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DREPHALYS: DIVISION OF THIS SHOWY NEOTROPICAL GENUS, PLUS A NEW SPECIES AND THE IMMATURES AND FOOD PLANTS OF TWO SPECIES FROM COSTA RICAN DRY FOREST (HESPERIIDAE: PYRGINAE)

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ABSTRACT. Mainly on the basis of many male and female genitalic characters, *Drephalys* splits cleanly into two subgenera: *Drephalys* (*Drephalys*) Watson 1893 (= *Paradros* Watson 1893), with at least 16 species, and ***Drephalys* (*Paradrephalys*) Burns, new subgenus** (type species *Hesperia dumeril* Latreille 1824), with at least 7 species. Although these showy, diurnal, neotropical pyrgine hesperiids generally are rare in collections, two species have been reared repeatedly in the tropical dry forests of the Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica: ***Drephalys* (*Drephalys*) *kidonoi* Burns, new species**, and *D. (D.) alcmon* (Cramer). In the ACG, larvae of *D. kidonoi* (N = 236) eat *Roupala montana* Aublet (Proteaceae), and larvae of *D. alcmon* (N = 70) eat *Hirtella racemosa* Lamarck (Chrysobalanaceae). In Panama, as well, *D. alcmon* eats *Hirtella racemosa*; but in Pará, Brazil, it eats the *Hirtella* relatives *Couepia* and *Parinari* (Chrysobalanaceae), whereas *D. (D.) eous* (Hewitson) eats *Vochysia vismiaefolia* Spruce (Vochysiaceae). As far as we can tell (admittedly not far), different species of *Drephalys* (*Drephalys*) seem to be specializing on food plants in taxonomically unallied families. Larvae of these three *Drephalys* (*Drephalys*) species share a basically similar color pattern, which is distinctive. With a development time of 45–55 days from newly-eclosed larva to prepupa, *D. kidonoi* is one of the slower-growing of some 190 species of pyrgines reared in the ACG. Adults of *D. kidonoi* apparently breed chiefly during the first half of the dry season, when other dry-forest skippers have emigrated or are sexually dormant. While *D. kidonoi* still is known only from Guanacaste, Costa Rica, *D. alcmon* ranges far more widely—from eastern Peru and central Brazil all the way to Guatemala, at least (it has not previously been reported from Central America). Despite close genitalic similarities that mark *D. kidonoi* as the sister species of *D. helixus* (the type species of *Drephalys*), *D. kidonoi* departs sharply in color pattern from it and all other species of *Drephalys*, apparently to mimic several common species of the silver-spotted skippers *Epargyreus* with which it is sympatric. We illustrate comparatively the larvae, pupae, adults, and genitalia of species of *Drephalys* (*Drephalys*) that are central to this paper.

Additional key words: *Drephalys* (*Drephalys*) *alcmon*; *Drephalys* (*Drephalys*) *kidonoi* Burns, new species; *Drephalys* (*Paradrephalys*) Burns, new subgenus; *Hirtella racemosa* (Chrysobalanaceae); *Roupala montana* (Proteaceae).

Once more, taxonomy and ecology join forces for the greater good.

A several-decade inventory of Lepidoptera larvae in the tropical dry forests of the Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica (Janzen & Hallwachs 1998) currently is focusing on the HesperIIDae or skipper butterflies (Burns & Janzen in prep.). Of some 190 species of pyrgine hesperiids now reared, at least two are new. The first, *Cephise nuspesez* Burns, joined a number of “known” species—which were buried in the wrong genus or in synonymy—to swell *Cephise* from a monotypic to a polytypic neotropical genus, tightly characterized by many aspects of

genitalic form (in both sexes), by a unique feature of the labial palpus, and by shared larval food plants (in the Malpighiaceae and Combretaceae) (Burns 1996). The fact that some species of *Cephise* have long hindwing tails while others do not, may explain why these skippers had never been seen as related, much less congeneric; but presence or absence of tails, though striking, can be taxonomically trivial. The second reared new species, *Drephalys kidonoi*, debuts here.

Because one ought not describe a new species without considering its taxonomic setting, Burns examined the genus *Drephalys* in as much detail as available material would allow. Unfortunately, this neotropical

genus of showy, medium large skippers is remarkably rare in collections. To illustrate, when Evans (1952) treated *Drephalys* (the most recent overall review), he included two taxa that were not represented in the vast hesperiid holdings of The Natural History Museum (BMNH); and he described three new species from single (or, in one case, a pair of) specimens. Evans also described what he called a new subspecies (*D. orian-der oria*, from Honduras) from just 3 specimens (*oria* Evans is actually a separate species, distinct from *oriander* [Hewitson] though related to it). One of the two new species of *Drephalys* that Mielke (1968) described from far southeastern Brazil (Santa Catarina) was based on a single male. One of the two new species that Austin (1995) described from westcentral Brazil (Rondônia) was based on 4 specimens. In reviewing a meager accumulation of *Drephalys* to develop a context for *D. kidonoi*, Burns already has discovered five more new species, represented by scant samples of 8, 6, 3, 1, and 1.

In sharp contrast, we have a huge sample of *D. kidonoi*—the type series amounts to 53 adults from Guanacaste—obtained almost entirely by rearing from 236 larvae found in nature. (Adults are far fewer than larvae because, in the course of rearing, many larvae were lost to parasitoids, fungi, and other diseases; and because some healthy reared adults were released.) Even though the larvae can be located with fair ease, only one adult has been caught in the wild. This, along with the general scarcity of *Drephalys* in collections, suggests adult behavior that tends to keep the skippers and their potential human captors apart. However, *Drephalys* is definitely diurnal, not crepuscular and/or nocturnal like some tropical skippers; and males are known to hilltop, though only for a very limited and specific period in any given day (Mielke 1968, pers. comm., Casagrande & Mielke 1992).

Watson (1893:34) proposed the genus *Drephalys* (with the type species *helixus* Hewitson) but did not define it well. Eleven genera later in the same paper, Watson (1893:39) also proposed the genus *Paradros* (with the type species *phoenice* Hewitson). Godman and Salvin (1894:349) immediately set these genera side by side, observing “There can be no doubt that *Drephalys* should be placed next *Paradros*, and the only question that arises is whether these two genera ought not to be merged into one.” While Mabille and Boulet (1919) still kept them separate but adjacent, Evans (1952:23) correctly listed *Paradros* as a synonym of *Drephalys*, remarking that “Typically these 2 genera appear very different, but they are connected by intermediate species and the genitalia conform to a general pattern.” Although his statement is partly true,

Drephalys as treated by Evans is gravely polyphyletic. Burns (1999) addressed this problem by removing morphologic misfits to the new and unrelated genus *Pseudodrephalys*.

Any lingering questions about the generic limits of *Drephalys* have no bearing on the inclusion of *kidonoi* for the simple reason that *kidonoi* is the sister species of *helixus*. Since *helixus* is the type species of *Drephalys*, the sister species *kidonoi* must also go in *Drephalys*. It will be treated together with *helixus* to document their similarity.

Drephalys heraclides Bell (1942:1), which is yet another species described from a single male (this time from “Peru”), was said in the original description to be “extremely like *helixus*.” Though Bell further noted that “The form of the male genitalia is similar in the two species, but the details materially differ,” he did not elaborate. Still known only from the holotype, *heraclides* is one of those taxa Evans (1952) never saw; and, as a result, he conservatively called it a subspecies of *D. helixus*. This is wrong. Study of the holotype of *heraclides* (borrowed from AMNH) and of Bell’s (1942:fig. 1) illustration of its genitalia (because the slide of its genitalia has been lost) shows not only that *D. heraclides* is a distinct species of *Drephalys* but also that it is morphologically farther from *D. helixus* than is *D. kidonoi*.

In connection with five species of *Drephalys* occurring in Rondônia, Brazil, Austin (1995:127) commented that “There appear to be a number of species groups in *Drephalys* with quite different genitalia of both sexes.” Even after Burns’s (1999) transfer of a pair of incredibly misplaced species—*atinas* (Mabille) and *hypargus* (Mabille)—from *Drephalys* to the distant new genus *Pseudodrephalys*, *Drephalys* is genitally complex. This complexity can be resolved into two readily characterizable groups that are highly distinct. Despite their differences, each is apparently the other’s nearest relative; so at this point in the analysis of hesperiid biodiversity, it is better to treat them as subgenera than as separate genera. A similarly cautious approach was taken in recognizing—but not overemphasizing—two useful, valid, well-differentiated divisions of the dusky wing skippers of the genus *Erynnis*: *Erynnis* (*Erynnis*) and *Erynnis* (*Erynnides*) (Burns 1964).

Drephalys (*Drephalys*) Watson, 1893:34
= *Paradros* Watson, 1893:39.

Type species. *Eudamus helixus* Hewitson (1877:320).

Male genitalia. Uncus with pair of caudally projecting prongs that form **U** (Figs. 1, 3) or **V** in dorsal or ventral view. In lateral view, juxta either at level of vinculum or considerably anterior to it (Figs. 2, 4). If present, any dorsal projection from sacculus (i.e., sclero-

TABLE 1. Species of *Drephalys* (*Drephalys*).

<i>alcmon</i> (Cramer)	<i>olva</i> Evans
<i>eous</i> (Hewitson)	<i>olvina</i> Evans
<i>helixus</i> (Hewitson)	<i>opifex</i> Evans
<i>heraclides</i> Bell	<i>phoenice</i> (Hewitson)
<i>kidonoi</i> Burns	<i>phoenicoides</i> (Mabille & Boulet)
<i>miersi</i> Mielke	4 undescribed species
<i>mourei</i> Mielke	

tized, anteroventral portion of inner lamina of valva) arises from proximal part of sacculus (Figs. 2, 4); apart from this projection, sacculus slopes sharply downward from anterior to posterior in lateral view (Figs. 2, 4). At least slightly dentate process arising from distal end of valva curves mostly mediad (Figs. 1, 3), but sometimes also dorsad (Figs. 2, 4) or caudad (or even cephalad so as to be recurved). Below this dentate, medially curved process, ventrodiscal corner of valva usually rounded and extended slightly (Figs. 2, 4) to moderately caudad, but sometimes prolonged into blunt point. Above the dentate, medially curved process, dorsodistal corner of valva ranges from completely undeveloped or slightly developed (Figs. 1–4) to a small to large process, variable in orientation and degree of dentation (rarely none). Aedeagus with very short to very long subterminal to terminal (Figs. 1–4) titillator on left side. Vesica long, delicate, fingerlike, with 1–14 needlelike cornuti (almost always in cluster) at distal end (Figs. 1, 3). In dorsal or ventral view, anterior end of saccus pointed (Figs. 1, 3), keeled, or narrowly rounded.

Female genitalia. Posterior portion of ductus bursae, which is well-sclerotized, extending well anterior of sterigma (Figs. 5–8) and flattened dorsoventrally, at least anterior (Figs. 6, 8). Thereafter, ductus bursae both narrow and long (Figs. 5–8). Altogether, bursa copulatrix takes rather indirect course from posterior to anterior (Figs. 5–8) (except in some individuals of *D. alcmon* [Cramer] and presumably also *D. mourei* Mielke [female unknown]). Lamella antevaginalis and lamella postvaginalis distinct from each other (Figs. 5–8) rather than fused and inseparable. Lamella antevaginalis a more or less simple, narrow band which may (Figs. 5–8) or may not be sclerotized midventrally; it forms conspicuous, paired, more or less caudally pointing, sharp projections immediately lateral to ostium bursae (Figs. 5–8) (except in *D. alcmon* and presumably *D. mourei*). Lamella postvaginalis a ventrally convex plate with midventral **U** or **V** in its posterior margin (Figs. 5–8).

Costal fold of male. Well-developed to vestigial or absent.

Wingshape. Hindwing elongate (Figs. 9–20), appreciably longer than wide (more so in males [Figs. 9, 10, 13, 14, 17, 18] than in females [Figs. 11, 12, 15, 16, 19, 20]), and clearly lobed at end of vein 1b (Figs. 9–16, 19, 20 [lobes of male in Figs. 17, 18 damaged]).

Included species. N = 16 (Table 1).

Drephalys (*Paradrephalys*) Burns, new subgenus

Type species. *Hesperia dumeril* Latreille (1824:757).

Male genitalia. Uncus truncate, with no long caudally projecting prongs in dorsal or ventral view. In lateral view, juxta begins at level of vinculum and extends posteriorly beneath aedeagus. Tall, dorsal projection arises from distal part of sacculus (i.e., sclerotized, anteroventral portion of inner lamina of valva); apart from this projection, sacculus nearly or quite uniform in height from anterior to posterior in lateral view. Process arising from middle part of dorsal margin of valva extends mostly caudad, usually becoming at least slightly dentate distally. Narrow, slightly dentate process arising from distal end of valva extends mostly dorsad to overlap aforementioned process. Valva at its ventrodiscal corner so totally undeveloped as to be “chinless” in lateral view. Aedeagus short, relatively stout, and devoid of titillators (although sometimes very finely dentate ventrolaterally or midlaterally, on one or both sides, slightly before its posterior tip). Short, fat vesica everts caudally but especially to right and sports numerous (11–33) needlelike cornuti in several loose assem-

TABLE 2. Species of *Drephalys* (*Paradrephalys*).

<i>croceus</i> Austin	<i>talboti</i> (Le Cerf)
<i>dumeril</i> (Latreille)	<i>tortus</i> Austin
<i>oria</i> Evans	1 undescribed species
<i>oriander</i> (Hewitson)	

blages. In dorsal or ventral view, anterior end of saccus expanded or broadly rounded.

Female genitalia. Posteriormost portion of ductus bursae a cylindrical tube, well-sclerotized—except for broad, middorsal, clear strip—and so short that it extends only slightly anterior of sterigma. Sterigma reflects major fusion between lamellae antevaginalis and postvaginalis. At posterior end of ductus bursae, parts of lamella antevaginalis that are closely appressed to its sides meet midventrally to form (in ventral view) a large **U** or **V** (which opens caudally) just ventrad of ostium bursae. Posterior to this, lamella postvaginalis forms another large (and similarly oriented) midventral **U** or **V**. All of the above framed laterally by paired, (essentially) parallel, large, thin, vertical plates extending ventrad from sterigma (so as to be seen on edge in ventral view). Although these long, thin plates closely flank the central equipment, they leave a deep fissure on either side of it. Immediately dorsal and lateral to all of above—about halfway up sides of sterigma—a conspicuous, somewhat fingerlike and caudally pointing, unsclerotized area extends two-thirds distance from anterior to posterior margin of sterigma. Seen ventrally, entire sterigma tends to look long, narrow, and more or less rectangular. Immediately anterior of point where posterior sclerotized tube of ductus bursae becomes membranous, ductus swells to large sac (which may have folded, sclerotized plate in its walls) and then constricts sharply before expanding anteriorly into corpus bursae. Altogether, bursa copulatrix takes rather direct course from posterior to anterior.

Costal fold of male. Well-developed.

Wingshape. Hindwing roundish, nearly as wide as long (more so in females than in males), and barely lobed at end of space 1b.

Included species. N = 7 (Table 2).

The *helixus/kidonoi* species pair of *Drephalys* (*Drephalys*)

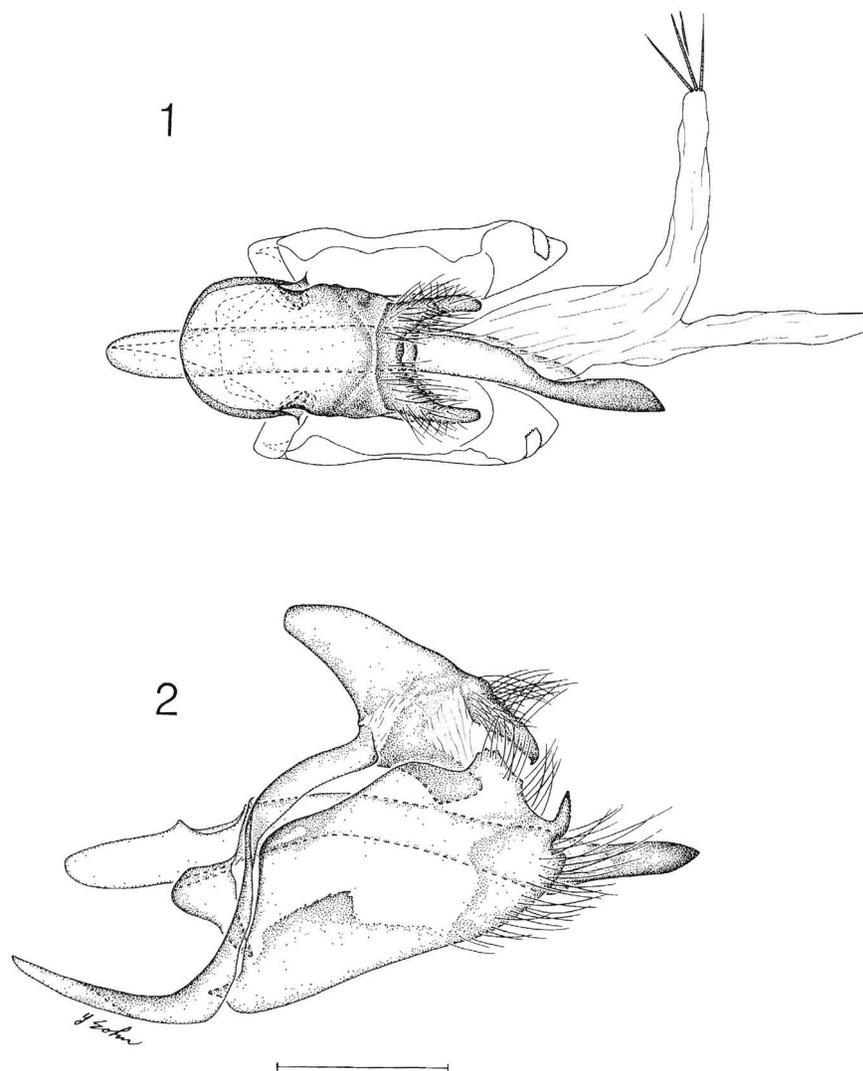
Male genitalia. Dorsal projection arising from proximal part of sacculus uniquely long from anterior to posterior and finely dentate dorsally (Figs. 2, 4). In dorsal or ventral view, saccus tapers anteriorly to extremely delicate, sharp point (Figs. 1, 3). In lateral view, distal end of valva roughly truncate, with no major development of dorsodistal corner, but with narrow, finely dentate process (which extends mediad, dorsad, and caudad) arising closer to ventrodiscal corner of valva than to dorsodistal corner (Figs. 2, 4).

Female genitalia. Anteriorly, where the well-sclerotized posterior portion of the ductus bursae abruptly becomes membranous and sharply decreases in diameter, a large, blind, membranous sac extends at least slightly to the right; and the narrowed, membranous ductus bursae angles dorsad, perpendicular to its sclerotized course, before continuing anteriorly to the corpus bursae (Figs. 5–8).

Costal fold of male. Narrow (*helixus*) or almost vestigial (*kidonoi*).

Number of antennal nudum segments. High (Table 3). Although there are too few specimens of other species of *Drephalys* to include the conspicuously variable nudum in the preceding subgeneric characterizations with confidence, there are enough to indicate that the mean number of nudum segments is greater in *helixus* and *kidonoi* than it is in other species of *Drephalys*. Moreover, the mean number of nudum segments is clearly greater in females than it is in males (Table 3). Evans (1952:6) said for *Drephalys* “Nudum typically 16/15, arcuate or hooked”; but his total of 31 segments is a little too low to be typical for this genus.

Palpus. Third segment of palpus (which in *Drephalys* and its relatives is not centered on the second segment but, instead, shifted



FIGS. 1, 2. Male genitalia of *Drephalys* (*Drephalys*) *kidonoi* (paratype) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 92-SRNP-445) (J. M. Burns genitalic dissection no. X-3422) (USNM); scale = 1.0 mm. **1**, Tegumen, uncus, gnathos, and aedeagus [all stippled] with everted vesica and cornuti (plus cut, everted sperm duct), as well as both valvae, vinculum, juxta, and saccus [all outlined] in dorsal view. Rotating the genitalia until the top of the tegumen/uncus is about flat makes the underlying structures look shorter than they do in the lower figure (but the scale is the same in both figures). **2**, Complete genitalia (minus right valva and everted vesica and cornuti) in left lateral view.

conspicuously laterad—see Burns 1999:figs. 19, 20) unusually short, protruding less far anterior of second segment than in other species of *Drephalys*. (Note that in *Drephalys* generally, the third segment of the palpus is shorter in males than it is in conspecific females.)

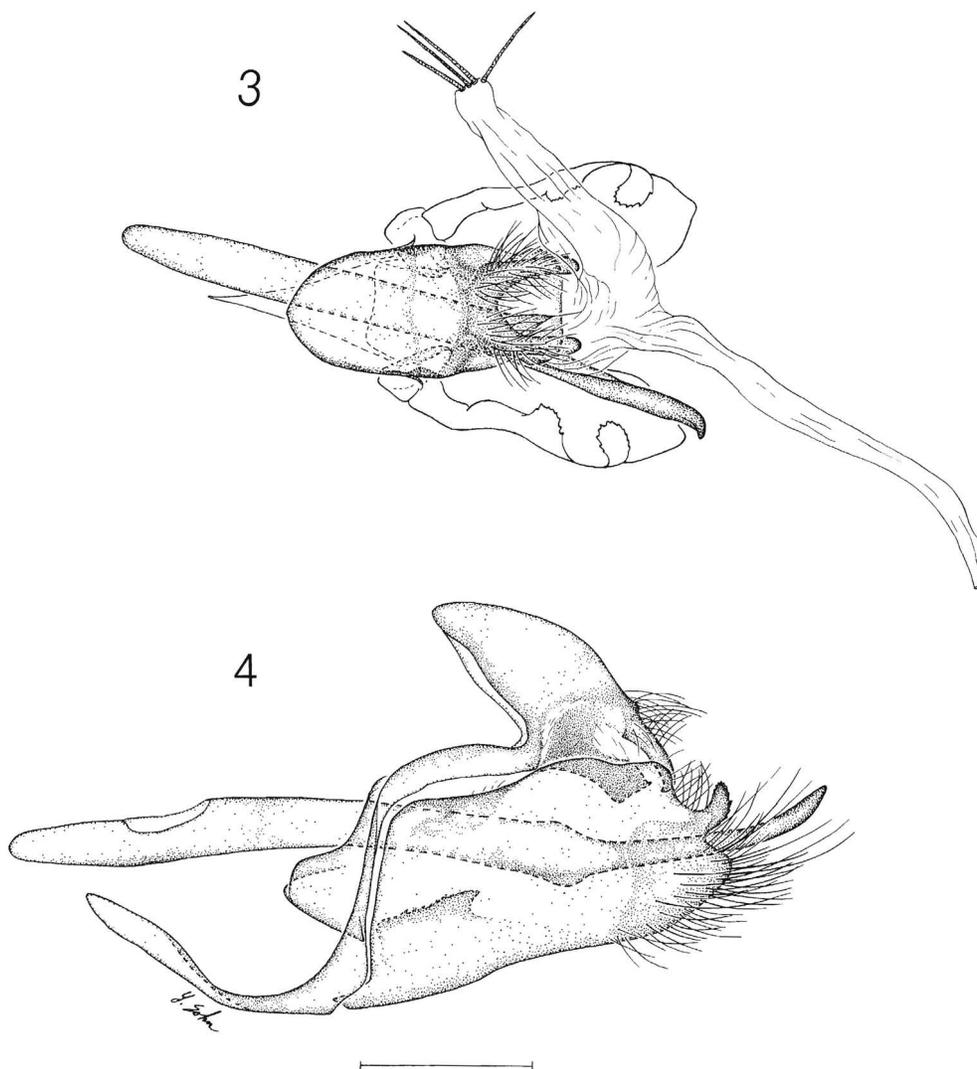
TABLE 3. Number of antennal nudum segments in sister species of *Drephalys* (*Drephalys*).

Species	Sex	N	Range	Mean
<i>D. helixus</i>	♂	18	33–37	35.3
"	♀	1	40	40
<i>D. kidonoi</i>	♂	27	30–42	35.0
"	♀	22	34–51	40.8

Size. Among the larger species of *Drephalys*. As usual in hesperiids, males average smaller than coexisting females (Table 4). Although *helixus* from Panama looks a little larger than *kidonoi* (Table 4), the difference may not be real: all specimens of *helixus* are wild-caught whereas all measured specimens of *kidonoi* are reared, with the likely result that most are appreciably stunted.

Drephalys (*Drephalys*) *kidonoi* Burns, new species

Male genitalia. Aedeagus shorter than that of *helixus*, owing mainly to titillator. Titillator (i.e., caudal extension of left side of aedeagus, beginning where vesica emerges) shorter by half, as well as stouter (Figs. 1, 2), than that of *helixus* (Figs. 3, 4) and not turned slightly up at distal end. Saccus also shorter (a condition almost certainly correlated with the reduced aedeagal length). Body of aede-



FIGS. 3, 4. Male genitalia of *Drephalys (Drephalys) helix* from Rodman, 8°58'N 79°35'W, Canal Zone, PANAMA, 22 December 1972 (G. B. Small) (J. M. Burns genitalic dissection no. X-4254) (USNM); scale = 1.0 mm. **3**, Tegumen, uncus, gnathos, and aedeagus [all stippled] with everted vesica and cornuti (plus cut, everted sperm duct), as well as both valvae, vinculum, juxta, and saccus [all outlined] in dorsal view. Rotating the genitalia until the top of the tegumen/uncus is about flat makes the underlying structures look shorter than they do in the lower figure (but the scale is the same in both figures). The oblique position of the aedeagus is unnatural. **4**, Complete genitalia (minus right valva and everted vesica and cornuti) in left lateral view.

gus, in lateral view (Fig. 2), bowed more dorsad than in *helix* (Fig. 4). Process arising from distal end of valva a little less conspicuously dentate (Figs. 1, 2) than in *helix* (Figs. 3, 4) and straight along its dorsal margin (Figs. 1, 2) rather than slightly convex as in *helix* (Figs. 3, 4).

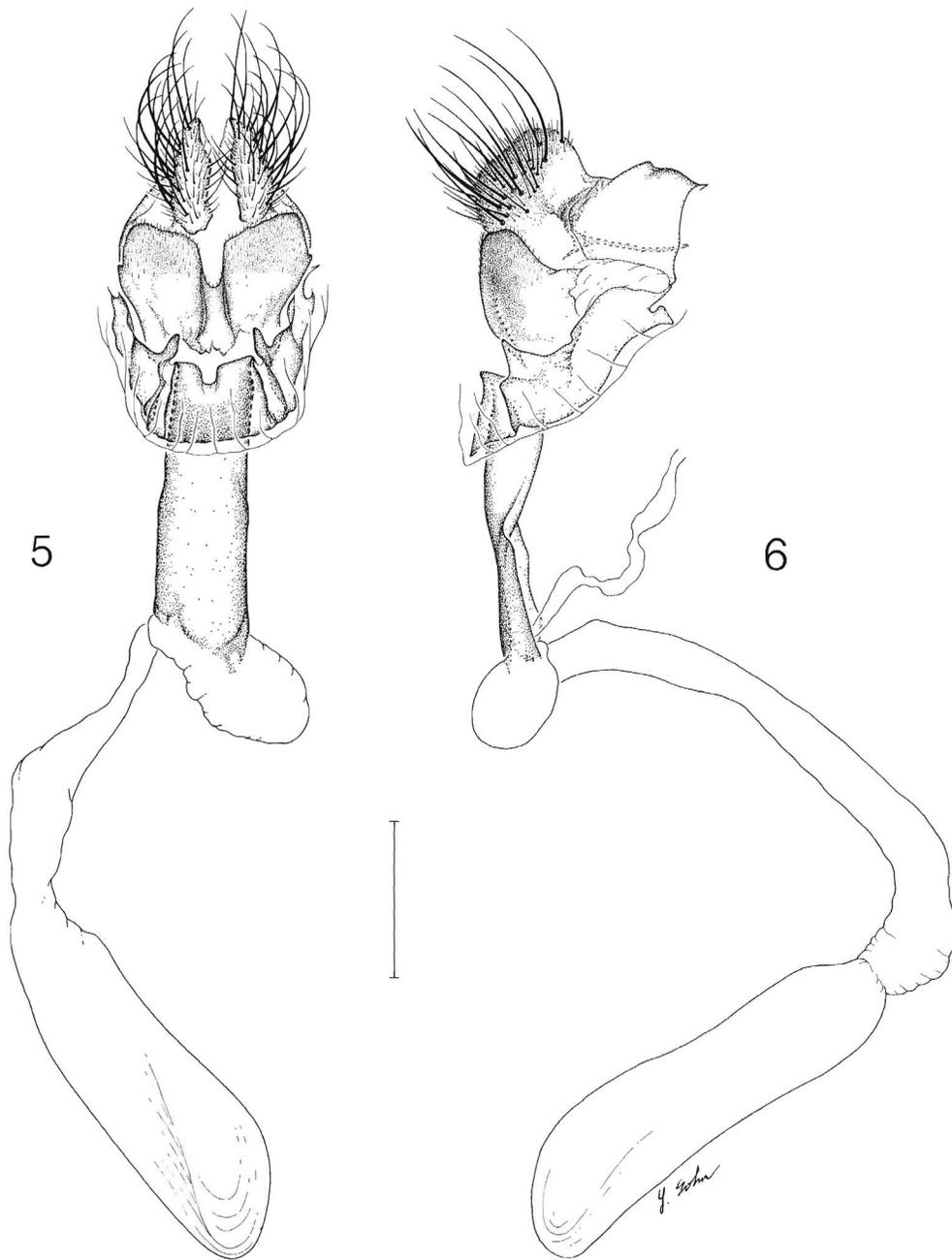
TABLE 4. Forewing length (mm) in sister species of *Drephalys (Drephalys)*.

Species	Locality	Sex	N	Range	Mean
<i>D. helix</i>	Brazil	♂	3	22.7–23.9	23.20
"	Panama	♂	15	20.6–22.2	21.49
"	"	♀	1	23.6	23.6
<i>D. kidonoi</i>	Costa Rica	♂	28	17.0–22.0	20.22
"	"	♀	24	19.0–24.7	22.22

Female genitalia. Lamella postvaginalis deeply notched midventrally in its posterior margin and grooved midventrally along its entire length (Fig. 5) rather than shallowly notched and grooveless as in *helix* (Fig. 7). Immediately farther anterior, at posterior end of ductus bursae, at least a small midventral notch (Fig. 5) not present in *helix* (Fig. 7). Sclerotized portion of ductus bursae flattened dorsoventrally in its anterior half (Fig. 6) instead of its anterior two-thirds as in *helix* (Fig. 8). Paired, caudally pointed projections from lamella antevaginalis (immediately lateral to ostium bursae) shorter, less delicate, and originating farther posterior (Figs. 5, 6) than in *helix* (Figs. 7, 8).

Costal fold of male. Present but exceedingly narrow (much narrower than that of *helix*)—almost vestigial.

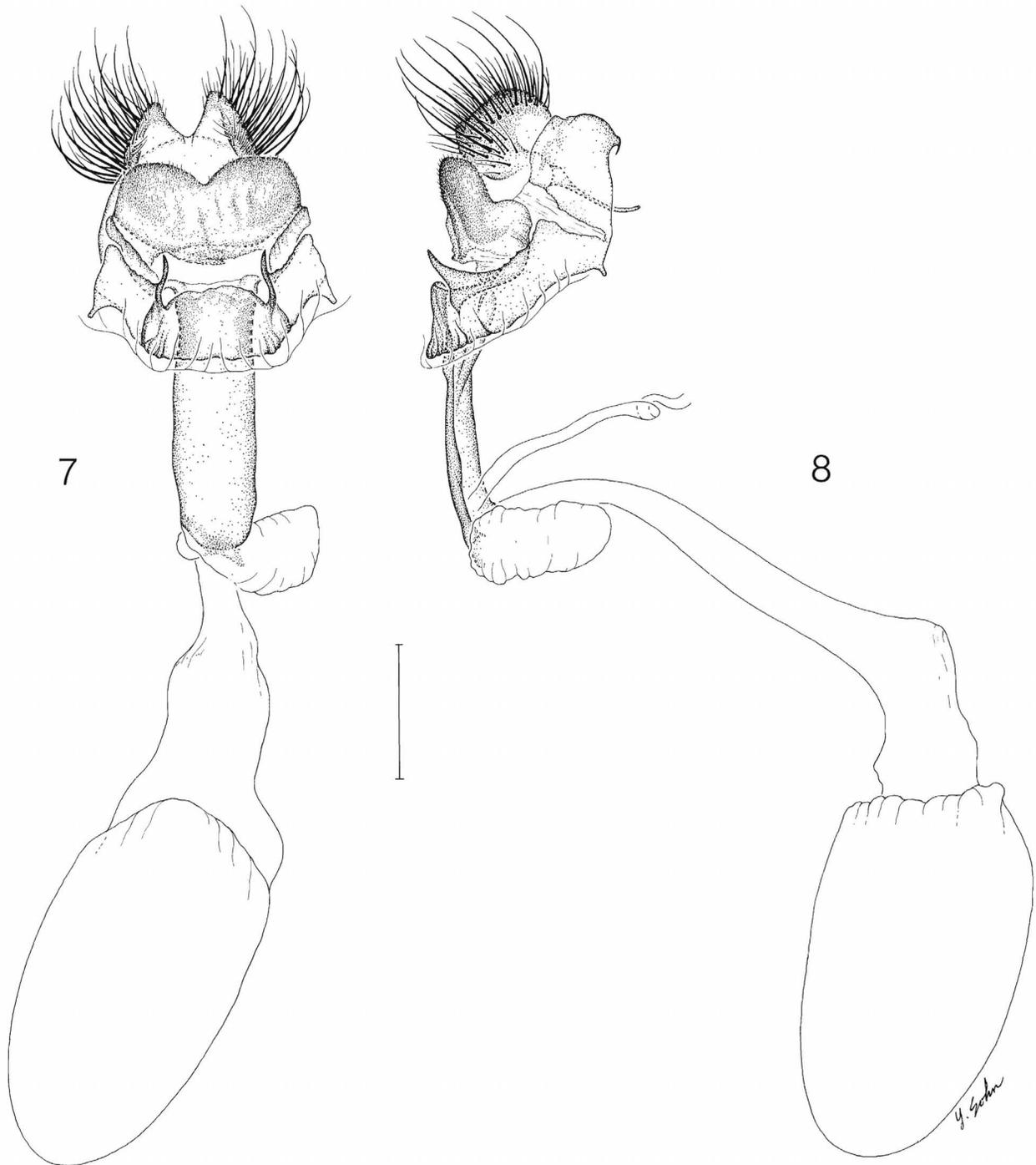
Facies/mimicry. Unique among species of *Drephalys: kidonoi* (Figs. 9–12) departs sharply from a more usual *Drephalys* appearance (as, for example, in *helix* [Figs. 13–16]) to suggest several



FIGS. 5, 6. Female genitalia of *Drephalys (Drephalys) kidonoi* (paratype) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 92-SRNP-480) (J. M. Burns genitalic dissection no. X-3423) (USNM); scale = 1.0 mm. **5**, Ovipositor lobes, sterigma, and bursa copulatrix in ventral view. **6**, The same, plus part of the ductus seminalis, terminal abdominal tergite, and posterior apophysis, in right lateral view.

common species of the silver-spotted skippers *Epargyreus* with which it is sympatric. On the forewing, this involves (a) eliminating (Figs. 9–12) the spot in space 1b (Figs. 13–20); (b) reducing to tiny points or, more often, completely eliminating (Figs. 9–12) the small subapical spots in spaces 6, 7, and 8 (Figs. 13–20); (c) reducing (Figs. 11, 12) or eliminating (Figs. 9, 10) the outer cell spot (Figs. 13–20); and (d) suppressing (Figs. 10, 12) the yellow coloration along the proximal half of the ventral costal margin (Figs. 14, 16, 18,

20). On the hindwing, this involves (dorsally) more or less suppressing (Figs. 9, 11) what is normally a conspicuous double row of spots (Figs. 13, 15); and (ventrally) shortening and making less regular (Figs. 10, 12) a conspicuous central white stripe (Figs. 14, 16). On both wings, this involves (dorsally) intensifying the color of proximal scales—to an orangy yellow—to heighten the contrast with more distal ones (Figs. 9, 11); and (ventrally) adding lavender overscaling broadly along the outer margins (Figs. 10, 12). The total effect is one

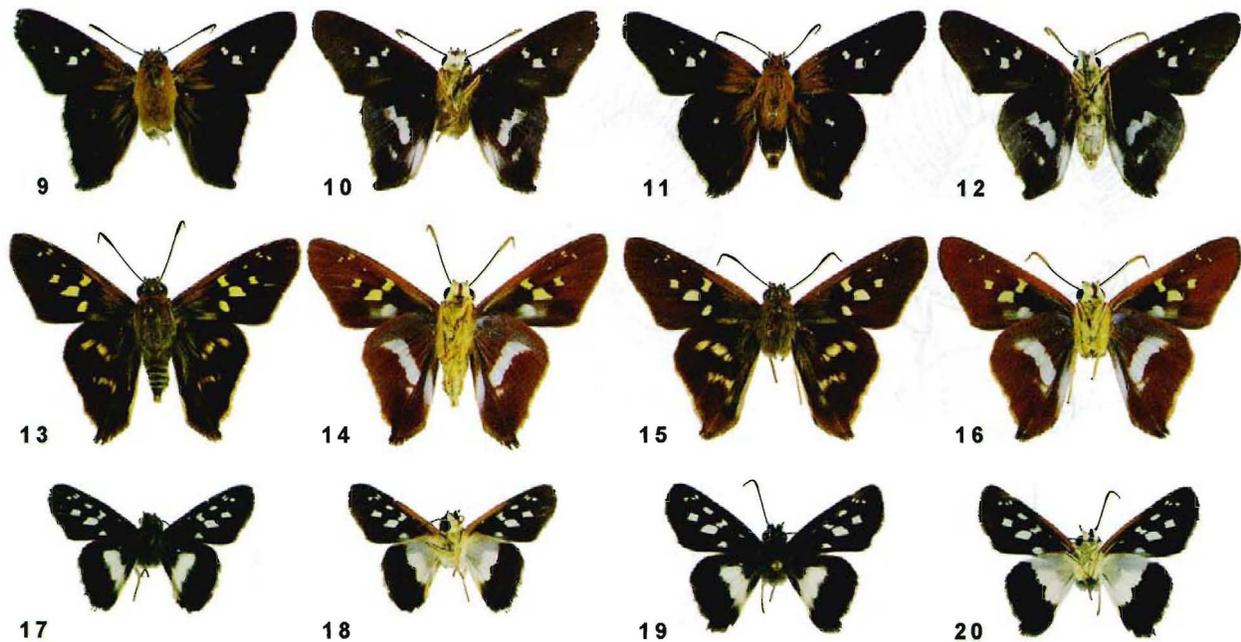


FIGS. 7, 8. Female genitalia of *Drephalys (Drephalys) helix* from Rodman Naval Station, Canal Zone, PANAMA, 9 January 1972 (S. S. Nicolay) (J. M. Burns genitalic dissection no. X-4263) (USNM); scale = 1.0 mm. **7**, Ovipositor lobes (by chance, wider apart than in Fig. 5), sterigma, and bursa copulatrix in ventral view. **8**, The same, plus part of the ductus seminalis, terminal abdominal tergite, and posterior apophysis, in right lateral view.

of apparent mimicry. Because the hindwing is a little less elongate in *kidonoi* (Figs. 9–12) than it is in *helix* (Figs. 13–16), *kidonoi* even approaches the wingshape of *Epargyreus*.

Larval food plant. *Roupala montana* Aublet (Proteaceae).

Types. *Holotype*: COSTA RICA, PROVINCIA GUANACASTE, Area de Conservacion Guanacaste, Sector Poco Sol, Poco Sol, 270 m, Janzen & Hallwachs rearing voucher 91-SRNP-2736, adult emergence date 20 Feb 1992, ♂, genitalia no. X-4243 J. M. Burns 1997;



FIGS. 9–20. Males and females of *Drephalys* (*Drephalys*) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA (reared) and from Rodman, Canal Zone, PANAMA (wild-caught) in dorsal (odd-numbered) and ventral (even-numbered) views ($\times 0.85$) (all USNM). **9, 10**, *D. kidonoi* ♂, holotype, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 91-SRNP-2736) (J. M. Burns genitalic dissection no. X-4243). **11, 12**, *D. kidonoi* ♀, paratype, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 92-SRNP-345). **13, 14**, *D. helixus* ♂, PANAMA, 28 November 1974, G. B. Small. **15, 16**, *D. helixus* ♀, PANAMA, 9 January 1972, S. S. Nicolay (J. M. Burns genitalic dissection no. X-4263). **17, 18**, *D. alcmon* ♂, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 96-SRNP-1047) (J. M. Burns genitalic dissection no. X-4248). **19, 20**, *D. alcmon* ♀, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 96-SRNP-1090) (J. M. Burns genitalic dissection no. X-4249).

deposited in National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes $N = 52$ (27 ♂, 25 ♀). *Reared Paratypes (with emergence dates)*: COSTA RICA, PROVINCIA GUANACASTE, Area de Conservacion Guanacaste: Sector El Hacha, Casa Oeste, 420 m, 93-SRNP-8708, 21 Jan 94, ♀; 93-SRNP-8712, 17 Mar 94, ♂; 93-SRNP-8738, 22 Jan 94, ♀; 93-SRNP-8740, 17 Jan 94, ♂; 94-SRNP-19, 5 Mar 94, ♂; 94-SRNP-20, ♀, X-4489; 94-SRNP-22, 31 Jan 94, ♀; 94-SRNP-25, 24 Jan 94, ♂; 94-SRNP-27, 11 Mar 94, ♂; 94-SRNP-29, ♀, ♂; 94-SRNP-31, 22 Feb 94, ♂; 94-SRNP-32, 5 Mar 94, ♂. Sector El Hacha, Vado Rio El Hacha, 290 m, 94-SRNP-879, 2 Jun 94, ♀; 94-SRNP-882, 11 Jul 94, ♂, X-4246. Sector Orosi, Estacion Maritza, 520 m, 95-SRNP-378, 14 Mar 95, ♂, X-4491. Sector Poco Sol, Poco Sol, 270 m, 91-SRNP-2737, 21 Feb 92, ♀; 92-SRNP-361, 20 Mar 92, ♂; 92-SRNP-379, 21 Mar 92, ♀; 92-SRNP-380, 5 Mar 92, ♀, X-4244; 92-SRNP-385, 27 Mar 92, ♀; 92-SRNP-386, 18 Apr 92, ♀; 92-SRNP-400, 21 Mar 92, ♀, X-4247; 92-SRNP-403, 23 Mar 92, ♂; 92-SRNP-410, 5 Mar 92, ♀; 92-SRNP-419, 14 Mar 92, ♀; 92-SRNP-426, 15 Apr 92, ♂; 92-SRNP-433, 10 Mar 92, ♂, X-4245; 92-SRNP-435, 21 Mar 92, ♂; 92-SRNP-437, 24 Mar 92, ♂; 92-SRNP-438, 15 Apr 92, ♀; 92-SRNP-441, 12 Mar 92, ♂, X-4487; 92-SRNP-444, 18 Mar 92, ♂; 92-SRNP-445, 29 Feb 92, ♂, X-3422; 92-SRNP-450, 18 Mar 92, ♀, X-4488; 92-SRNP-455, 15 Mar 92, ♀; 92-SRNP-458, 5 Apr 92, ♂; 92-SRNP-466, 30 Mar 92, ♂; 92-SRNP-470, 21 Apr 92, ♀; 92-SRNP-473, 5 Apr 92, ♀; 92-SRNP-477, 2 Mar 92, ♂, X-4278; 92-SRNP-480, 6 Mar 92, ♀, X-3423; 92-SRNP-498, 15 Apr 92, ♂; 92-SRNP-639, 29 Apr 92, ♀. Sector Poco Sol, Quebrada Aserradero, 160 m, 92-SRNP-354, 7 Apr 92, ♀; 92-SRNP-366, 13 Mar 92, ♂; 92-SRNP-370, 3 Mar 92, ♀; 92-SRNP-377, 23 Mar 92, ♂; 92-SRNP-698, 9 Jun 92, ♂; 94-SRNP-641, 8 May 94, ♂. Sector Santa Rosa, Cruz de Piedra, 290 m, 92-SRNP-345, 29 Feb 92, ♀. Sector Santa Rosa, Porton de Los Perros, 300 m, 94-SRNP-870, ♀, X-4490.

Wild-caught paratype: COSTA RICA, PROVINCIA GUANACASTE, Comelco, 8 km N Bagaces, 50 m, 24 May 1972, ♀, P. A. Opler (CAS).

Etymology. Named in honor of Dr. Hiroshi Kidono of the Japan International Cooperation Agency who is an enthusiastic and dedicated supporter of the INBio and ACG parataxonomists' research on the caterpillars of the HesperIIDae of Costa Rica.

NATURAL HISTORY OF *DREPHALYS KIDONOI* AND *DREPHALYS ALCMON*

As stated above, just one adult of *D. kidonoi* has been collected in nature, although larvae have often been found eating both new and mature leaves of *Roupala montana* (Proteaceae), the only known host plant. This shrubby tree is abundant on the poor soils and rocky pastures in the central portion of the ACG at 100–500 m elevation (Figs. 31, 32). Since *R. montana* occurs throughout the dry forest remnants in Pacific coastal Mesoamerica, since it “ranges from Veracruz, Mexico, to Peru, Bolivia, and Brazil” (Burger 1983:14), and since adults of *D. kidonoi* elude collectors, we infer that this skipper is more widespread. In this connection, note that its sister species, *D. helixus*, is represented (a) in the USNM by 14 ♂ 1 ♀, all taken at a single, hilltop locality (Rodman) in the former Canal

Zone of Panama (on 12 different days in 5 different years), (b) in the AMNH by 1 ♂ from Balboa in the former Canal Zone of Panama, and (c) in the BMNH by 6 ♂, all from Panama (Evans 1952)—which suggests a geographically limited species. But it most certainly is not: Mielke, Miers, and Casagrande (Mielke pers. comm.) have caught 28 ♂ of *D. helixus* (only 1 or 2 on any given day, and always on hilltops) very far away in the southern Brazilian states of Santa Catarina (24 ♂ at Joinville) and São Paulo (3 ♂ at Morro do Diabo, Teodoro Sampaio) and in the city of Rio de Janeiro (1 ♂) (specimens in UFPR, 3 of them donated to USNM and examined by Burns); and C. Callaghan has caught 1 ♂ (on a hilltop at km 500 of the Belo Horizonte-Brasília highway) in Minas Gerais, the next Brazilian state to the north (specimen seen by Burns).

Drephalys kidonoi larvae (Figs. 21–23) are unlikely to be confused with any other hesperiid larvae known from the ACG. The dorsal and lateral part of the body is sharply, and rather narrowly, banded black on a whitish to greenish white background, while the head (which is slightly rugose) is pale to dark orange and devoid of markings. The black bands are broken by the whitish ground color just anterior to the spiracles on all segments but the first two and the last three. This banded color pattern starts to appear in the second instar; the first instar larva is green (once it has fed) with a black head. When the larva changes to a prepupa, the ground color becomes creamy, and the black bands, light beige (Fig. 23). The head may become lighter orange at this time.

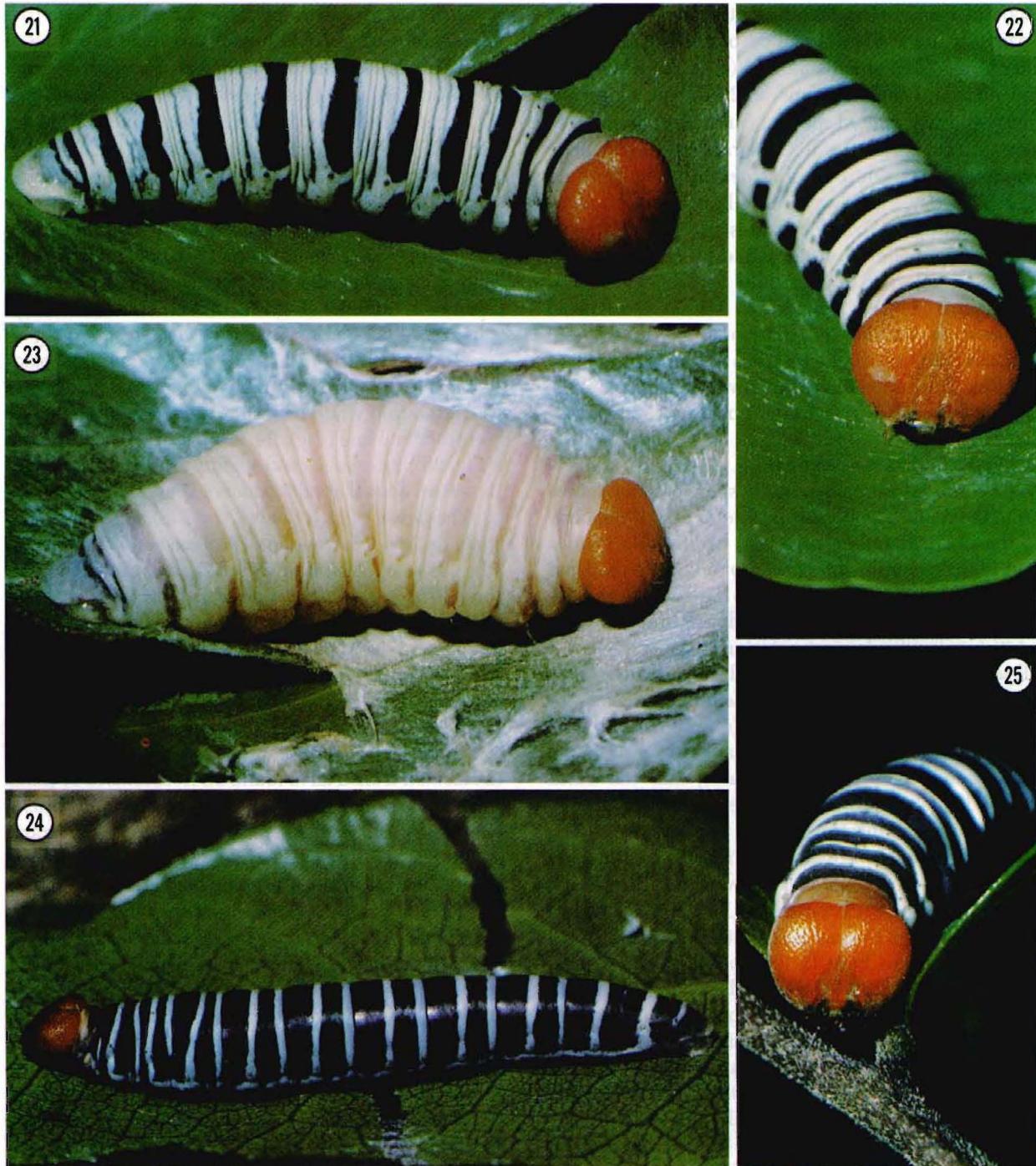
Drephalys alcmon (Cramer) (Figs. 17–20), the only other species of *Drephalys* known from the ACG, ranges widely from Guatemala (1 ♀ from Cayuga in USNM) through Central and South America to Brazil and southeastern Peru (1 ♀ from ~30 km SW Puerto Maldonado in USNM)—as well as the island of Trinidad (Cock 1984). Brazilian specimens come from northern and central states—Roraima: Ilha de Maraca, Alto Alegre (UFPR); Rondônia: Fazenda Rancho Grande, Cacauplândia (Austin 1995, UFPR), Fazenda Urupa, Candeias do Jamari (UFPR); Pará (Evans 1952): Belém (Moss 1949), 15 km S Itaituba (USNM), Óbidos (UFPR), Santarém (UFPR); Mato Grosso: Alto Rio Arinos, Diamantino (USNM), Barra dos Bugres (UFPR), Fazenda Parana, Brasnorte (UFPR); Goiás: Goiás Velho (UFPR), Ilha do Bananal (UFPR); Pernambuco: Camaragibe, Recife (UFPR); and Espírito Santo: Linhares (UFPR). The latitude of the southernmost record (Linhares, Brazil, 19°25'S) is slightly higher than that of the northernmost record (Cayuga, Guatemala, 15°32'N). However, *D. alcmon*

probably occurs as far north as southern Mexico (the distribution of its larval food plant would allow this—see below). When he recorded *D. alcmon* from Rondônia, Brazil, Austin (1995:127) gave for the rest of its range only “northeastern South America.” In his list of BMNH holdings, Evans (1952:27) included, besides specimens from the Guianas and Amazonian Brazil, “1 ♀ ‘Honduras’”; but the quotation marks were his way of questioning the accuracy of a locality label.

Adults of *D. alcmon* (Figs. 17–20) are superficially and morphologically well removed from the sister species *D. kidonoi* (Figs. 9–12) and *D. helixus* (Figs. 13–16). Although the larva of *D. alcmon* shares a general color pattern with that of *D. kidonoi*, its black bands are so broad that the white ground color is reduced to thin white bands connected to a thin, white ventrolateral line (Figs. 24, 25). Viewed from the front (Fig. 25), its orange (and slightly rugose) head bulges less than does that of *D. kidonoi* (Fig. 22).

The larvae of *D. kidonoi* (N = 236) apparently feed only on *Roupala montana* (Proteaceae). In the ACG, the larvae of *D. alcmon* (N = 70) apparently feed only on *Hirtella racemosa* Lamarck (Chrysobalanaceae) (Burns & Janzen in prep., Janzen & Hallwachs 1998), a quite unrelated plant—but a common one that spans the neotropics from central and southern Mexico to southeastern Peru, Bolivia, and northeastern São Paulo, Brazil (Prance & Campbell 1988, Prance 1989). In 1998, Aiello (pers. comm.) reared an adult male of *D. alcmon* from a larva found on *H. racemosa* in Loma del Río, Arraiján, Panama province, Panama (Aiello Lot 98-9). But in the vicinity of Belém, Pará, Brazil, Moss (1949:59) reared *D. alcmon* from larvae found on two food plants that were incompletely determined as “*Parinarium* or *Couepia*, Rosaceae.” “*Parinarium*” is presumably *Parinari*; and both *Parinari* and *Couepia* are now in the Chrysobalanaceae, along with *Hirtella*. Indeed, *Couepia* and *Hirtella* are sister genera, extremely closely related (Prance pers. comm.). Moss (1949:59) reared one other species of *Drephalys*, *D. eous* (Hewitson), whose “larval shelters [he] commonly observed in the forest on the leaves of . . . *Vochysia vismiaefolia* Spruce” (Vochysiaceae). So far (but admittedly it is not very far), different species of *Drephalys* seem to be specializing on food plants in taxonomically unallied families (Proteaceae, Chrysobalanaceae, and Vochysiaceae).

The drawings of last instar *Drephalys* larvae in Moss (1949:pl. I) are both black-and-white and small. Still, his *D. eous* larva (fig. 9) closely resembles our *D. kidonoi* larva (Figs. 21–23). However, his *D. alcmon* larva (fig. 11) is one in which every other vertical, thin, white band of ground color fails to reach the horizon-

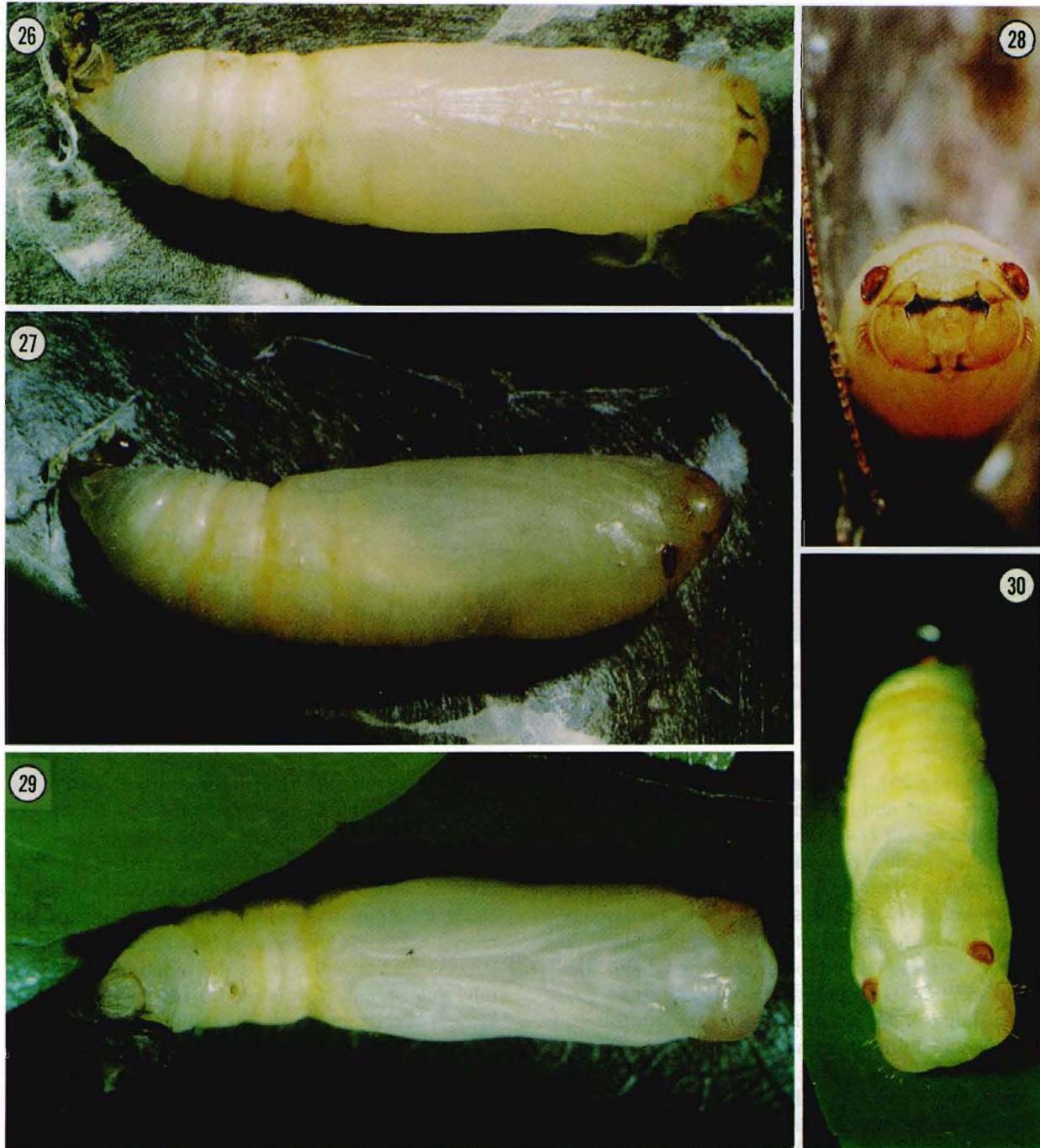


FIGS. 21–25. Larvae of two species of *Drephalys* (*Drephalys*) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA. **21**, *D. kidonoi* last instar larva in dorsolateral view (93-SRNP-8715, 11 January 1994). **22**, *D. kidonoi* last instar larva in anterior view (93-SRNP-8715, 11 January 1994). **23**, *D. kidonoi* prepupal larva in dorsolateral view (94-SRNP-147, 11 January 1994). **24**, *D. alcmon* penultimate instar larva in dorsolateral view (94-SRNP-8577, 10 October 1994). **25**, *D. alcmon* last instar larva in anterior view (96-SRNP-1091, 22 May 1996).

tal, thin, white ventrolateral line, something that happens only once, near the anterior end, in our examples of *D. alcmon* (Figs. 24, 25).

For both *D. eous* and *D. alcmon*, Moss (1949:59) notes that “the pupa squeaks audibly when touched.”

In all instars, the larva of *D. kidonoi* forms its shelter by silking together two halves of a leaflet (*R. montana* has pinnately compound leaves), thus folding the leaflet along its midrib so that its upper surface is inside the shelter. Search for larvae is greatly facilitated

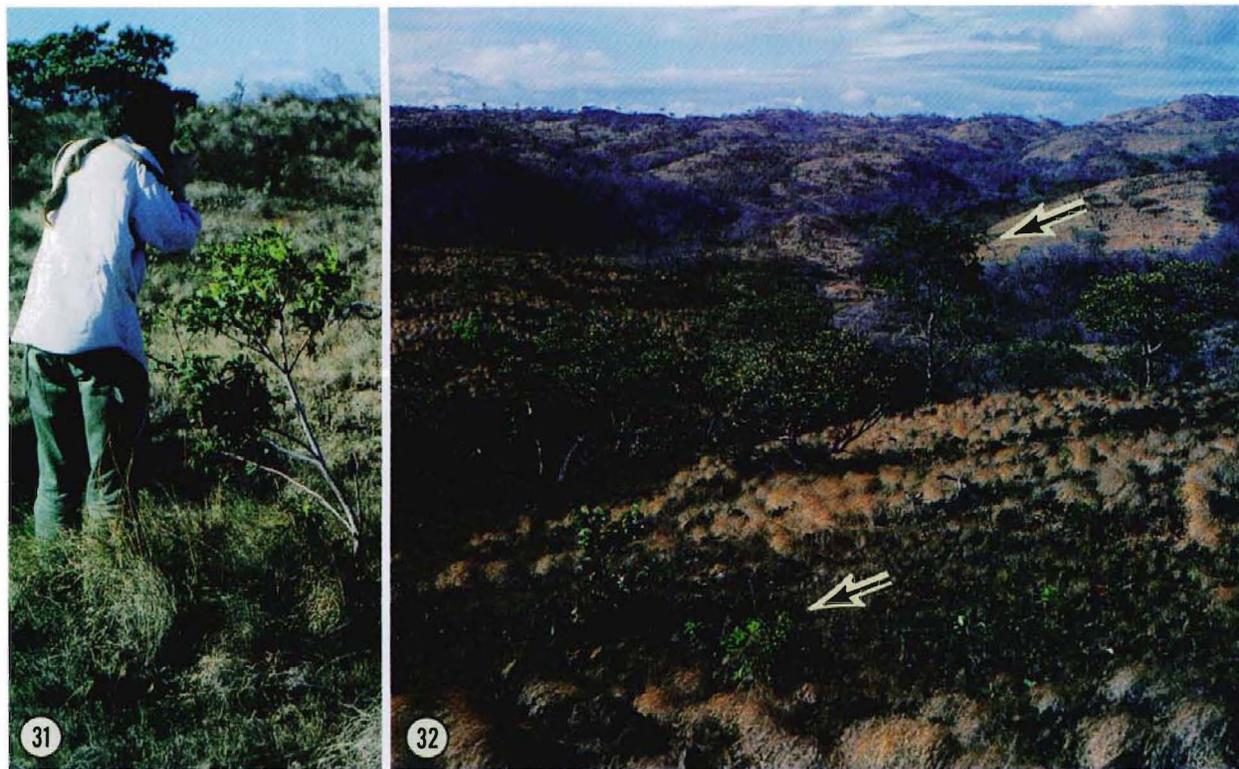


FIGS. 26–30. Pupae of two species of *Drephalys* (*Drephalys*) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA. **26**, *D. kidonoi* in ventral view (93-SRNP-8708, 11 January 1994). **27**, *D. kidonoi* in lateral view (93-SRNP-8708, 11 January 1994). **28**, *D. kidonoi* in anterior view (93-SRNP-8708, 11 January 1994). **29**, *D. alcmon* in ventral view (96-SRNP-1090, 22 May 1996). **30**, *D. alcmon* in anterodorsal view (96-SRNP-1090, 22 May 1996).

by looking for shelters on young saplings and sucker shoots, where the folded leaflets are easier to see and where they may also be more abundant. However, the larvae are occasionally encountered at all heights above the ground and on leaves of all ages. The larva walks out of the shelter to feed at night and remains

within it by day. The larva of *D. alcmon* lightly silks together two leaves to form its shelter.

The pupa of *D. kidonoi* (Figs. 26–28) is largely ivory white. It has a pair of conspicuous pink/orange/brown-colored thoracic spiracles (false eyespots) and a black/brown “mustache” between the ivory-colored



FIGS. 31, 32. *Roupala montana* (Proteaceae)—larval food plant of *Drephalys* (*Drephalys*) *kidonoi*—in the Santa Elena Sector of the Area de Conservación Guanacaste, Guanacaste, COSTA RICA, during the dry season. 31, Sapling (1 m tall) at the age commonly used as larval food (15 January 1986). 32, Sapling (lower arrow) and adult tree (upper arrow) in their general habitat (8 April 1985).

true eyes (Fig. 28). The true eyes turn red several days before eclosion and become dark brown the day before. The pupa of *D. alcmon* (Figs. 29, 30) is likewise ivory white with a pair of conspicuous pink/brown (false eye-like) thoracic spiracles, but it lacks the dark “mustache” (Fig. 30). The striking “face” on the anterior end of both species’ pupae is part of a pupal defense against diurnal vertebrate predators that is commonplace in ACG hesperiids (Janzen in prep.).

The pupa of *D. kidonoi* rests in the whitish and densely silked pupation chamber that is constructed from the last larval shelter. The last instar larval skin remains in the pupal chamber and lodges close to the point where the cremaster attaches to the silked walls.

In captivity, the larva takes 45–55 days to develop from a newly-hatched first instar to prepupa. This puts *D. kidonoi* among the slower-growing pyrgine larvae that have been reared in the ACG (Janzen & Hallwachs 1998). Slowness of growth probably is related to feeding on leaves that range from newly expanded to very old and tough. The last instar larva remains 3–4 days in the prepupal stage and 16–18 days in the pupal stage. Such durations are normal for a pyrgine hesperiid of this body weight. There is no hint of prepupal

or pupal dormancy, either in the wet season or in the (very hot and dry) ACG dry season.

More than 90% of the 236 larvae collected between 1991 and 1997 were found in the first half of the ACG dry season (late December through March) (Janzen 1993). Four pupae were found in the wild in mid-February 1992, and adults eclosed from them a week later. However, a few larvae were also found in April, May, July, August, and November. It would appear that *D. kidonoi* breeds mainly during the first half of the dry season. At this time, almost all other species of Hesperidae that breed in this dry forest are sexually dormant adults on site, are dormant prepupae (very rarely), or have migrated out of these dry forests into nearby riparian bottomlands or the more distant evergreen, montane, cloud or rain forests to the east of the ACG dry forests.

The ACG habitat currently occupied by the food plant, *Roupala montana*, is extensive, deforested, windswept, highly insolated, and dry (Fig. 32). Most, if not all, of this habitat has been generated by centuries of logging and burning, which have left large areas as rocky plains and knolls with low, sparse, native grasses and three species of widely scattered, stunted, and rel-

atively fire-resistant trees: *Curatella americana* L. (Dilleniaceae), *Byrsonima crassifolia* (L.) DC (Malpighiaceae), and *Roupala montana* (Janzen 1988:fig. 26). In some of the old pastures, *R. montana* is the only species of tree present. All three of these fire-tolerant tree species are vertebrate-dispersed. Originally, the *D. kidonoi* population may well have persisted on a fragmented and low density *R. montana* population growing on cliff faces, ravine banks, and rocky outcrops scattered throughout the original old growth dry forest blanketing the ACG landscape.

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