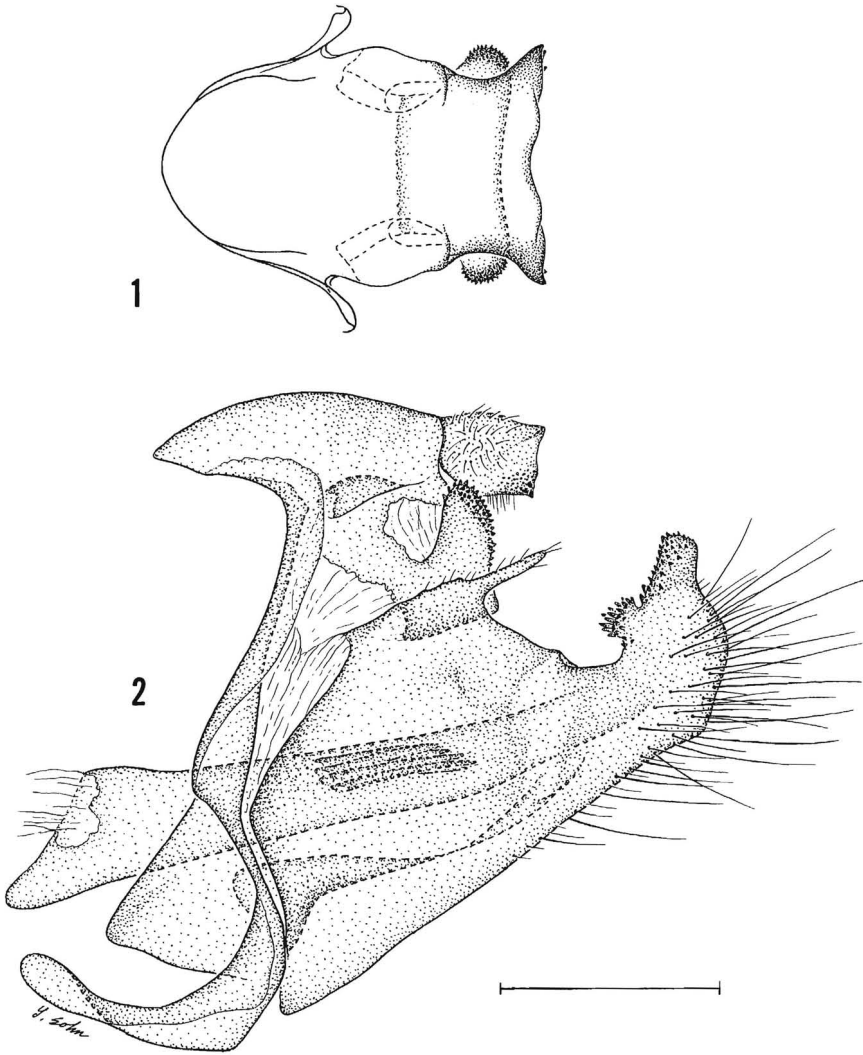
As currently constituted, the genus *Typhedanus* includes five species with long hindwing tails and six without (Evans 1952, Freeman 1977, Mielke 1979). *Typhedanus* ranges from the United States (southern Texas) to central Argentina (Hayward 1948).

CEPHISE

The genus *Cephise* embraces species with long hindwing tails as well as species with strong hindwing lobes (Figs. 28–51)—but not as currently constituted. Evans (1952:136, 153) proposed *Cephise* (in his *Celaenorrhinus* group of genera, with the admonition “systematic position . . . doubtful”) for what he considered the single species *cephise* (Herrich-Schäffer), comprising two genitally differentiated subspecies, *cephise* and *hydarnes* (Mabille); and he listed several synonyms under these names. In reality, Evans’s *Cephise* is a complex of species, ranging from at least as far north as San Luis Potosí, Mexico (Freeman 1970), to Peru, Paraguay, and Misiones, Argentina (Hayward 1948), with hindwings that are “strongly lobed at [the] tornus” (Evans 1952:136).

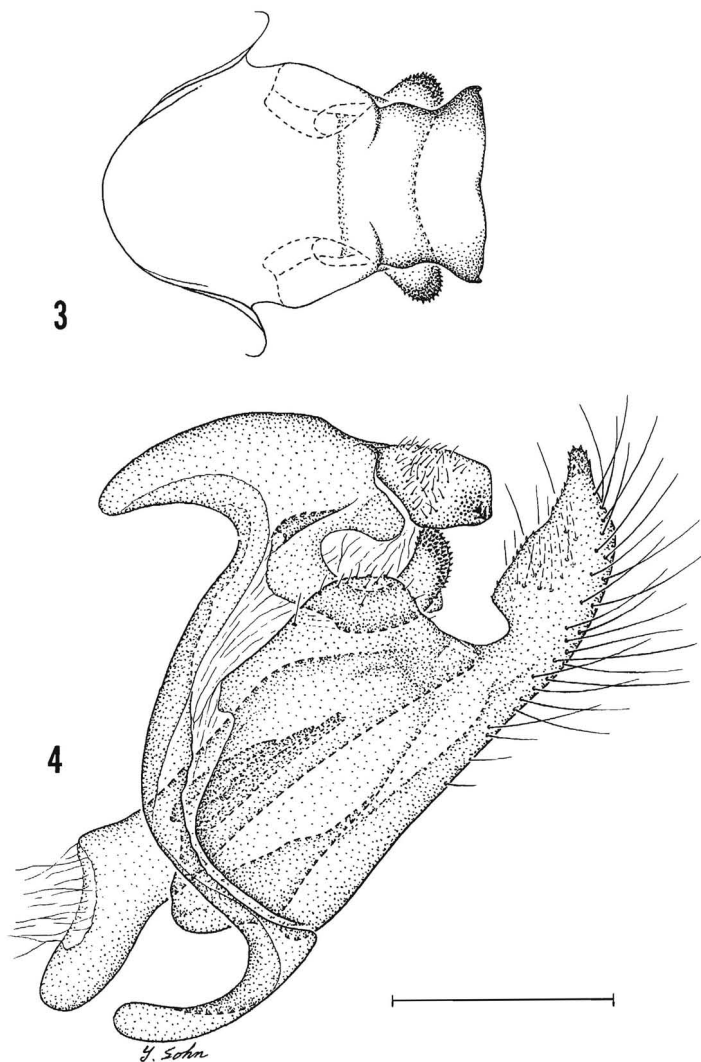
Evans (1952:67) called *Polythrix* “a compact genus in respect of general appearance, characterised by the spot in space 3 of the forewing being approximate to the central spots and the apical spots being in a straight line. Hindwing elongate with a long tail.” But appearances can be deceiving. Like other genera in his *Urbanus* group (and elsewhere), *Polythrix* is polyphyletic, partly because two of the thirteen species Evans included are long-tailed species of *Cephise*: *Cephise auginulus* (Godman & Salvin), **new combination** (Figs. 40–43) (see next paragraph), and *Cephise callias* (Mabille), **new combination**. A *Polythrix* later described by Freeman (1977) is yet another tailed *Cephise*: *Cephise guatemalaensis* (Freeman), **new combination** (Figs. 48–51). (However, *Polythrix kanshul* Shuey, recently described from southern Mexico and central Panama, is a true *Polythrix* because [a] Shuey [1991] showed, with genitalic characters, that *kanshul* forms a monophyletic lineage with *P. metallescens* [Mabille] as well as *P. eudoxus* [Stoll] and [b] *metallescens* is the type of *Polythrix*.) Like their tailless counterparts, the tailed species of *Cephise* collectively span most of the neotropics from San Luis Potosí and Veracruz, Mexico, to at least Brazil (Plötz 1881) and Bolivia (Evans 1952).

I am resurrecting the name *auginulus*, which Evans (1952:70) listed with *aelius* Plötz and *callicina* Schaus as synonyms of *Polythrix procerus* (Plötz), because I doubt that *auginulus* and *procerus* are the same. Although the precise identity of *procerus* eludes me, that of *auginulus* does not: Godman and Salvin (1893), in describing *auginulus* from two males from Mexico (Veracruz) and Guatemala (type locality), provided a good figure of the genitalia (vol. 3, pl. 75, fig. 22), along with color figures of the dorsal and ventral surfaces of the whole animal. Godman (1907) stated, after examining Plötz’s unpublished color figures of American skipper species, that neither *procerus* nor *aelius* (each described by



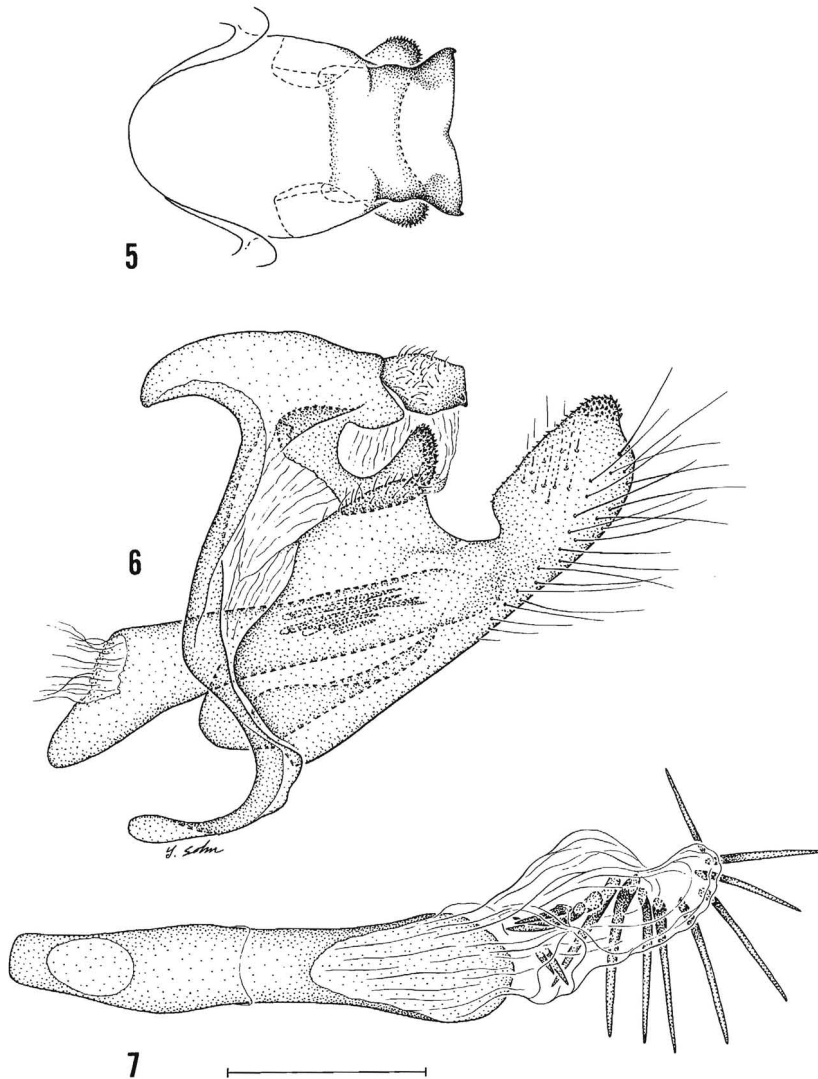
FIGS. 1, 2. Male genitalia of *Cephise hydarnes* (sensu Hayward 1948 and Evans 1952) from PARAGUAY (J. M. Burns genitalic dissection no. X-1400) (USNM). Scale=1.0 mm. **1**, Tegumen, uncus, and gnathos in dorsal view. **2**, Complete genitalia (minus right valva, which is not entirely symmetrical with the left valva), with vesica retracted and cornuti bundled, in left lateral view.

Plötz from Pará) was in the Godman and Salvin collection. In other words, these Brazilian skippers did not look to Godman exactly like his Mexican/Guatemalan *auginulus*. From my perusal of the original descriptions of *procerus* and *aelius* (Plötz 1881), I suspect that these skip-

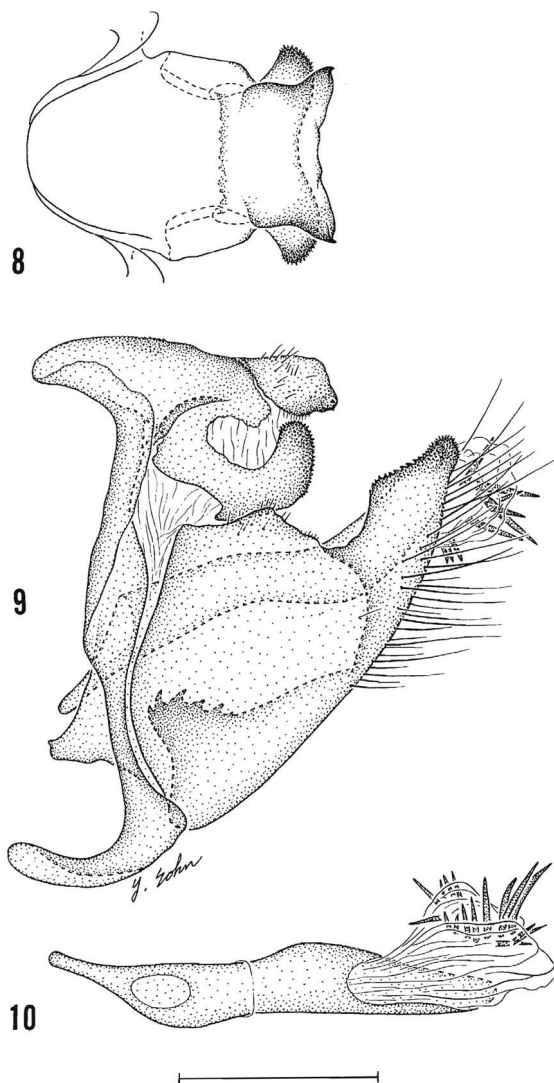


FIGS. 3, 4. Male genitalia of *Cephise orima* (holotype of *Nascus orima* Schaus) from Petrópolis, BRAZIL (X-1401) (USNM). Scale=1.0 mm. **3**, Tegumen, uncus, and gnathos in dorsal view. **4**, Complete genitalia (minus right valva), with vesica retracted and cornuti bundled, in left lateral view.

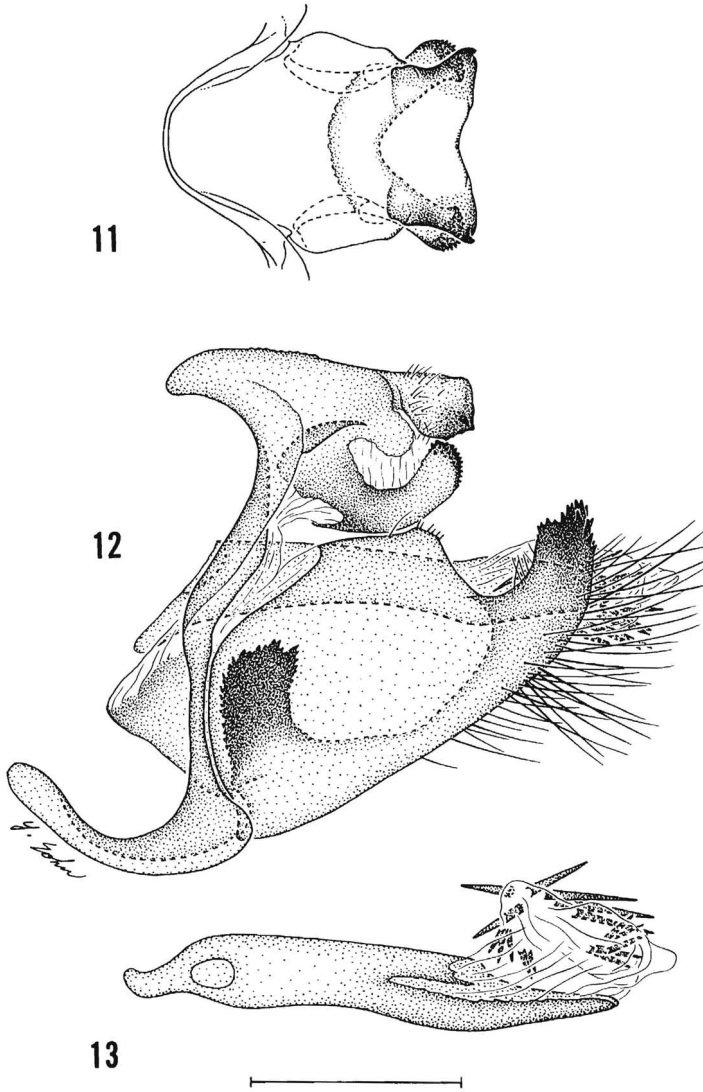
pers differ not only from *auginulus* but also from each other. For years I have mistrusted Evans's synonymies. Now, having clearly shown (Burns 1994b) that the four synonyms listed by Evans (1955) under *Mellana clavus* Erichson are four separate species (in two different species groups) of *Anatrytone* and that *clavus* itself is a species of *Wallengrenia*,



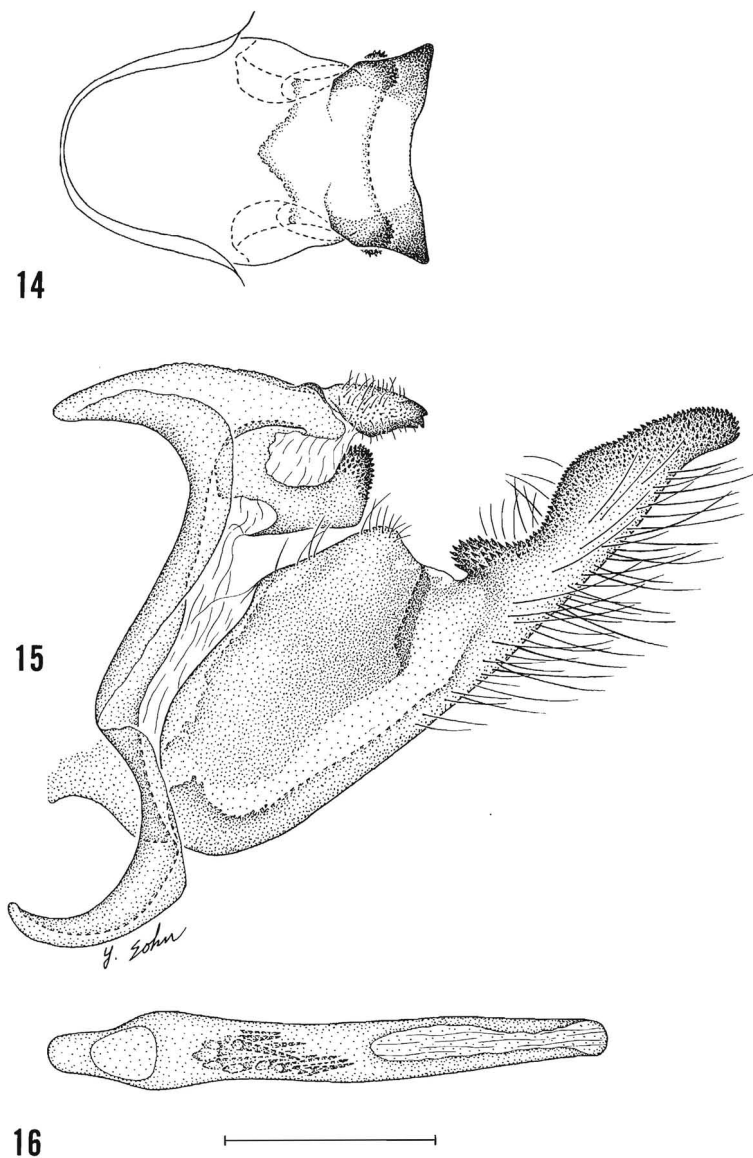
FIGS. 5-7. Male genitalia of *Cephise nuspesez* from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (USNM). Scale=1.0 mm. **5**, Tegumen, uncus, and gnathos in dorsal view (holotype, Santa Rosa Sector, rearing voucher 81-SRNP-646, dissection X-1345). **6**, Complete genitalia (minus right valva), with vesica retracted and cornuti bundled, in left lateral view (holotype, Santa Rosa Sector, rearing voucher 81-SRNP-646, dissection X-1345). **7**, Aedeagus, with vesica everted and cornuti splayed, in dorsal view (paratype, Guanacaste Sector, rearing voucher 91-SRNP-2079, dissection X-3735).



FIGS. 8–10. Male genitalia of *Cephise auginulus* from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 92-SRNP-3959, dissection X-3828) (USNM). Scale=1.0 mm. **8**, Tegumen, uncus, and gnathos in dorsal view. **9**, Complete genitalia (minus right valva), with vesica everted and cornuti splayed, in left lateral view. **10**, Aedeagus, with vesica everted and cornuti splayed, in dorsal view.



FIGS. 11–13. Male genitalia of *Cephise* nr. *callias* from Saül, 200–450 m, 3°37' N, 53°43' W, FRENCH GUIANA, 16 November 1993, D. J. Harvey (X-3900) (USNM). Scale=1.0 mm. **11**, Tegumen, uncus, and gnathos in dorsal view. **12**, Complete genitalia (minus right valva), with vesica everted and cornuti splayed, in left lateral view. **13**, Aedeagus, with vesica everted and cornuti splayed, in dorsal view.



FIGS. 14–16. Male genitalia of *Cephise guatemalaensis* (holotype of *Polythrix guatemalaensis* Freeman) from Sayaxché, Petén, GUATEMALA, 23 August 1963, E. C. Welling (Freeman genitalic dissection no. H-674) (AMNH). Scale=1.0 mm. **14**, Tegumen, uncus, and gnathos in dorsal view (split in uncus plus adjacent tegumen, and torn perimeter of tegumen, repaired). **15**, Genitalia (minus right valva, aedeagus, and portions of juxta) in left lateral view. (Repair includes reassembly and additions to the missing, inner, anteroventral corner of the left valva working from what remains in the corresponding position on the right valva [which may not be everything as it, too, is damaged].) **16**, Aedeagus, with vesica retracted and cornuti bundled, in dorsal view.

I am more skeptical than ever. I have examined the holotype of *Eudamus callicina* which Schaus (1902:425) described from a lone female from Honduras, with the comment "closely allied to *E. callias* Mabille." His comment is correct since *callicina* (Figs. 38, 39) is the same as *auginulus* (Figs. 40–43)—and a junior synonym of it.

The genitalia of *Cephise* exhibit a basic pattern in each sex. Most notable in males is the truncate uncus, with two or three small teeth at each posterolateral corner (Figs. 1–6, 8, 9, 11, 12, 14, 15). On either side of the uncus, the underlying, undivided gnathos sends up a thumb-shaped projection that is densely and finely dentate distally and posteriorly (Figs. 1–6, 8, 9, 11, 12, 14, 15). Because the many, tiny, close-set gnathosteeth are both conical and short, they create a nubbly surface. At rest within the aedeagus, the cornuti suggest a bundle of spines (Figs. 2, 4, 6, 16); but when the vesica everts, the cornuti dissociate in a stunning burst of spines (Figs. 7, 10, 13). In lateral view, the valva presents a large proximal end, followed by a more or less **U**-shaped notch and a ventrodorsal extension that is finely to coarsely dentate dorsally and distally (Figs. 2, 4, 6, 9, 12, 15). The anteroventral, innermost edge of the valva extends more or less broadly and bluntly dorsad (Figs. 2, 4, 6, 9, 12, 15).

In females, heavy sclerotization around the ostium bursae and the caudalmost part of the ductus bursae is essentially **Y**-shaped in ventral view (Figs. 17, 18, 20–22). Arising from the sides of the sterigma and flanking the **Y** are paired, heavily sclerotized, ventromedially directed, and more or less serrate to pointed plates, which usually look wicked (Figs. 17–22). The top of the **Y** forms a funneling entryway, while the stem of the **Y** constitutes the beginning of the ductus bursae proper. Here the ductus bursae is midventral in position and narrow in diameter; the sclerotization (i.e., the stem of the **Y**) is limited, abruptly switching to membrane; and even the short, sclerotized **Y**-stem is unsclerotized in a dorsal, longitudinal strip (Figs. 17–22). Anteriad, the membranous ductus bursae angles at least slightly to the left and increases at least slightly in diameter (Figs. 17, 18, 20–22); and (with one known exception) a sizable, well-sclerotized piece wraps around it without completely encircling it (Figs. 17–21). (In the maverick species, the sclerotization, though still sizable, is light [Fig. 22]; and it is divided longitudinally into two separate, flanking strips instead of the single wrap-around.) The corpus bursae is wholly membranous.

Immediately dorsad of the entire sterigma is a single, distinctive sac with an elaborately crinkled surface somewhat like that of the longer, paired sacs extending anteriad of the sterigma in females of such genera as *Proteides*, *Aguna*, *Codatractus*, *Urbanus*, *Astraptus*, *Calliades*, *Autochton*, *Thessia*, *Achalarus*, *Thorybes*, and *Cabares*. The anterior apophyses are rudimentary or absent while the posterior apophyses are

short, delicate, and, in lateral view, bowed ventrad (Fig. 19). On the paired ovipositor lobes, setae near the midventral line are shorter, sparser, and more delicate than peripheral setae, which are not only longer, denser, and more robust, but also directed outward and backward (Fig. 17), imparting a sort of saintly radiance in an aedeagal-eye view. No major setae are directed inward, toward each other, from the inner, ventral edges of the ovipositor lobes as they often are in *Urbanus* group females (Fig. 23).

The preceding generic characterization is distilled from genitalic dissections of 23 males in 7 species and 17 females in 6 species.

As you would predict, the skippers sharing this genitalic pattern have more than that in common. The palpi of *Cephise* are remarkable. At the distal end of the first segment, some of the scales that tightly clothe the palpus turn sharply outward across the ventral edge of the eye. Magnified, and seen from below, this projection of scales resembles a shelf nearly perpendicular to the body of the palpus (Figs. 24, 26); from in front, it looks like a triangle beneath the eye (Figs. 25, 27), often conspicuous because the exposed inner sides of the turned out scales tend to be paler than the outer sides of most other visible palpal scales (Fig. 27). Dark hairs always extend beyond the pale, turned out, shingle-like scales and usually curve ventrad (Figs. 24–27). Males express this peculiar projection of palpal scales more fully than do females. In either sex, it is more obvious in reared than in wild-caught specimens, owing to the wear and tear of skipper living.

Males of *Cephise* have a well-developed costal fold (Figs. 28, 32, 34, 40, 44, 48). They also have wonderfully furry metathoracic legs with wide rows of long hairs: down the femur, one row of less dense, paler hairs that tend to curl at the tips; and down the tibia, two rows of denser, darker hairs that tend to stay straight. These are not the same as the metatibial tufts of many and various pyrgine skippers.

The total number of nudum segments in *Cephise* ranges from 21 to 26 (usually 23, 24, or 25), with only 4 to 6 (usually 5 or 6) of the segments on the basal part of the antennal club before the apiculus (Table 1). The apiculus is about as long as, and decidedly more slender than, the basal part of the club and is sharply reflexed. Because—as in so many skippers—it is often not entirely clear where the basal part ends and the bent back apiculus begins, a line of demarcation between them (à la nudum counts of Evans) is somewhat arbitrary. I counted nudum segments in 100 specimens.

Instead of the monotypic genus that Evans (1952) envisioned, *Cephise* is a polytypic genus that may ultimately include as many as a dozen species, rather evenly divided between tailed and tailless. As I indicated in resurrecting *auginulus* for one of the tailed species, it is hard

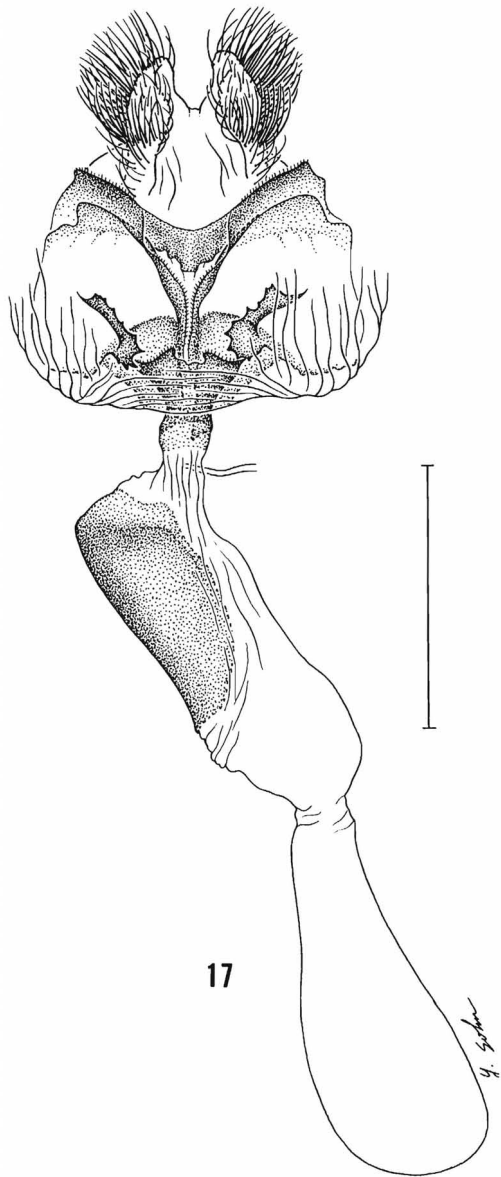
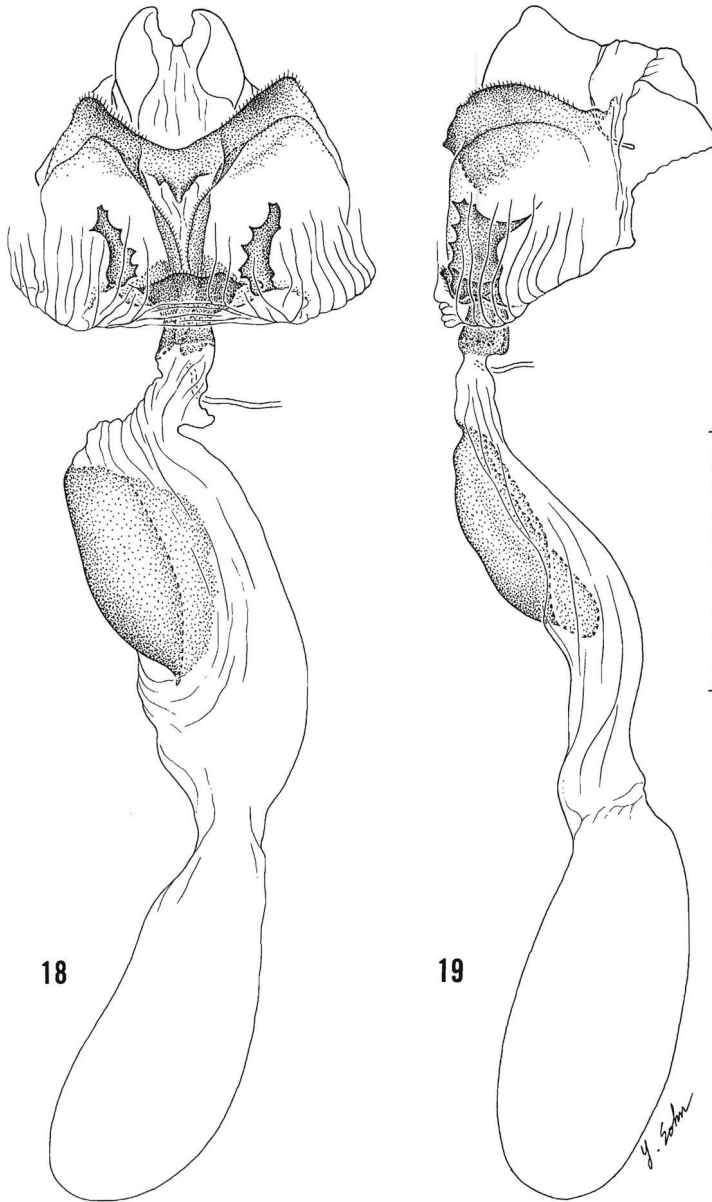
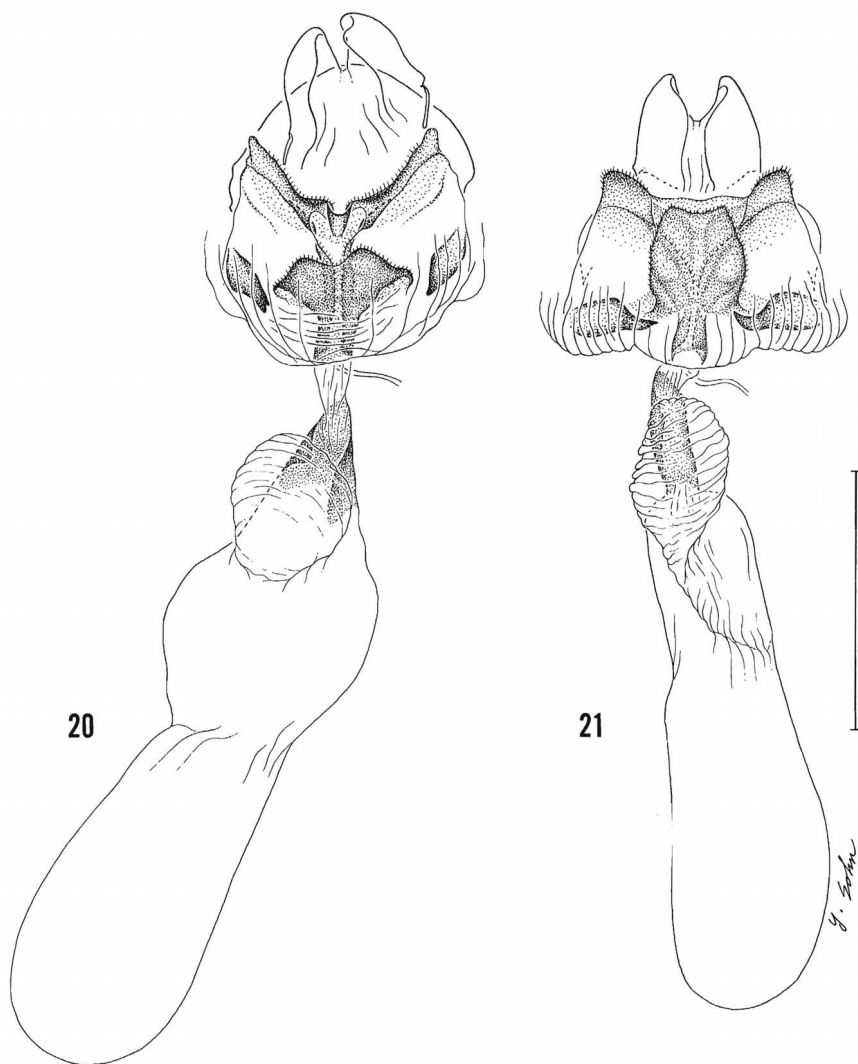


FIG. 17. Female genitalia of *Cephise orita* (holotype of *Nascus orita* Schaus) supposedly from PERU but probably from BOLIVIA (X-3885) (USNM). Ovipositor lobes (with an indication of their setae), sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. Scale=2.0 mm.



FIGS. 18, 19. Female genitalia of *Cephise nuspesez* (paratype) from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 93-SRNP-6334, dissection X-3745) (USNM). Scale=2.0 mm. **18**, Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. **19**, The same, plus posterior apophysis and an indication of a terminal abdominal tergite, in right lateral view.



FIGS. 20, 21. Female genitalia of two species of *Cephise*. Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. Scale=2.0 mm. **20**, *Cephise auginulus* (holotype of *Eudamus callicina* Schaus) from HONDURAS (X-3884) (USNM). **21**, *Cephise* nr. *callias* from Paraiso, Canal Zone, PANAMA, 19 June 1978, G. B. Small Jr. (X-3886) (USNM).

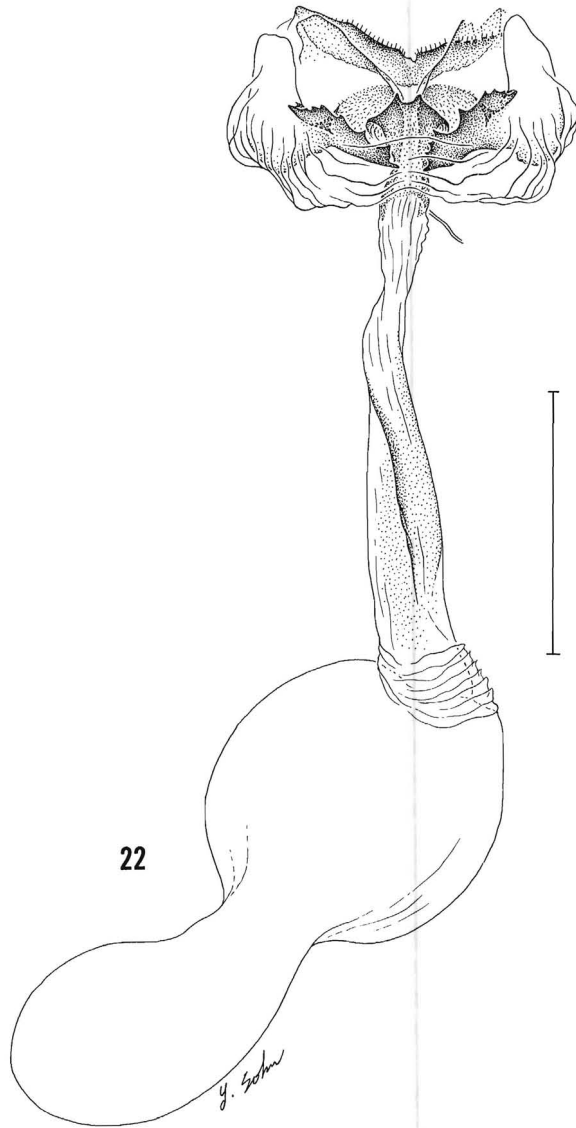


FIG. 22. Female genitalia of *Cephise guatemalaensis* (allotype of *Polythrix guatemalaensis* Freeman) from X-Can, Quintana Roo, MEXICO, 26 July 1962, E. C. Welling (X-3901) (AMNH). Sterigma, bursa copulatrix, and part of ductus seminalis in ventral view. Scale=2.0 mm. Development of posterior margin of sterigma a bit abnormal, with dorsal layer slightly atrophied, and ventral layer somewhat hypertrophied, on right side. Distalmost extension of hypertrophied right ventral layer, and both ovipositor lobes, not shown because damaged.

TABLE 1. Frequency of antennal nudum variants in species of *Cephise*.

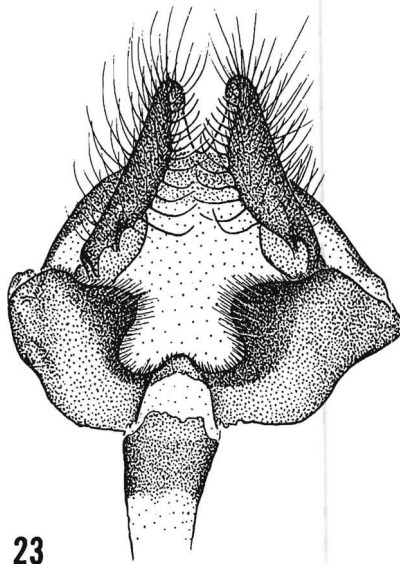
Species	Mean	Number of nudum segments						N
		21	22	23	24	25	26	
<i>C. nuspesez</i>	24.6	—	1	3	15	26	6	51
<i>C. auginulus</i>	23.5	1	7	12	13	6	2	41
<i>C. guatemalaensis</i>	23.5	—	—	1	1	—	—	2
<i>C. nr. callias</i>	24.0	—	—	—	2	—	—	2
<i>C. orima</i>	23.5	—	—	1	1	—	—	2
<i>C. hydarnes</i>	23.5	—	—	1	1	—	—	2

to assign names from a heap of seeming synonyms. Evans (1952:154) recognized a single, wide-ranging, tailless (lobed) species with the two subspecies *cephise* and *hydarnes*, which, from his own caricatures (Evans 1952:pl. 23, D.6), are genitally too divergent to be anything but separate species (a point made by Freeman 1970). Evans gave three synonyms—*zopyrus* Plötz (1881), described from a female from Surinam; *glarus* Mabille (1888), described from a male from the lower Amazon; and *orita* Schaus (1902), described from a female from Peru—for *cephise* Herrich-Schäffer (1869), which was described from a male from no one knows where. And he gave two synonyms—*maneros* Mabille (1888), described from a female from Brazil; and *orima* Schaus (1902), described from a male from Petrópolis, Brazil—for *hydarnes* Mabille (1876), which was described from a female from eastern Brazil. There is no guarantee that these really are synonyms or even that the names *cephise* and *hydarnes* are correctly applied. I know from close examination of Schaus's type, on the one hand, and Evans's text and genitalia figures, on the other, that, contrary to Evans, *orima* is not a synonym of *hydarnes*—at least not of *hydarnes* sensu Evans. Compare the male genitalia of the type of *orima* Schaus (Figs. 3, 4) with those of *hydarnes* in the sense of Evans (1952) and also of Hayward (1948) before him (Figs. 1, 2)—and keep in mind that the lone specimen from which Mabille (1876) described *hydarnes* was female instead of male. The taxonomic stew thickens because *Cephise* is geographically widespread and rare in collections, which makes it harder to detect sibling species and to associate sexes correctly.

Although I lack the material for general treatment of species, my unique handle on *Cephise* is a pair of long, cumulative series of reared specimens from one locality (Guanacaste Conservation Area) in northwestern Costa Rica: 17♂ 11♀ of the tailed *C. auginulus* and 39♂ 30♀ of a new tailless species, *C. nuspesez*. Besides their great utility for assessing sexual dimorphism and individual variation, these series point to a critical evolutionary pattern in *Cephise*: the larvae of both species eat plants in the two families Malpighiaceae and Combretaceae. *Cephise auginu-*

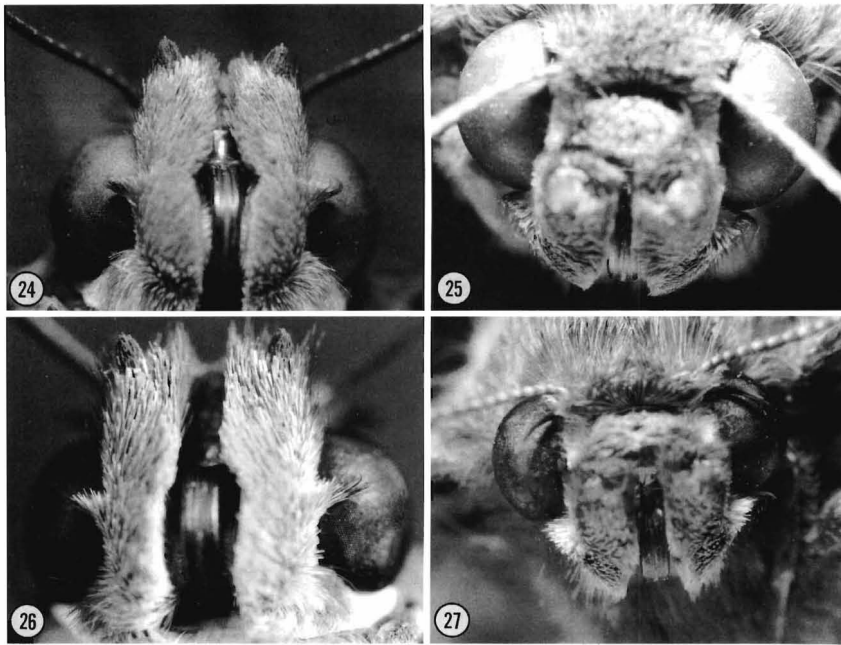
TABLE 2. Larval foodplants of two species of *Cephus* in the Guanacaste Conservation Area of northwestern Costa Rica (Janzen & Burns, unpubl. data). Numbers show males and females reared from each plant species between 1981 and 1995.

	<i>C. mispesei</i> (tailless)		<i>C. auginulus</i> (tailed)	
	♂	♀	♂	♀
COMBRETACEAE				
<i>Combretum farinosum</i> H.B.K.	1	1	7	4
ERYTHROXYLACEAE				
<i>Erythroxylum havanense</i> Jacq.	—	—	—	1
MALPIGHIACEAE				
<i>Banisteriopsis muricata</i> (Cav.) Cuatrec.	1	1	3	3
<i>Heteropteris laurifolia</i> A. Juss.	2	1	1	—
<i>Heteropteris obovata</i> (Small) Cuatrec. & Croat	25	20	1	1
<i>Hiraea reclinata</i> Jacq.	2	2	2	1
<i>Mascagnia polycarpa</i> T. S. Brandegees	8	5	—	—
RUBIACEAE				
<i>Calycophyllum candidissimum</i> (Vahl) DC.	—	—	2	1
	<u>39</u>	<u>30</u>	<u>16</u>	<u>11</u>



23

FIG. 23. Beginning of ductus bursae, sterigma, and especially the ovipositor lobes of female *Autochthon cellus* (Boisduval & Le Conte), in ventral view, to show major setae directed inward, toward each other, from inner, ventral edges of those lobes, as usual for *Urbanus* group females. Specimen from Hda. Montecristo, Cerro Miramundo, 2300 m, Metapán, EL SALVADOR, 21 May 1972, S. & L. Steinhauser (J. M. Burns 1378) (AME).



FIGS. 24–27. Distinctive prominent scaling (beneath eyes) at distal ends of first palpal segments in reared males of *Cephise* from the Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (USNM), in ventral (left) and anterior (right) views. **24, 25**, *Cephise nuspesez* (a tailless species), rearing voucher 94-SRNP-7535. **26, 27**, *Cephise auginulus* (a tailed species), rearing voucher 93-SRNP-5721.

lus is more catholic because it also eats plants in two other families (Erythroxylaceae and Rubiaceae) for a total of seven known species of food-plants; but, significantly, it eats five of the six plants that *Cephise nuspesez* eats (Table 2).

At this point I have fulfilled my primary purpose of expanding the genus *Cephise* conceptually and redefining it. However, in the course of conveying a modified generic gestalt, I have illustrated not only the reared tailless and tailed species that I have in series but also various odd specimens at hand—especially all three relevant Schaus types (USNM), and their genitalia, in order to promote correct application of specific names in the future. For now, I can do no more with species than describe the new one and offer various comparative comments.

The male of the new species from Costa Rica superficially looks like the type of *Cephise orima* from Petrópolis, Brazil, and is genitally so close to it that in 1982, when I had only one Costa Rican specimen, I could not exclude the possibility that their slight genitalic differences

stemmed from individual variation. Much later, in a series of Costa Rican males, the differences held, indicating separate species.

Cephise nuspesez, new species

(Figs. 5–7, 18, 19, 28–31)

Male genitalia (Figs. 5–7). Differences between *nuspesez* and most other figured species of *Cephise* (Figs. 1, 2, 8–16) extensive and obvious, but differences between *nuspesez* and *orima* (Figs. 3, 4) limited (chiefly to valva) and relatively subtle: in lateral view, valva of *nuspesez* (Fig. 6) neither as high proximally nor as attenuate (and twisted) distally as that of *orima* (Fig. 4), and dorsodistal corner of proximal section of valva, in *nuspesez*, with short, backward projection (long and slender in *hydarnes* [Fig. 2]) not present in *orima*.

Female genitalia (Figs. 18, 19). Most like those of *orita* (Fig. 17); but, in *nuspesez*, medial edges of paired, heavily sclerotized, ventromedially directed, sterigmal plates flanking **Y** more nearly parallel to midventral line in ventral view, and sclerotized roof of flared part of **Y** more restricted, extending less far caudad.

Facies (Figs. 28–31). As in other tailless (lobed) species of *Cephise*, strong sexual dimorphism in forewing hyaline spots: pale yellow in male, white in female. (In tailed species such dimorphism ranges from slightly less pronounced [*guatemalaensis*] to unapparent [*auginulus*].) Band-and-spots pattern of ventral hindwing weak (Figs. 29, 31) as in other tailless species (Figs. 33, 35, 37) plus *auginulus* (Figs. 39, 41, 43), not strong as in the tailed *callias*, nr. *callias* (Figs. 45, 47), and *guatemalaensis* (Figs. 49, 51). Narrow white fringe on outer margin of hindwing checkered (Figs. 28–31) as in other tailless species (Figs. 34–37) and, to lesser degree, *guatemalaensis* (Figs. 50, 51), instead of unchecked as in remaining tailed species (Figs. 38–43, 46, 47). Pale outer edging (in space 1c) to dark band of ventral hindwing weak (Fig. 29) to nonexistent (Fig. 31), rather than strong as in *orita* (Fig. 37).

Size. Close to that of other species of *Cephise*, with females averaging 1 mm more than males in forewing length: mean forewing length in males 21.3 mm, range 19.6–22.9 mm, n 34; in females, mean 22.3 mm, range 20.8–24.0 mm, n 24. (Measurements perhaps a bit below those of wild-caught adults, on average; but artificial rearing time highly variable, depending on instar of larva when found [which varied from first to last].)

Nudum (Table 1). Mean number of nudum segments 24.6 (range 22–26, n 51); on average, one segment more than in *auginulus*.

Types. *Holotype*: COSTA RICA, GUANACASTE PROVINCE, Guanacaste Conservation Area, Santa Rosa Sector (10°51'N, 85°37'W), D. H. Janzen & W. Hallwachs, rearing voucher 81-SRNP-646, ♂, Genitalia No. X-1345 J. M. Burns 1981; deposited in National Museum of Natural History, Smithsonian Institution (USNM). *Paratypes*: 38♂ 30♀, COSTA RICA, GUANACASTE PROVINCE, Guanacaste Conservation Area, dry forest, rain forest, and transitional, D. H. Janzen & W. Hallwachs, rearing vouchers between 1989 and 1995; deposited in USNM and in Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica. 1♀, COSTA RICA, GUANACASTE PROVINCE, Comelco, 8 km N Bagaces, 50 m, 18 January 1974, P. A. Opler; in collection of C. D. MacNeill.

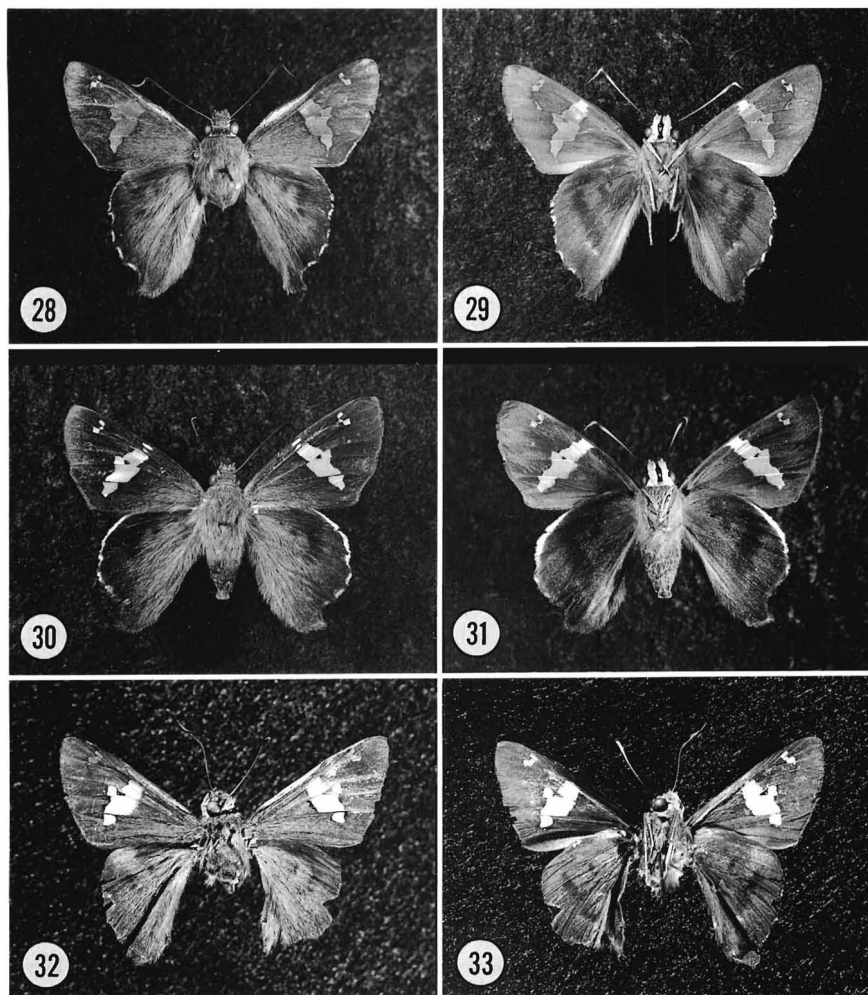
I have seen 2♂ 1♀ *Cephise* from 6 mi (ca. 10 km) S Ciudad Valles, SAN LUIS POTOSI, MEXICO, June 1969, H. A. Freeman, in the American Museum of Natural History, New York, which I suspect may be *nuspesez*; but not having seen their genitalia, I cannot be sure.

Etymology. The name of this new species is a noun in apposition which phonetically says that this species is new. The combination *Cephise nuspesez* is deliberately euphonious.

Peculiarities of some species of *Cephise*

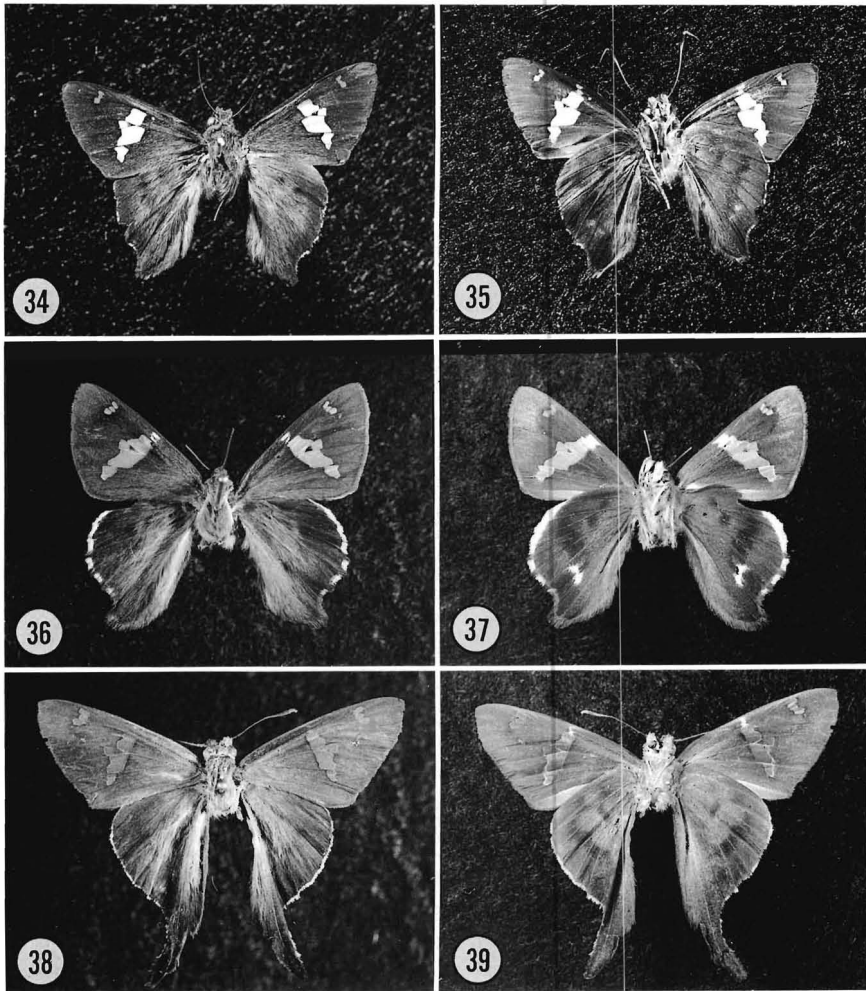
Judging from Evans (1952:pl. 23, fig. D.6.*cephise*), the valva of *Cephise cephise* is about like that of *orima* and *nuspesez* except for a long, slender, backward projection, from the dorsodistal corner of its proximal section, as in *hydarnes* (Fig. 2; Evans 1952:pl. 23, fig. D.6.*hydarnes*).

I refer to one of the tailed species of *Cephise* as “near *callias*” for the



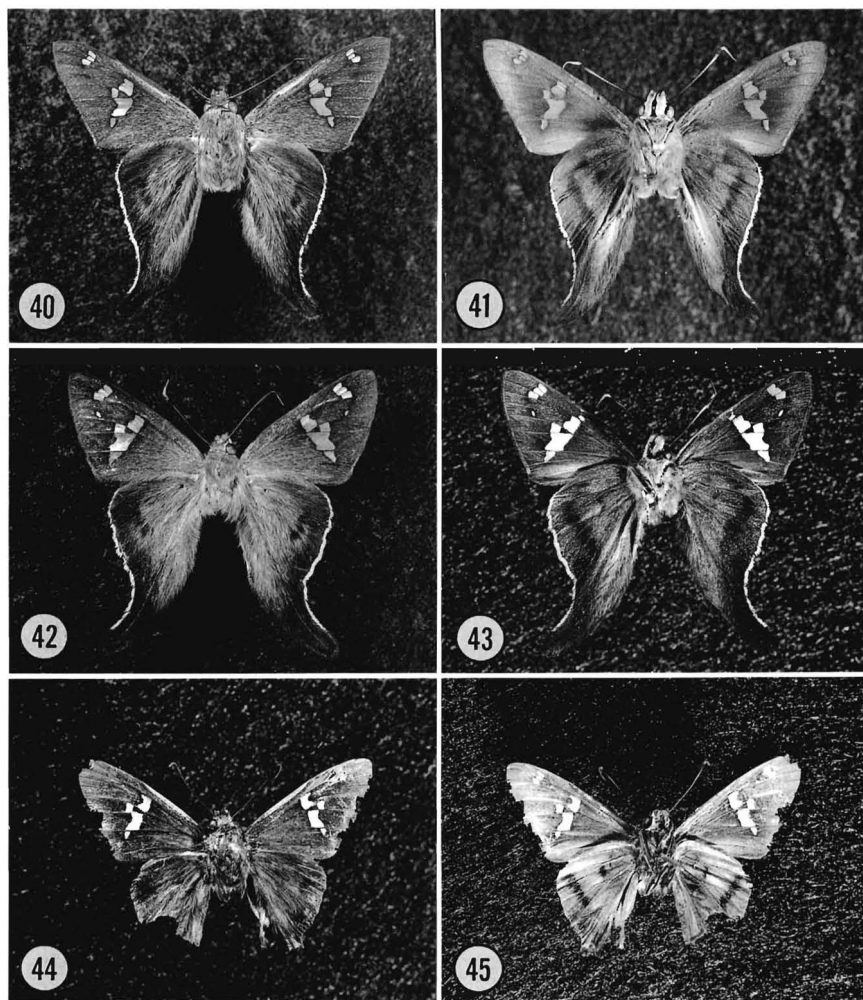
FIGS. 28–33. Adults of *Cephise* in dorsal (left) and ventral (right) views (all $\times 1$, USNM). **28, 29**, *C. nuspesez* δ , holotype, Santa Rosa Sector, Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 81-SRNP-646, dissection X-1345). **30, 31**, *C. nuspesez* f , paratype, Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 94-SRNP-7524). **32, 33**, *C. hydarnes* δ , PARAGUAY (X-1400).

following reasons. Both the brief original description of *callias*, with a black and white figure (Mabille 1888), and a fuller, subsequent description, with a much better color figure (Mabille & Vuillot 1891), mention and show a bold distal spot in space 7 of the ventral hindwing as well as a bold proximal spot in the same space. The bold distal spot is missing



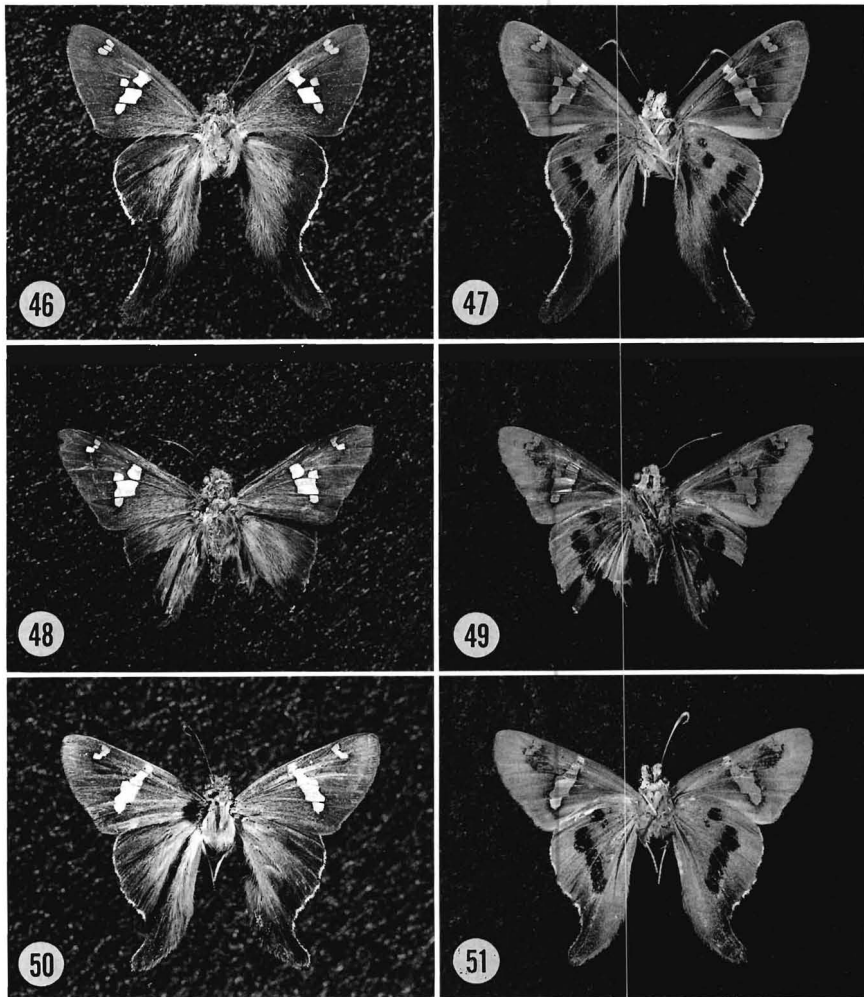
FIGS. 34–39. Holotypes of species of *Cephise* described by Schaus in dorsal (left) and ventral (right) views (all $\times 1$, USNM). 34, 35, *C. orima* ♂, Petrópolis, BRAZIL (X-1401). 36, 37, *C. orita* ♀, supposedly from PERU but probably from BOLIVIA (X-3885). 38, 39, *C. callicina* (= *auginulus*) ♀, HONDURAS (X-3884).

not only from my lone male (Fig. 45) whose genitalia (Figs. 11–13) approximate Evans's (1952:pl. 15, fig. C.7.6) caricature of *callias* genitalia but also from the lone female (Fig. 47) that I tentatively associate with this male. These specimens come, respectively, from French Guiana and Panama, to either side of Porto Cabello, Venezuela, the source of the lone female from which *callias* was described (Mabille & Vuillot 1891).



FIGS. 40–45. Adults of *Cephise* in dorsal (left) and ventral (right) views (all $\times 1$, USNM). 40, 41, *C. auginulus* δ , Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 93-SRNP-3800, dissection X-3801). 42, 43, *C. auginulus* δ , Guanacaste Conservation Area, Guanacaste, COSTA RICA, D. H. Janzen & W. Hallwachs (rearing voucher 93-SRNP-3647, dissection X-3881). 44, 45, *C. nr. callias* δ , Saül, 200–450 m, 3°37' N, 53°43' W, FRENCH GUIANA, 16 November 1993, D. J. Harvey (X-3900).

Although the spot difference may involve individual variation, the male and female in question may represent a *callias* sibling. Evans's lone specimen from which he figured the male genitalia of what he considered *callias*, came from Bolivia (Evans 1952). Since it is already clear



FIGS. 46–51. Adults of *Cephise* in dorsal (left) and ventral (right) views (all $\times 1$). **46**, **47**, *C. nr. callias* ♀, Paraíso, Canal Zone, PANAMA, 19 June 1978, G. B. Small Jr. (X-3886) (USNM). **48**, **49**, *C. guatemalaensis* ♂, holotype, Sayaxché, Petén, GUATEMALA, 23 August 1963, E. C. Welling (Freeman genitalic dissection no. H-674) (AMNH). **50**, **51**, *C. guatemalaensis* ♀, allotype, X-Can, Quintana Roo, MEXICO, 26 July 1962, E. C. Welling (X-3901) (AMNH).

that genitalia can be closely similar in separate species of *Cephise*, far more specimens are needed.

The dorsal extension of the anteroventral, innermost edge of the valva is hypertrophied and dentate (in different ways) in the tailed species *auginulus* (Fig. 9; Godman & Salvin 1893, pl. 75, fig. 22) and *nr. callias*

(Fig. 12). (This may also be true of *guatemalaensis* [Fig. 15], but damage in the genitalic dissection of the only known male precludes judgment.) The juxta is visibly enlarged anteriorly in the tailed species *auginulus* (Fig. 9), nr. *callias* (Fig. 12), and perhaps *guatemalaensis* (Fig. 15)—though here again, damage in the critical region makes it hard to interpret. However, the juxta is hugely enlarged anteriorly in the tailless *hydarnes* (Fig. 2).

The distal end of the valva is the most strikingly variable feature across all figured species (Figs. 2, 4, 6, 9, 12, 15). The dentate, distal ends of the valvae are conspicuously asymmetric in *hydarnes*, with the right valva longer than the left. The distal end of the uncus is extra wide in *hydarnes* (Fig. 1) and in *guatemalaensis* (Fig. 14). The anterior end of the aedeagus is exceptionally long and narrow, and usually is curved downward and bent slightly to the right, in *auginulus* (Figs. 9, 10).

The ductus bursae exhibits three major variations: one in the tailless *orita* (Fig. 17) and *nuspesez* (Figs. 18, 19), a second in the tailed *auginulus* (Fig. 20) and nr. *callias* (Fig. 21), and a third—the most outré—in the tailed *guatemalaensis* (Fig. 22). The paired, heavily sclerotized, sterigmal plates flanking the **Y** are more elaborate in the tailless *orita* (Fig. 17) and *nuspesez* (Figs. 18, 19), and especially in the tailed *guatemalaensis* (Fig. 22), than they are in the tailed *auginulus* (Fig. 20) and nr. *callias*, which is the simplest of all (Fig. 21). On the other hand, nr. *callias* has a unique, large, midventral, caudally projecting plate developed from the floor of the **Y** (Fig. 21). A small, narrow, rounded, midventral ridge, which distinctly notches the posterior margin of the lamella postvaginalis midventrally, is unique to *auginulus* (Fig. 20).

Judging from the female (Figs. 50, 51) because they are completely broken off of the male (Figs. 48, 49), the hindwing tails of *guatemalaensis* are significantly shorter than those of the other tailed species (Figs. 38–47). The female of *guatemalaensis* (Figs. 50, 51) is the only specimen of *Cephise* I have seen (out of 135 examined) that lacks a small, dark, more or less triangular bit of ground color between the small hyaline spot in space 3 and the large hyaline spots in space 2 and the cell of the forewing (Figs. 28–49). Since this is the sole known female of *guatemalaensis*, I cannot say whether such variation in the hyaline band is individual or meaningful.

The morphology of *Cephise* indicates a genus that is highly distinct but also internally complex with a long evolutionary history.

THE *CYDA* GROUP OF *CODATRACTUS*

Although the species *cyda* Godman has been in *Codatractus* from the beginning, when Lindsey (1921) proposed this name to replace *Heteropia* Mabille (a junior homonym), the other two species now joining

cyda to form a distinctive, compact group of tailless *Codatractus* have never been near this genus. Both *Codatractus mysie* (Dyar), **new combination**, and *Codatractus uvydixa* (Dyar), **new combination**, were originally described in *Thorybes* early in this century (Dyar 1904, 1914); and since then they have had a nomenclatural history more checkered than the fringes of their wings (Figs. 79–84).

This is particularly true of *mysie* which, because it was described from the “Patagonia Mountains, Arizona,” became part of the U.S. fauna and had to be treated repeatedly, whether it was known or not. It was placed in *Eudamus* (*Phaedinus*) [sic] by Skinner (1911), in *Phoedinus* by Lindsey (1921) and Lindsey et al. (1931), in *Cogia* (*Phoedinus*) by Skinner & Williams (1922), in *Caicella* (a Hemming replacement name) by Bell (1938), Hoffmann (1941), and Tilden (1949), and was argued back to *Phoedinus* by Tilden (1975), where he left it (Tilden & Smith 1986). Meanwhile, Evans (1952) listed both *mysie* and *uvyidixa* (which was described from the “Sierra de Guerrero, Mexico”) as synonyms of *Thorybes valeriana* (Plötz), though he added that *uvyidixa* was “Possibly a sub-species.” Thereafter, Miller (1970), MacNeill (1975), Miller and Brown (1981), and Scott (1986) all dealt with *mysie* as *Thorybes valeriana*. On the other hand, Llorente-Bousquets, Luis-Martínez, and Vargas-Fernández (1990) listed *mysie* and *uvyidixa* as species of *Thorybes* separate from *Thorybes valeriana*. Ferris (1989), following both Tilden’s (1949) argument for the validity of *mysie* as a species and Evans’s (1953) placement of *Phoedinus* as a junior synonym of *Cogia*, put *mysie* in *Cogia*. As a result, *mysie* still goes by totally different names in contemporary butterfly books: *Cogia mysie* according to Bailowitz and Brock (1991:43) who, however, “strongly feel that *mysie* is sufficiently distinct in phenotype and behavior to warrant placement in its own genus”; and *Thorybes valeriana* according to Brown et al. (1992).

The name *valeriana* cannot apply to *mysie* or *uvyidixa*. At the British Museum of Natural History I closely studied Plötz’s unpublished color painting of his *Eudamus valeriana*, and have directly compared an excellent color photograph of it with many specimens of *Codatractus*, including *mysie* and *uvyidixa*. Besides serious discrepancies in color pattern, each antenna of the painted skipper has a club with a long and only moderately swollen body that abruptly dwindles to a very short, delicate, and sharply reflexed apiculus. All species of *Codatractus*, including all three species of the *cyda* group, have an unusual antennal club: it is basally stout and apically tapered but evenly arcuate throughout its length—nothing is sharply reflexed, and it is impossible to distinguish an apiculus (Figs. 79–90).

Characterization of the *cyda* group. In the *cyda* group, as opposed to the rest of *Codatractus*, the distal segment of the palpus is ex-

TABLE 3. Forewing length (mm) in males of the *cyda* group of *Codattractus*.

Species	N	Range	Mean	SE	SD	CV
<i>C. mysie</i>	37	18.7–23.7	21.05	0.19	1.13	5.37
<i>C. cyda</i>	12	22.5–25.4	24.33	0.23	0.78	3.21
<i>C. uvydixa</i>	31	24.5–27.9	26.49	0.15	0.82	3.11

ceptionally long. (As in all species of *Codattractus*, males lack a costal fold.)

In the male genitalia of *Codattractus* the valva is distally divided into dorsal and ventral parts; the ventral part extends dorsad just posterior to the dorsal part and becomes dentate distally (Figs. 52–58). In lateral view the dorsal extension is more smoothly curved and broader in the *cyda* group (Figs. 52–56)—especially in *cyda* (Fig. 56) and *uvydixa* (Figs. 54, 55)—than in any other species of *Codattractus* (Figs. 57, 58). (To represent the “other species of *Codattractus*” in visual comparisons with the *cyda* group, I have selected *C. imalena* [Butler], a tailless species and the type of the genus, and *C. carlos* Evans, a tailed species. But my written characterizations come from close comparisons of all the species in the genus.) In profile the tegumen is more humped in the *cyda* group (Figs. 52–56) than in any other species of *Codattractus* (Figs. 57, 58). In dorsal view the distal end of the uncus is narrow and essentially undivided in the *cyda* group (Figs. 59–63) but wide and deeply bilobed in three species (Fig. 64) to very wide and deeply divided into prongs in all other species of *Codattractus* (Fig. 65). The elaborate cornutus within the aedeagus suggests a fan with many sharp fingers in the *cyda* group (Figs. 52–56, 66–70), but has either a narrow, central shaft to which the longer, spike-like fingers attach (Figs. 57, 71) or little more than a base for their attachment, usually in two clusters (Figs. 58, 72), in other species of *Codattractus*.

In figuring and describing the male genitalia of *mysie*, Tilden (1949) erroneously wrote that “the aedeagus has but a single internal spicule”; and in figuring them (as *valeriana*), Miller (1970:fig. 3) erroneously showed nothing more than a single, simple spike inside the aedeagus. Neither saw the sharply fingered fan described here which is diagnostic of the *cyda* group.

In the female genitalia of *Codattractus* a large plate originates ventrad of the ostium bursae and extends posteriad to about the posterior edge of the lamella postvaginalis. Midventrally, in all species of *Codattractus* outside the *cyda* group, this elongate plate is shallowly to (usually) deeply (Fig. 77) or very deeply (Fig. 78) notched, leaving a pair of prongs still united anteriorly so as to hide the ostium bursae in ventral view (Figs. 77, 78). But in the *cyda* group the plate is divided all the way

TABLE 4. Frequency of antennal nudum variants in species of the *cyda* group of *Codatractus*.

Species	Mean	Number of nudum segments										N
		16	20	21	22	23	24	25	26	27	28	
<i>C. mysie</i>	22.3	1	2	6	12	18	5	—	—	—	—	44
<i>C. cyda</i>	25.4	—	—	—	—	—	—	7	3	1	—	11
<i>C. uvydixa</i>	26.4	—	—	—	—	—	—	5	9	13	2	29

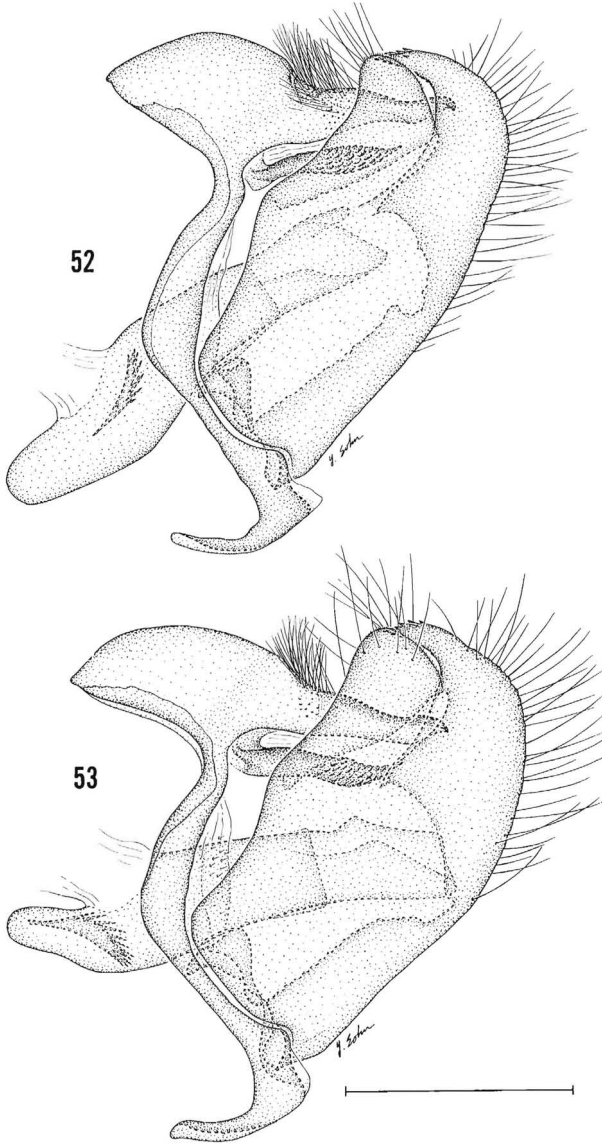
to its anterior end, splitting it into left and right halves and exposing the ostium bursae in ventral view (Figs. 73–76).

Distinguishing the species of the *cyda* group. Genitalia. Although *Codatractus mysie*, *C. uvydixa*, and *C. cyda* form a morphologically tight group, they do have their differences. The dorsal extension of the ventral division of the distal end of the valva is not as broad in lateral view in *mysie* (Figs. 52, 53) as it is in *uvydixa* (Figs. 54, 55) and *cyda* (Fig. 56). Put another way, in *uvydixa* the dorsal and ventral divisions of the valva are about equally broad (Figs. 54, 55), and in *cyda* the ventral division may even be slightly broader than the dorsal division (Fig. 56); but in *mysie* the ventral division is distinctly narrower than the dorsal division (Figs. 52, 53). The distal dentation of the dorsal extension of the ventral division is less in *mysie* (Figs. 52, 53) than it is in *uvydixa* (Figs. 54, 55) and *cyda* (Fig. 56). Most of the ventral surface of the paired lobes of the lamella postvaginalis is densely clothed with short setae in *uvydixa* (Figs. 74, 75) and *cyda* (Fig. 76), while dense setal clothing is limited to the posterior part of these lobes in *mysie* (Fig. 73). (Females of the *cyda* group are rare in collections; with additional material, this difference may not hold up.)

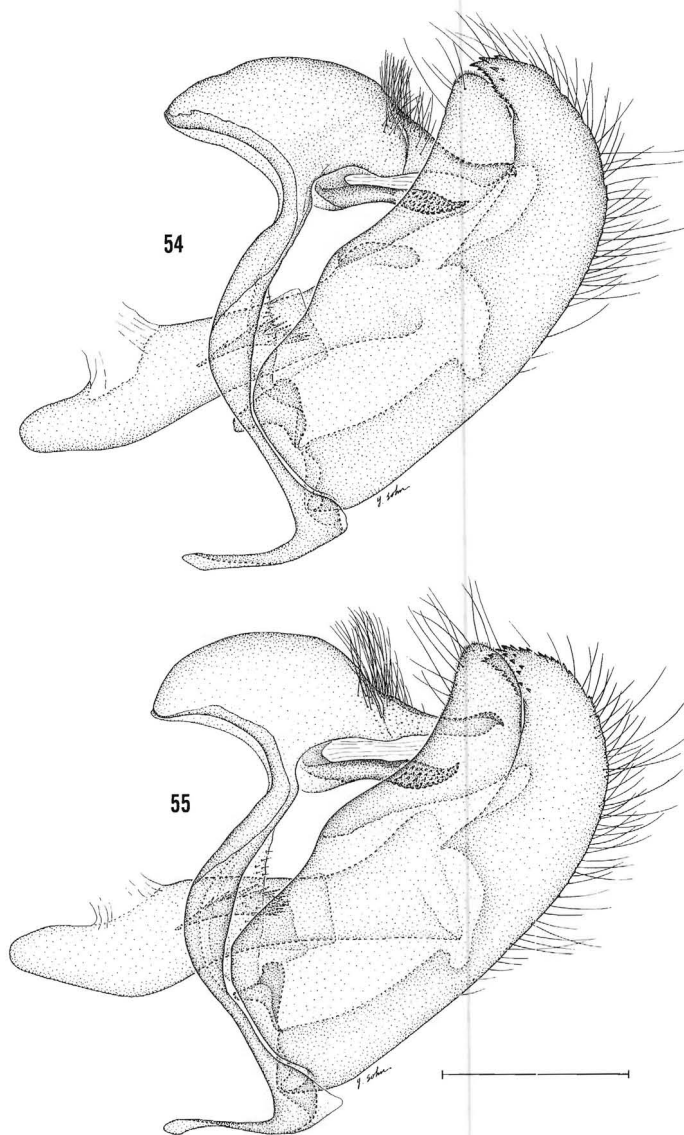
Size. The three species of the *cyda* group differ strikingly in size, with *uvydixa* the largest and *mysie* the smallest. (Indeed, *mysie* is the smallest species of *Codatractus*.) Males of *cyda* are over 3 mm more than males of *mysie* in average forewing length but still about 2 mm less than males of *uvydixa* (Table 3).

Antenna. Although *uvydixa* averages about 1 nudum segment more than *cyda* and 4 nudum segments more than *mysie*, what is so remarkable is that there is no overlap between *mysie* and the other two species in number of nudum segments (Table 4). I have never encountered such nudum variation among related species.

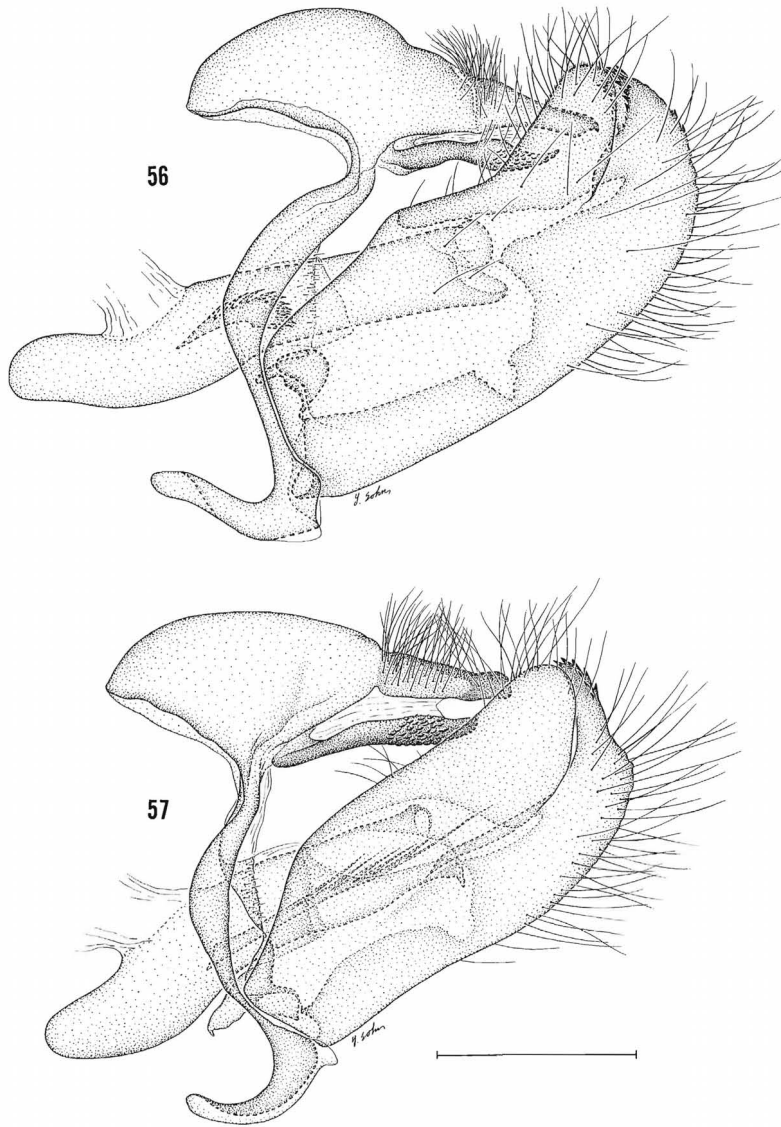
Facies. Both pairs of wings—especially the hindwings—are perceptibly narrower in *cyda* (Figs. 85, 86) than in *uvydixa* and *mysie* (Figs. 79–84). This is related to the fact that *cyda* has a small but unmistakable lobe at the end of hindwing vein 1b (Figs. 85, 86) that is reduced though still detectable in *uvydixa* (Figs. 81–84) and mostly to entirely (Figs. 79,



FIGS. 52, 53. Male genitalia (minus right valva) of *Codatractus mysie* (in the *cyda* group of *Codatractus*) in left lateral view (USNM). Scale=1.0 mm. **52**, Lectotype, Patagonia Mountains, Arizona, USA, 21 May 1903 (genitalic dissection no. W[illiam] D. F[ield] 2950). **53**, Cuesta Colorado, Hidalgo, MEXICO, 3 March 1981, W. H. Howe (J. M. Burns genitalic dissection no. X-1936).



FIGS. 54, 55. Male genitalia (minus right valva) of *Codatractus uydixa* (in the *cyda* group of *Codatractus*) in left lateral view (USNM). Scale=1.0 mm. **54**, Dark differentiate, Mazatlán, Sinaloa, MEXICO (X-1941). **55**, Holotype, Sierra de Guerrero, MEXICO, June 1913, R. Müller (X-1940).



FIGS. 56, 57. Male genitalia (minus right valva) of two species of *Codatractus* in left lateral view. Scale=1.0 mm. **56**, *C. cyda*, automatically in the *cyda* group of *Codatractus*, San Pedro Sula, HONDURAS, 1895, E. Wittkugel (J. M. Burns 1439) (BMNH). **57**, *C. imalena*, the type species of *Codatractus*, Avangarez, COSTA RICA, July (X-1371) (USNM).

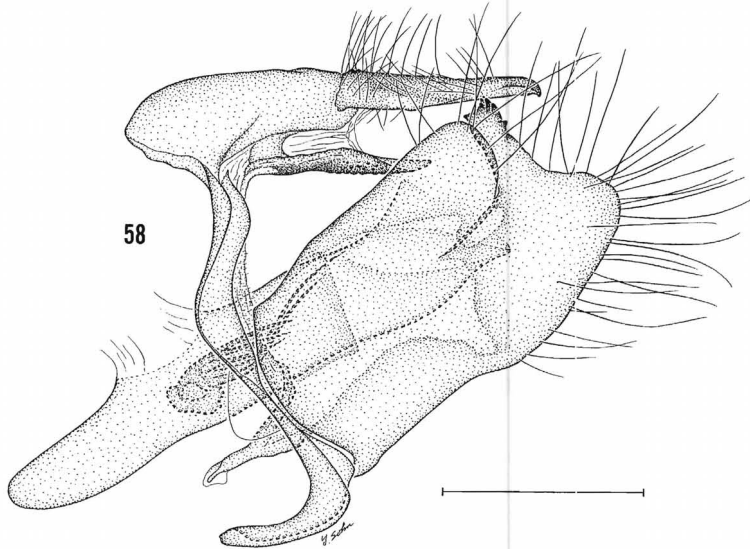
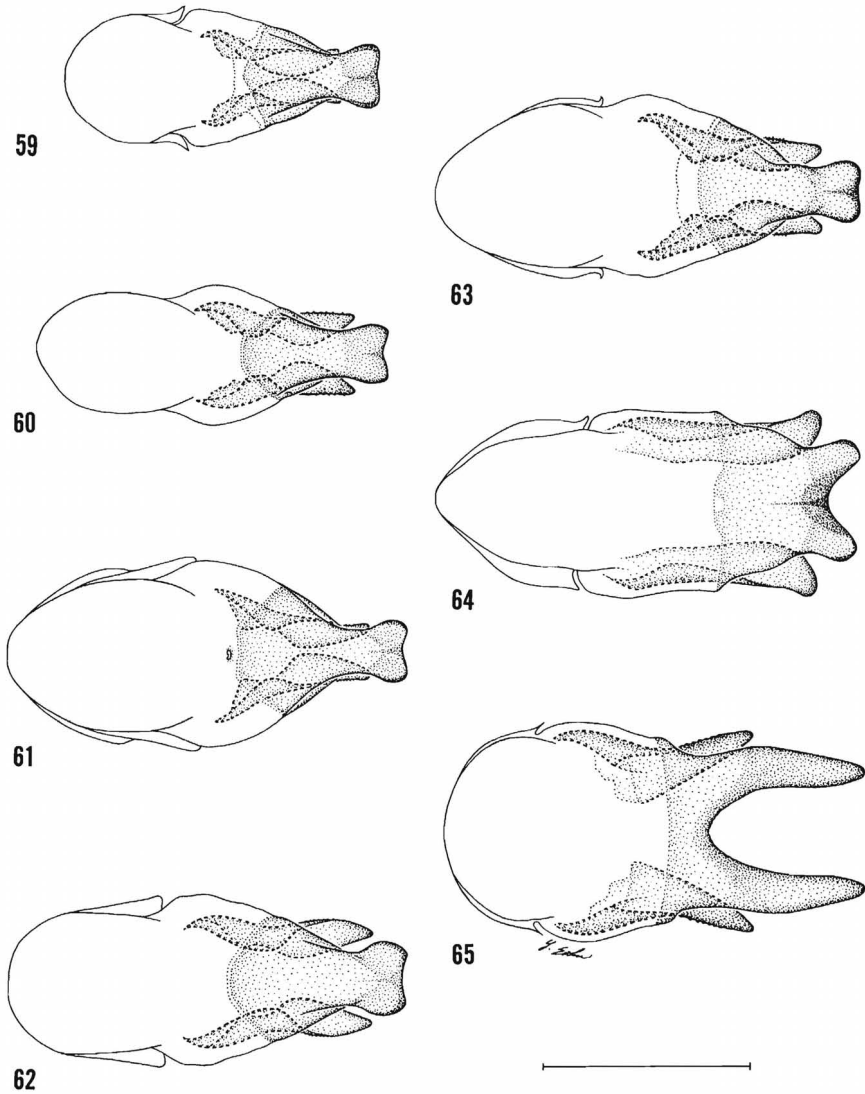


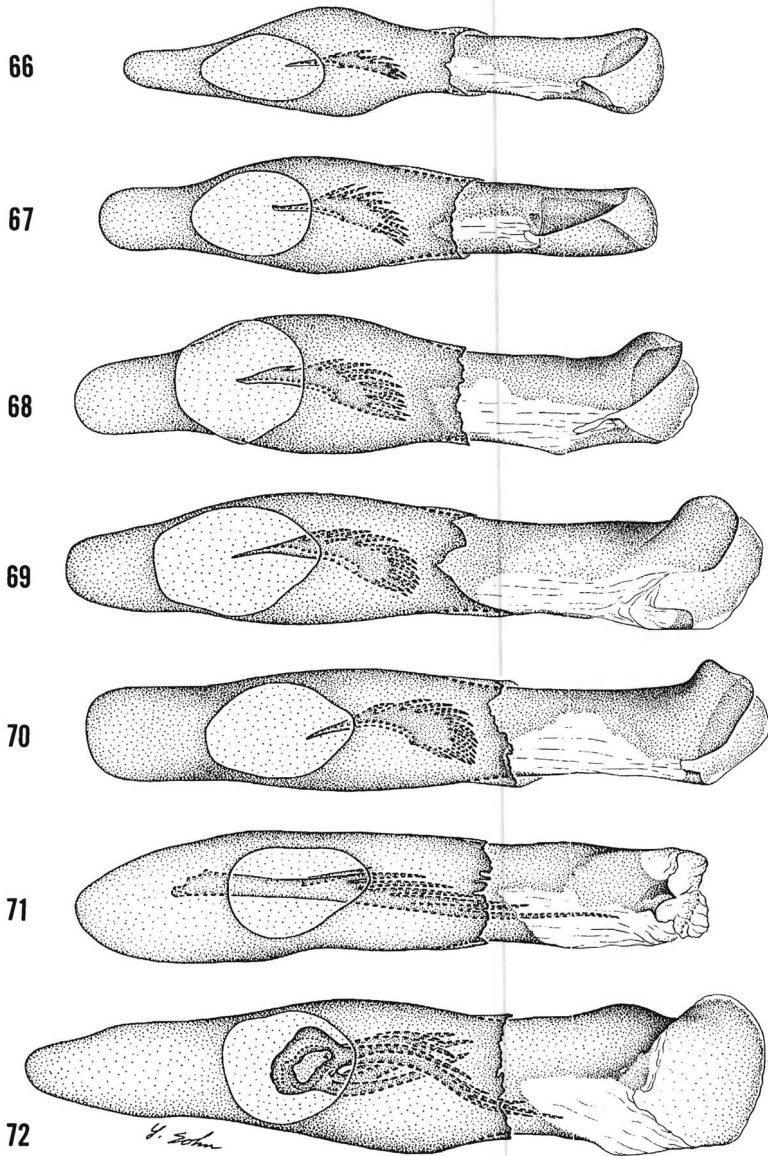
FIG. 58. Male genitalia (minus right valva) of *Codatractus carlos*, a tailed species, in left lateral view. Scale=1.0 mm. Córdoba, Veracruz, MEXICO, June 1909, R. Müller (J. M. Burns 1420) (USNM).

80) eliminated in *mysie* (*mysie* has the roundest wings of any species of *Codatractus*—compare Figs. 79–90). The hyaline spots of the forewing are expressed more fully by *cyda* (Figs. 85, 86) than by *uvydixa* (Figs. 81–84) and *mysie* (Figs. 79, 80). (As usual in skippers, such spots are expressed more fully by females than by males.) In general, the strong checkering of the wing fringes is slightly more discrete in *cyda* and *mysie* than it is in *uvydixa*.

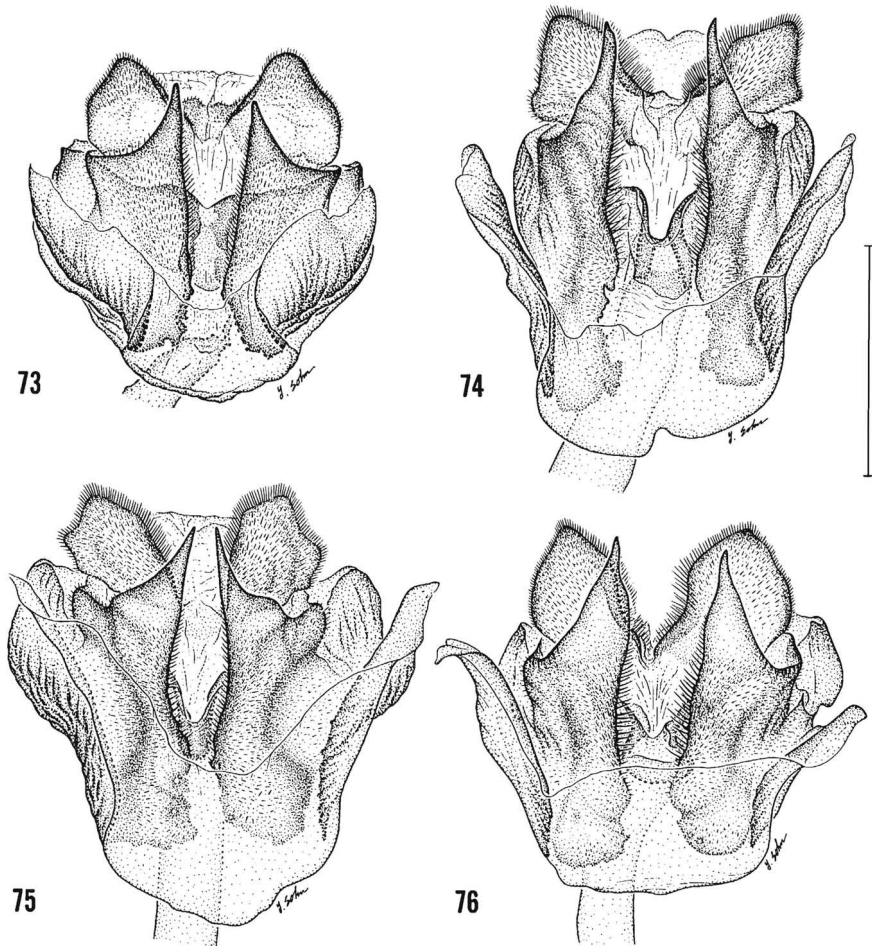
On the ventral hindwing, *cyda* always exhibits a strong white patch adjacent to the lower outer margin (Fig. 86). A similar patch, more variably—and less strongly—expressed, appears in those populations of *uvydixa* (in Chiapas, Puebla, and Guerrero—Fig. 84) that are geographically closer to *cyda*, but not in those populations of *uvydixa* that are farther away (in Colima, Jalisco, and Sinaloa—Fig. 82). The latter, which I simply call the “*uvydixa* dark differentiate,” look more like *mysie* (Fig. 80), except, of course, for their giant size. Dorsally, golden hairlike scales—on the basal half of the forewing (proximal to the hyaline spots), and over most of the hindwing below the costal margin—which contrast with the dark brown ground color in typical *uvydixa* (Fig. 83), are replaced by essentially concolorous hairs in the *uvydixa* dark differentiate (Fig. 81).



FIGS. 59-65. Tegumen, uncus, and gnathos of the male genitalia of five species of *Codatractus* (including all three species of the *cyda* group) in dorsal view. Scale=1.0 mm. **59**, *C. mysie*, lectotype, Arizona, USA (William] D. Field] 2950). **60**, *C. mysie*, Hidalgo, MEXICO (X-1936). **61**, *C. uvydixa*, dark differentiate, Sinaloa, MEXICO (X-1941). **62**, *C. uvydixa*, holotype, Sierra de Guerrero, MEXICO (X-1940). **63**, *C. cyda*, San Pedro Sula, HONDURAS (J. M. Burns 1439). **64**, *C. imalena*, the type species of *Codatractus*, Avangarez, COSTA RICA, July (X-1371). **65**, *C. carlos*, a tailed species, Veracruz, MEXICO (J. M. Burns 1420).

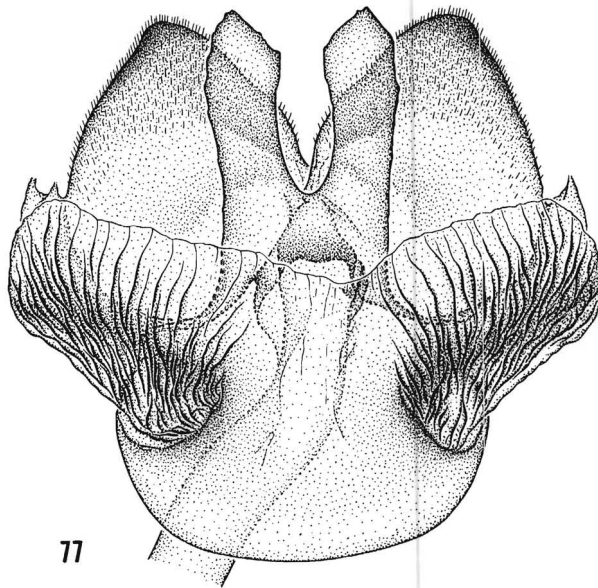


FIGS. 66–72. Aedeagus of the male genitalia of five species of *Codatractus* (including all three species of the *cyda* group) in dorsal view. All drawn to the same scale. **66**, *C. mysie*, lectotype, Arizona, USA (William D. Field 2950). **67**, *C. mysie*, Hidalgo, MEXICO (X-1936). **68**, *C. uvydixa*, dark differentiate, Sinaloa, MEXICO (X-1941). **69**, *C. uvydixa*, holotype, Sierra de Guerrero, MEXICO (X-1940). **70**, *C. cyda*, San Pedro Sula, HONDURAS (J. M. Burns 1439). **71**, *C. imalena*, the type species of *Codatractus*, Avangarez, COSTA RICA, July (X-1371). **72**, *C. carlos*, a tailed species, Veracruz, MEXICO (J. M. Burns 1420).

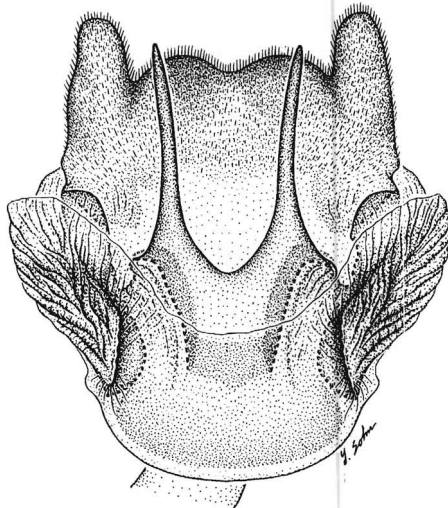


FIGS. 73–76. Sterigma and beginning of ductus bursae of the female genitalia of all three species of the *cyda* group of *Codatractus* in ventral view. Scale=1.0 mm. **73**, *C. mysie*, Guadalupe, MEXICO, R. Müller (X-1944) (USNM). **74**, *C. uvydixa*, Acahuizotla, Guerrero, MEXICO, July 1957, T. Escalante (X-2080) (AME). **75**, *C. uvydixa*, Las Delicias, 700 m, 60 km SW Comitán, Chiapas, MEXICO, June 1969, P. Hubbell (X-2081) (AMNH). **76**, *C. cyda*, Las Delicias, 700 m, 60 km SW Comitán, Chiapas, MEXICO, June 1969, P. Hubbell (X-2083) (AMNH).

Larval foodplants. *Codatractus mysie* oviposits on, and feeds as a larva on, *Tephrosia leiocarpa* Gray (Leguminosae) in southern Arizona (Roever 1990). This bolsters an emerging pattern. Other species of *Codatractus*, as far as known, also choose legumes: in southern Arizona the tailless *C. arizonensis* (Skinner) was seen to oviposit on *Eysenhardtia or-*

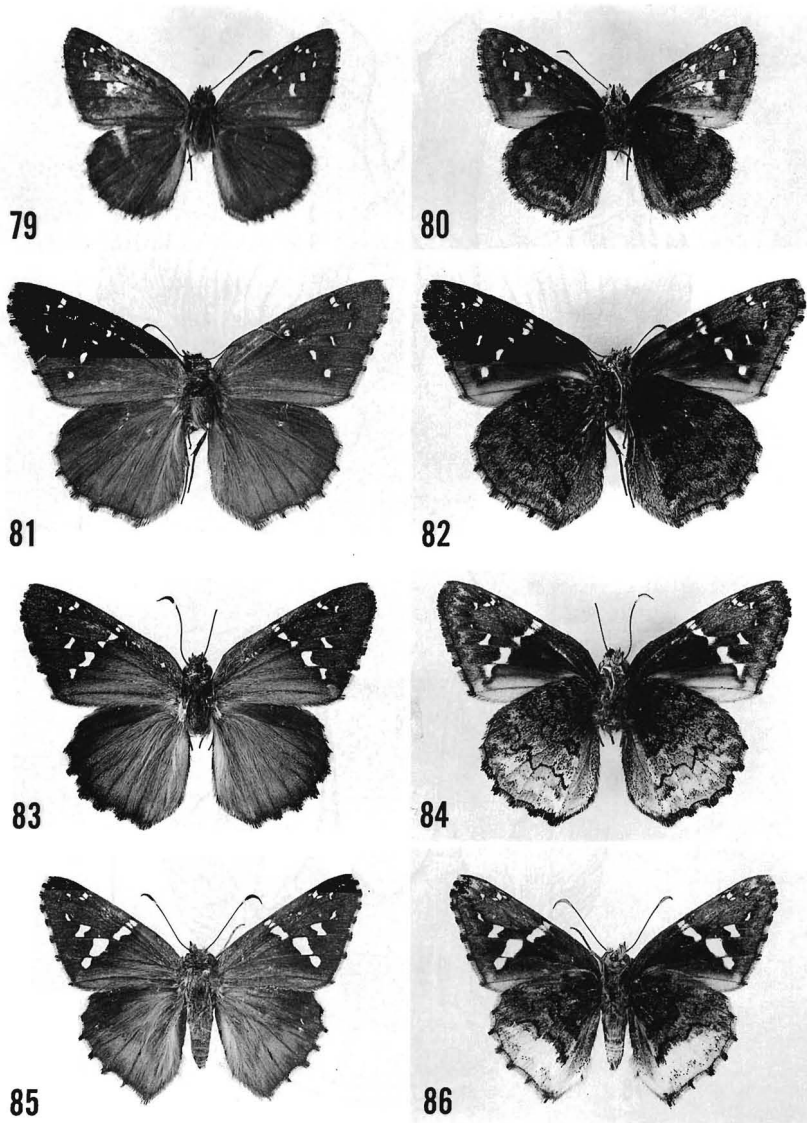


77

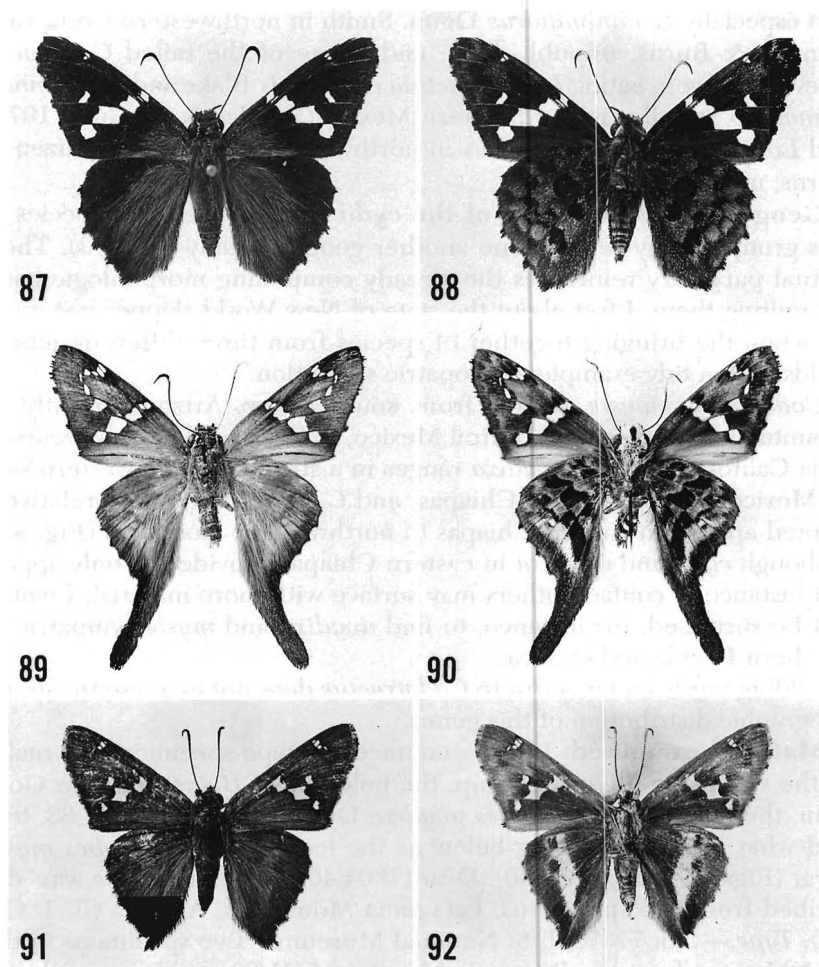


78

FIGS. 77, 78. Sterigma and beginning of ductus bursae of the female genitalia of two species of *Codattractus* in ventral view. Scale=1.0 mm. **77**, *C. imalena*, the type species of *Codattractus*, Cerro Campana, 2500 ft [760 m], PANAMA, 26 November 1964 (G. B. Small) (J. M. Burns 1433) (USNM). **78**, *C. carlos*, a tailed species, Cayuga, GUATEMALA, November (X-2025) (USNM).



FIGS. 79–86. Males of the *cyda* group of *Codatractus* in dorsal (left) and ventral (right) views (all $\times 0.95$). **79, 80**, *C. mysie*, lectotype, Patagonia Mountains, Arizona, USA, 21 May 1903 (W[illiam] D. F[ield] 2950) (USNM). **81, 82**, *C. uvydixa* dark differentiate, Mazatlán, Sinaloa, MEXICO (X-1942) (USNM). **83, 84**, *C. uvydixa*, holotype, Sierra de Guerrero, MEXICO, June 1913, R. Müller (X-1940) (USNM). **85, 86**, *C. cyda*, San Pedro Sula, HONDURAS, 1895, E. Wittkugel (BMNH).



FIGS. 87–92. Males of a tailless species of *Codatractus*, a tailed species of *Codatractus*, and a tailless species erroneously placed in *Codatractus* in dorsal (left) and ventral (right) views (all $\times 0.95$). **87, 88**, *C. imalena*, the type species of *Codatractus*, Cerro Hornito, 1200 m, Chiriquí, PANAMA, 27 July 1975, G. B. Small (USNM). **89, 90**, *C. carlos rowena* Evans, holotype, Patao, Güiría, VENEZUELA, August 1891 (BMNH). **91, 92**, Holotype of what Dyar called *Eudamus hyster*, Sierra de Guerrero, MEXICO, July 1913, R. Müller (J. M. Burns 1424) (USNM).

thocarpha (Gray) Wats. and larvae were found on it (Roever 1990 [gave plant as *E. polystachya* (Ortega) Sarg.], Bailowitz & Brock 1991); the tailless *C. melon* (Godman & Salvin) was reared from larvae on *Lonchocarpus acuminatus* (Schlechtendal) M. Sousa S., *L. orotinus* Pittier,

and especially *L. minimiflorus* Donn. Smith in northwestern Costa Rica (Janzen & Burns, unpubl. data); and larvae of the tailed *C. alcaeus* (Hewitson) were eating *Ichthyomethia communis* Blake and *Amerimnon granadillo* Standley in northeastern Mexico (Kendall & McGuire 1975) and *Lonchocarpus minimiflorus* in northwestern Costa Rica (Janzen & Burns, unpubl. data).

Geographic distribution of the *cyda* group. The three species of this group closely replace one another geographically (Fig. 93). Their virtual parapatry reinforces the already compelling morphologic basis for uniting them. I fret about the state of New World skipper systematics when the bringing together of species from three different genera yields such a tidy example of allopatric speciation.

Codatractus mysie ranges from southeastern Arizona, mostly in mountains of western and central Mexico, to Oaxaca—but also occurs in Baja California Sur; *C. uvydixa* ranges in a strip down the western side of Mexico from Sinaloa to Chiapas; and *C. cyda* occurs in a relatively limited area from eastern Chiapas to northwestern Honduras (Fig. 93). Although *cyda* and *uvydixa* in eastern Chiapas provide the only apparent instance of contact, others may surface with more material. I would not be surprised, for instance, to find *uvydixa* and *mysie* sympatric in southern Puebla and Oaxaca.

Adding *mysie* and *uvydixa* to *Codatractus* does not increase the grand geographic distribution of this genus.

Material examined. I have examined the type specimens (all male) of the species in the *cyda* group: the holotype of *Heteropia cyda* Godman, the holotype of *Thorybes uvydixa* Dyar (Figs. 55, 62, 69, 83, 84), and what I am designating below as the lectotype of *Thorybes mysie* Dyar (Figs. 52, 59, 66, 79, 80). Dyar (1904:40) wrote that *mysie* was “described from two specimens, Patagonia Mountains, Arizona (E. J. Oslar). *Type*.—No. 7737, U. S. National Museum.” Two specimens in the USNM come from the Patagonia Mts, Ariz, 5/21/03, and bear a red type label with that type number. The genitalia are gone from one but dissected and preserved from the other (“♂ genitalia, 1948, W.D.F. 2950”) which I proclaim the **lectotype**.

***Codatractus mysie*.** USA: ARIZONA: SANTA CRUZ COUNTY: Atascosa Mountains, Peña Blanca Lake, 4000 ft [1220 m], 31°24' N, 111°5' W, 5-VIII-1991, 2♀, J. M. & S. N. Burns (USNM). Pajarito Mountains, Alamo Canyon, 4000–4200 ft [1220–1280 m], K. Roever (Roever): 2-VIII-1974, 2♂; 27-VII-1978, 4♂ 1♀; 24-VII-1983, 1♂. Patagonia, 3 mi [5 km] SW, 2-VIII-1976, 1♂ 1♀, R. A. Bailowitz (USNM). Rt. 82, 3–4 mi [5–6 km] SW Patagonia, 3900–4100 ft [1190–1250 m], K. Roever (Roever): 24-VII-1977, 1♂; 18-VII-1986, 2♂; 24-VII-1986, 1♂ 1♀. Patagonia Mountains, 21-V-1903, 1♂ [LECTOTYPE] 1♀, Oslar (USNM). Patagonia Mountains, 3 mi [5 km] SSW Harshaw, 5400 ft [1645 m], 31°26' N, 110°43' W, 8-VIII-1991, 1♀, J. M. & S. N. Burns (USNM).

MEXICO: BAJA CALIFORNIA SUR: Ayo. Candelaria, 26-XI-1961, 1♂ (MacNeill). Bahía de la Concepcion, 10-IX-1968, 2♂, C. Callaghan (AME). CHIHUAHUA: Hidalgo

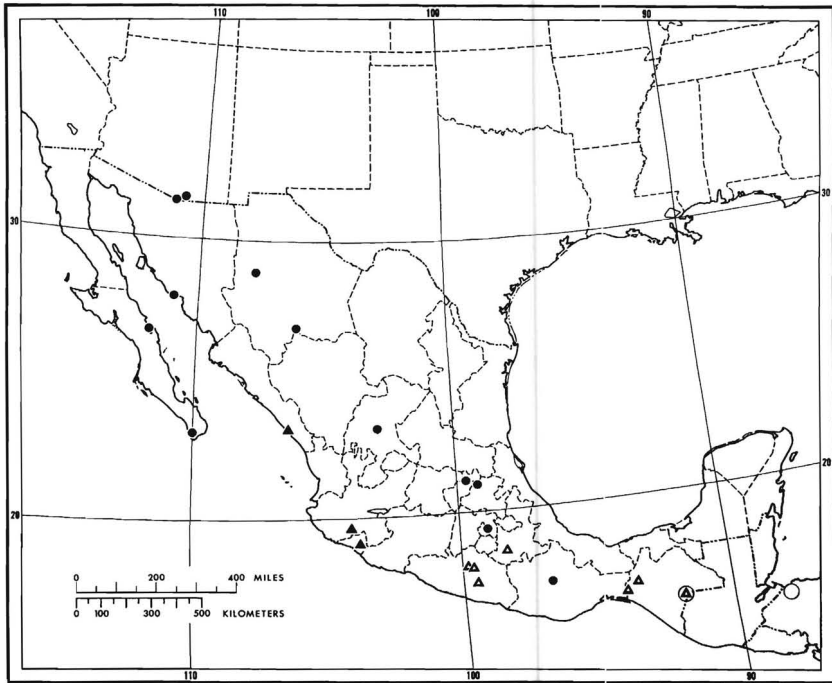
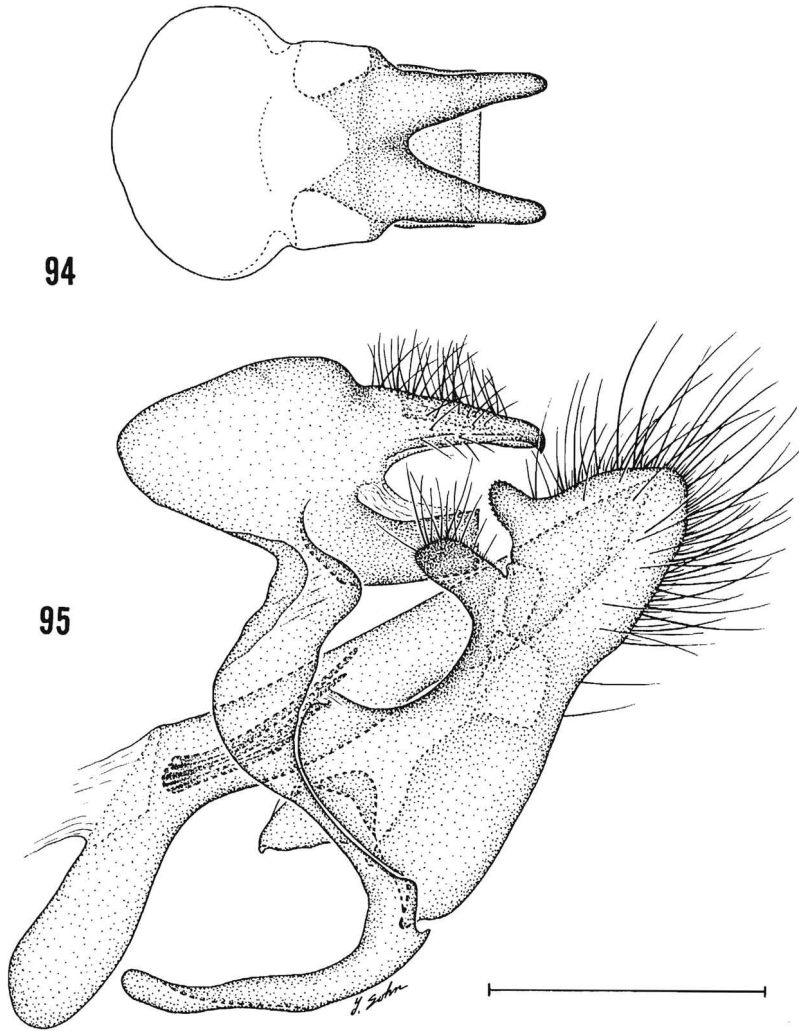


FIG. 93. Geographic distribution (based on specimens examined) of the *cyda* group of *Codatractus*, which strongly reflects allopatric speciation. Large open circles, *C. cyda*; open triangles, *C. uvydixa*; solid triangles, *C. uvydixa* dark differentiate; and small solid circles, *C. mysie*. Open symbols mark differentiates with considerable white on the ventral hindwing (see Figs. 83–86). The one known instance of sympatry involves *C. cyda* and *C. uvydixa* in eastern Chiapas, Mexico.

del Parral, 25 mi [40 km] W, 6800 ft [2075 m], 15-VII-1964, 1♂, J. Powell (MacNeill). Matachic, 7-VII-1947, 1♂, C. D. Michener (AMNH). DISTRITO FEDERAL: Los Reyes, 7500 ft [2285 m], 2-VII-1952, 4♂ 2♀, E. E. Gilbert, C. D. MacNeill (UCB, MacNeill). Sierra de Guadalupe, VII-1917, 1♂, C. C. Hoffmann (AMNH). HIDALGO: Cuesta Colorado, W. H. Howe: 15-III-1980, 2♂ (AMNH); 3-III-1981, 1♂ (USNM). OAXACA: Hwy. 175, 5 mi [8 km] N Oaxaca, 6000 ft [1830 m], J. Kemner (USNM): 22-VII-1988, 1♂, 26-VII-1991, 2♂. Hwy. 175, 5–10 mi [8–16 km] N Oaxaca, 6000–7000 ft [1830–2135 m], 3-VIII-1992, 1♂, J. Kemner (USNM). QUERETARO: Ahuacatlan, 19 km SSW, 1500 m, 21°16' N, 99°8' W, 16-III-1984, 1♂, J. Rawlins, D. Harvey, S. Thompson (CMNH). SONORA: Guaymas, Oslar (BMNH): 24-II-1903, 2♂; 25-II-1903, 1♀. ZACATECAS: Fresnillo, J. Stone (AMNH): 24-VI-1950, 1♂; 25-VI-1950, 1♂. STATE UNDETERMINED: Guadalupe, 1♂ 1♀, R. Müller (USNM).

***Codatractus uvydixa* dark differentiate.** MEXICO: COLIMA: La Salada, 1000 ft [305 m], R. Wind (AME): 21-V-1968, 1♂; 30-V-1968, 1♂. Salada, R. Wind (AMNH): 10-V-1967, 1♂; 11-V-1967, 1♂; 20-V-1967, 2♂ + 1♂ in private collection; 4-VI-1967, 1♂; 10-VI-1967, 1♂; 8-V-1968, 1♂. JALISCO: Zenzontla, SE El Grullo, 800 m, 8-VI-1994, 1♂, A. D. Warren. SINALOA: Mazatlan, 2♂ (USNM).

***Codatractus uvydixa*.** MEXICO: CHIAPAS: El Aguacero, 2-V-1988, 5♂, J. Kemner



FIGS. 94, 95. Male genitalia of holotype of *Eudamus hyster* Dyar, Sierra de Guerrero, MEXICO, July 1913, R. Müller (J. M. Burns 1424) (USNM). The species *hyster* was transferred to *Codatractus* where obviously it does not belong (compare true *Codatractus* male genitalia in Figs. 52–72). Scale=1.0 mm. **94**, Tegumen, uncus, and gnathos in dorsal view. **95**, Complete genitalia (minus right valva) in left lateral view.

(USNM); Las Delicias, 60 km SW Comitan, 700 m, VI-1969, 1♀, P. Hubbell (AMNH); Rizo de Oro, 25-IV-1972, 1♂, H. L. King (AME). GUERRERO: Acahuizotla, T. Escalante (AME): VII-1957, 2♂ 1♀; VII-1959, 1♂; XI-1960, 5♂. Balsas, 1♂ (AMNH). Mexcala, VIII-1958, 1♂, T. Escalante (AME). Sierra de Guerrero, VI-1913, 1♂ [HOLOTYPE], R. Müller (USNM). PUEBLA: Jaulillas, 18-V-1979, 1♂, J. R. Powers (USNM).

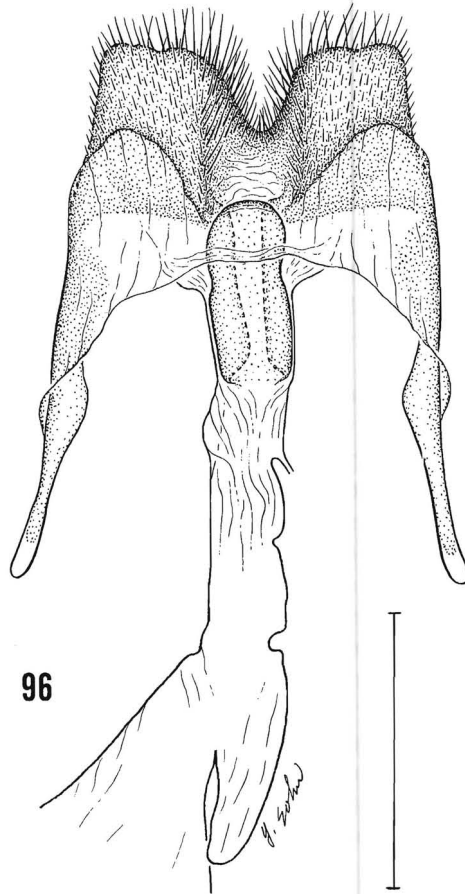


FIG. 96. Sterigma and ductus bursae of the female genitalia of *hyster* in ventral view (*hyster* obviously does not belong in *Codattractus*: compare true *Codattractus* female genitalia in Figs. 73–78). Scale=1.0 mm. 12 mi [19.3 km] W Ocozocoautla, 2500 ft [760 m], Chiapas, MEXICO, 26 July 1952, E. E. Gilbert, C. D. MacNeill (X-2042) (MacNeill).

Codattractus cyda. HONDURAS: San Pedro Sula, 1895, 10♂, E. Wittkugel (BMNH) [HOLOTYPE lacks year and first name of collector]. MEXICO: CHIAPAS: Las Delicias, 60 km SW Comitan, 700 m, VI-1969, 2♂ 1♀, P. Hubbell (AMNH).

The *hysterectomy* of *Codattractus*

One species put in *Codattractus* by Evans (1952:80) does not belong: what was described—again from the “Sierra de Guerrero, Mexico,” by Dyar (1916)—as *Eudamus hyster*. Evans (1952:42) had reservations about his own pigeonholing; for, after remarking that “*hyster* has usually been placed next *asander* in the genus *Aguna*, but structurally it is very

different," he went on to say that "it has been moved to *Codattractus*, where it is better placed, though not a perfect fit."

Clearly the genitalia of *hyster* in the male (Figs. 94, 95) as well as the female (Fig. 96) do not conform with those of male (Figs. 52–72) and female (Figs. 73–78) *Codattractus*. Besides the total differences in *hyster's* female genitalia and the salient differences in the shape and relative proportions of its male valva, note that the gnathos of *hyster* is continuous across its distal end (Fig. 94) instead of divided into left and right sclerotized parts (Figs. 59–65) as it is in all species of *Codattractus*; that the saccus is long (Fig. 95) instead of short (Figs. 52–58) as it is in all species of *Codattractus*; and that the aedeagus is relatively much longer (Fig. 95) than it is (Figs. 52–58) in any species of *Codattractus*. Moreover, the pattern of *hyster's* ventral hindwing (Fig. 92) does not really fit the *Codattractus* mold (Figs. 80, 82, 84, 86, 88, 90).

Some behavior of *hyster* is also aberrant. Warren (1995, pers. comm.), who observed *hyster* together with several species of *Codattractus* along small creeks in Jalisco, Mexico, says that *hyster* perched mainly on small branches just above or next to the water but *Codattractus*, mainly on mud; that *hyster* was less easily disturbed, less fast and direct in its flight, and less deliberate about alighting than *Codattractus*; and that *hyster* did not attract perched *Codattractus*, which did, however, fly up at other *Codattractus*. Kendall (1976) reported that larvae of *hyster*, in Tamaulipas, Mexico, were gregarious, rather than solitary like other skipper larvae (which include the known larvae of *Codattractus*).

Although I am still unsure where it goes, I am formally removing *hyster* from *Codattractus*. Better unattached than misplaced. This is the first *hysterectomy* I have ever performed, and *Codattractus* is instantly healthier for it.

ACKNOWLEDGMENTS

The following individuals and institutions generously provided material: Lee D. Miller and the Allyn Museum of Entomology (AME), Florida Museum of Natural History, Sarasota, Florida; Frederick H. Rindge and the American Museum of Natural History (AMNH), New York, New York; C. Don MacNeill and the California Academy of Sciences (CAS), San Francisco, California; John E. Rawlins and the Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania; Jerry A. Powell and the Essig Museum of Entomology, University of California, Berkeley (UCB), California; Philip R. Ackery and The Natural History Museum (BMNH), London, England; National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; Richard A. Bailowitz, H. Avery Freeman, Daniel H. Janzen, John Kemner, C. Don MacNeill, David K. Parshall, Jack R. Powers, Kilian Roeber, and Andrew D. Warren.

Richard G. Robbins, B. Adrienne B. Venables, and Elizabeth A. Klafter dissected genitalia. Except for Fig. 23, which is the work of George L. Venable, Young Sohn drew the genitalic illustrations and mounted all figures. Carl C. Hansen took the photographs in Figs. 24–51 and Victor E. Krantz, those in Figs. 79–92. Andrew D. Warren offered field observations on skipper behavior, Jim P. Brock obtained the best current name for the species of *Eysenhardtia* in Arizona, Donald J. Harvey tracked down some critical literature,

and Jerry A. Louton calculated the statistics on size in Table 3. S. Dillon Ripley and the Fluid Research Fund of the Smithsonian Institution got me to what was still the British Museum (Natural History). Stanwyn G. Shetler and the Research Opportunities Fund of the Smithsonian Institution supported relevant fieldwork in Arizona. Sarah N. Burns assisted in many and various ways in Washington, London, and Arizona. John A. Shuey and Daniel H. Janzen each reviewed the manuscript from one angle and Arthur M. Shapiro (a virtual anglewing), from five. Thank you, thank you, thank you . . .

LITERATURE CITED

- BAILOWITZ, R. A. & J. P. BROCK. 1991. Butterflies of southeastern Arizona. Sonoran Arthropod Studies, Inc., Tucson, Arizona. ix + 342 pp.
- BELL, E. L. 1938. A catalogue of the original descriptions of the Rhopalocera found north of the Mexican Border. Part One. The Hesperioidea. Bull. Cheyenne Mountain Mus. 1:H-1-H-35.
- BROWN, J. W., H. G. REAL & D. K. FAULKNER. 1992. Butterflies of Baja California. Lepid. Res. Foundation, Inc., Beverly Hills, California. v + 129 pp., 8 pls.
- BURNS, J. M. 1987. The big shift: *nabokovi* from *Atalopedes* to *Hesperia* (Hesperiidae). J. Lepid. Soc. 41:173-186.
- . 1989. Phylogeny and zoogeography of the bigger and better genus *Atalopedes* (Hesperiidae). J. Lepid. Soc. 43:11-32.
- . 1990. *Amblyscirtes*: problems with species, species groups, the limits of the genus, and genus groups beyond—a look at what is wrong with the skipper classification of Evans (Hesperiidae). J. Lepid. Soc. 44:11-27.
- . 1992. Genitalic recasting of *Poanes* and *Paratrytone* (Hesperiidae). J. Lepid. Soc. 46:1-23.
- . 1994a. Split skippers: Mexican genus *Poanopsis* goes in the *origenes* group—and *Yvretta* forms the *rhesus* group—of *Polites* (Hesperiidae). J. Lepid. Soc. 48:24-45.
- . 1994b. Genitalia at the generic level: *Atrytone* restricted, *Anatrytone* resurrected, new genus *Quasimellana*—and yes! we have no *Mellanas* (Hesperiidae). J. Lepid. Soc. 48:273-337.
- DYAR, H. C. 1904. New species of North American Lepidoptera and a new limacodid larva. J. New York Entomol. Soc. 12:39-44.
- . 1914. Descriptions of new species and genera of Lepidoptera from Mexico. Proc. U.S. Natl. Mus. 47:365-409.
- . 1916. Descriptions of new Lepidoptera from Mexico. Proc. U.S. Natl. Mus. 51:1-37.
- EVANS, W. H. 1952. A catalogue of the American Hesperidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part II. Pyrginae. Section I. British Museum, London. 178 pp., pls. 10-25.
- . 1953. A catalogue of the American Hesperidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part III. Pyrginae. Section 2. British Museum, London. 246 pp., pls. 26-53.
- FERRIS, C. D. 1989. Supplement to: A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. No. 3. vii + 103 pp.
- FREEMAN, H. A. 1970. Notes on the genus *Cephise* Evans, with a new record for Mexico (Hesperiidae). J. Lepid. Soc. 24:68-69.
- . 1977. Six new species of Hesperidae from Mexico. J. Lepid. Soc. 31:89-99.
- GODMAN, F. D. 1907. Notes on the American species of Hesperidae described by Plötz. Ann. Mag. Nat. Hist. Ser. 7, 20:132-155.
- GODMAN, F. D. & O. SALVIN. 1879-1901. Biologia Centrali-Americana; Insecta; Lepidoptera-Rhopalocera. Vol. 2, 782 pp.; Vol. 3, 113 pls.
- HAYWARD, K. J. 1948. Genera et species animalium argentatorum. Vol. 1. Insecta, Lepidoptera, Hesperidae, Pyrrhopyginae and Pyrginae. Guillermo Kraft Ltda., Buenos Aires. 389 pp., 27 pls.
- HOFFMANN, C. C. 1941. Catalogo sistematico y zoogeografico de los Lepidopteros Mexicanos. Segunda parte. Hesperioidea. Anales Inst. Biol. [Mexico] 12:237-294.

- KENDALL, R. O. 1976. Larval foodplants for thirty species of skippers (Lepidoptera: Hesperidae) from Mexico. *Bull. Allyn Mus.* No. 39. 9 pp.
- KENDALL, R. O. & W. W. MCGUIRE. 1975. Larval foodplants for twenty-one species of skippers (Lepidoptera: Hesperidae) from Mexico. *Bull. Allyn Mus.* No. 27. 7 pp.
- LINDSEY, A. W. 1921. The Hesperioidea of America north of Mexico. *Univ. Iowa Stud. Nat. Hist.* 9(4):1-114.
- LINDSEY, A. W., E. L. BELL & R. C. WILLIAMS JR. 1931. The Hesperioidea of North America. *Denison Univ. Bull., J. Sci. Lab.* 26:1-142.
- LLORENTE-BOUSQUETS, J., A. LUIS-MARTÍNEZ, & I. VARGAS-FERNÁNDEZ. 1990. *Catálogo sistemático de los Hesperioidea de México*. Publ. Esp. Mus. Zool. (Univ. Nac. Autónoma México) No. 1. 70 pp.
- MABILLE, P. 1888. Diagnoses de Lépidoptères (Hespérides) nouveaux. *Le Naturaliste* yr. 10, ser. 2, no. 27:98-99.
- MABILLE, P. & VUILLOT. 1891. *Novitates Lepidopterologicae*, fasc. 4:25-33, pl. IV.
- MACNEILL, C. D. 1975. Family Hesperidae, pp. 423-578. *In* Howe, W. H. (ed.), *The butterflies of North America*. Doubleday & Co., Inc., Garden City, New York.
- MIELKE, O. H. H. 1979. *Das neue Arten* de *Typhedanus* Butler (Lepidoptera, Hesperidae). *Rev. bras. Entomol.* 23:1-8.
- MILLER, L. D. 1970. Reports on the Margaret M. Cary-Carnegie Museum expedition to Baja California, Mexico, 1961. 7. The family Hesperidae (Lepidoptera). *Ann. Carnegie Mus.* 41:169-200.
- MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. *Lepid. Soc. Mem.* No. 2. vii + 280 pp.
- PLÖTZ, C. 1881. Die Hesperiden-Gattung *Goniurus* Hübn. und ihre Arten. *Bull. Soc. Impériale Naturalistes Moscou [Moscow]* 55(3):1-22.
- ROEVER, K. 1990. [observations in] 1989 Season Summary. *News Lepid. Soc.* No. 2, p. 15.
- SCHAUS, W. 1902. Descriptions of new American butterflies. *Proc. U.S. Nat. Mus.* 24:383-460.
- SCOTT, J. A. 1986. *The butterflies of North America*. Stanford Univ. Press, Stanford, California. xiii + 583 pp., 64 pls.
- SHUEY, J. A. [1991] "1989." A new *Polythrix* from Central America (Lepidoptera: Hesperidae). *J. Res. Lepid.* 28:277-282.
- SKINNER, H. 1911. The larger boreal American Hesperidae, including *Eudamus*, *Erycides*, *Pyrrhopyge*, and *Megathymus*. *Trans. Amer. Entomol. Soc.* 37:169-209, pl. X.
- SKINNER, H. & R. C. WILLIAMS JR. 1922. On the male genitalia of the larger Hesperidae of North America. *Trans. Am. Entomol. Soc.* 48:109-127.
- STEINHAUSER, S. R. 1989. Taxonomic notes and descriptions of new taxa in the neotropical Hesperidae. Part I. Pyrginae. *Bull. Allyn Mus.* No. 127. 70 pp.
- TILDEN, J. W. 1949. A note on *Caicella mysie* (Dyar) with a figure of the male genitalia. *Bull. Southern California Acad. Sci.* 48:4-6.
- . 1975. Hesperiid notes. *J. Lepid. Soc.* 29:60-62.
- TILDEN, J. W. & A. C. SMITH. 1986. *A field guide to western butterflies*. Houghton Mifflin Co., Boston. xii + 370 pp., 48 pls.
- WARREN, A. D. 1995. A new species of *Codattractus* from western Mexico (Lepidoptera: Hesperidae). *Tropical Lepid.* 6:21-25.

Received for publication 28 June 1995; revised and accepted 2 September 1995.