

EVOLUTION AND IDENTIFICATION OF THE NEW WORLD
HAIRSTREAK BUTTERFLIES (LYCAENIDAE: EUMAEINI):
ELIOT'S *TRICHONIS* SECTION AND
TRICHONIS HEWITSON

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ABSTRACT. I revise the lycaenid genus *Trichonis* Hewitson (Theclinae: Eumaeini), establish the new combination *Trichonis hyacinthus* Cramer, and make *Papilio theanus* Cramer 1777 a junior synonym of *P. hyacinthus* Cramer 1775. The genus consists of two species, *T. hyacinthus* and *T. immaculata*, which differ in wing pattern, forewing shape, color of androconial scales, and length of the third palpal segment. I then assess Eliot's higher classification of the Eumaeini. I examine leg, genitalia, and wing morphology, and conclude that Eliot's *Trichonis* Section is diphyletic. The unusual male foretarsus of *Trichonis* appears to have evolved independently three times in the Eumaeini.

Eliot (1973) and Clench (1964, pers. comm. 1978) proposed different higher classifications for the "New World hairstreaks" (Lycaenidae: Theclinae: Eumaeini). Eliot divided them into a *Trichonis* Section—for genera *Trichonis* Hewitson and *Micandra* Schatz—and an enormous *Eumaeus* Section—for the remaining genera (64 available names). Clench also divided these butterflies in two groups; in one he isolated *Eumaeus* Hübner (his Eumaeini), and in the other he lumped the remaining genera (his Strymonini).

The purpose of this paper is to assess the evidence for Eliot's provisional higher classification of the Eumaeini. Specifically, I consider whether the *Trichonis* Section is a monophyletic group. As basic information needed to answer this question, I revise *Trichonis*. *Micandra*, which Clench (1971) treated preliminarily, needed little work for the purpose of this paper. I then discuss the evidence for Eliot's classification.

GENUS *TRICHONIS*

Trichonis consists of two species known only from males, *T. theanus* Cramer (Fig. 1a, b) and *T. immaculata* Lathy (Fig. 2a, b). In 1865, Hewitson named *Trichonis*, primarily on the basis of an unusual male foretarsus in *T. theanus*, which he described as "exarticulate, robust, and broad beyond the middle" (Fig. 7a, b). Hewitson also illustrated the "female" of *T. theanus*, and described its foretarsus as "of the usual form, jointed and spined." Lathy (1930) pointed out that Hewitson's female was the male of a second species, which he named *T. immaculata*. Lathy did not, however, compare foreleg morphology of



FIG. 1. Adult *Trichonis hyacinthus*. (a) male upperside, (b) male underside, (c) female upperside, (d) female underside.

T. theanus and *T. immaculata*, nor did he discuss whether Hewitson's characterization of *Trichonis* was valid. No females have been associated with either species.

I propose that *Papilio hyacinthus* Cramer (Fig. 1c, d)—Cramer named all butterflies in *Papilio*—and a second phenotypically similar species (Fig. 2c, d) are the females of *T. theanus* and *T. immaculata*. Neither "female species" has been associated with males, but both share with *T. theanus* and *T. immaculata* a pastel blue or blue-green color on the frons and ventral wings that is unique among the Eumaeini. Both sexes have truncate forewings, and share similar geographical distributions. Further, genital morphology, which is discussed more fully later, indicates that both males and females belong to a similar section of the Eumaeini.

I associate female *T. hyacinthus* with male *T. theanus* and the new female with male *T. immaculata*. The bases for this action are distribution (Fig. 3) and forewing shape (Fig. 4). Briefly, *T. hyacinthus* and *T. theanus* are known only from the Guianas and Lower Amazon while the new female and *T. immaculata* occur there and in the Upper Amazon; the new female and a male of *T. immaculata* were collected

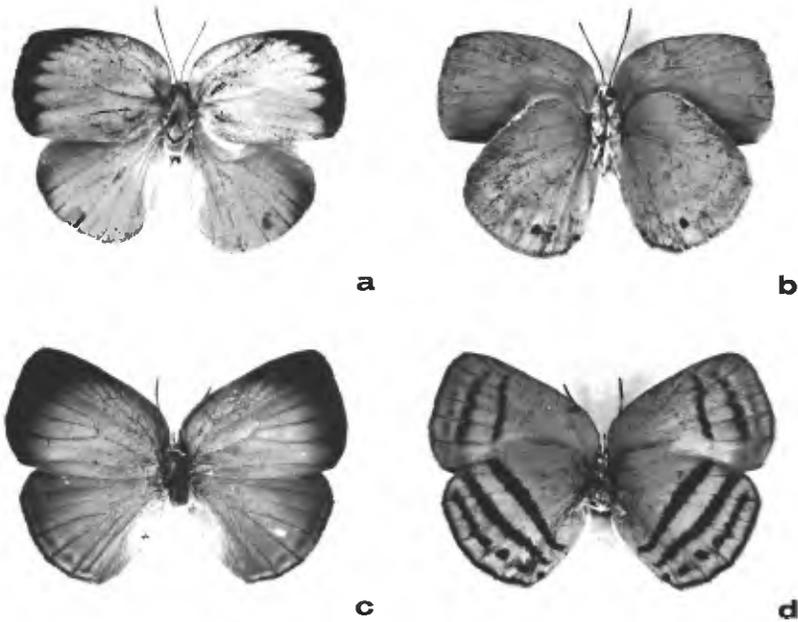


FIG. 2. Adult *Trichonis immaculata*. (a) male upperside, (b) male underside, (c) female upperside, (d) female underside.

at the same locality in northern Peru. As detailed below, the forewing apex is more truncate in male *T. immaculata* than in male *T. theanus* and in the new female than in female *T. hyacinthus*.

Characters unique to *Trichonis* include a pastel blue or blue-green frons and ventral ground color, and the genitalia, whose structure (Figs. 5 & 6) differs quantitatively from other eumaeines. I do not know which species or species group is its closest relative. *Trichonis* may be enlarged as our understanding of eumaeine phylogeny increases.

Key to *Trichonis* Species and Sexes

1. Ventral hindwings without transverse brown lines (Fig. 1b, 2b) (males) . . . 2
 Ventral hindwings with transverse brown lines (Fig. 1d, 2d) (females) . . . 3
2. Inner edge of dorsal forewing marginal band "smooth" (Fig. 1a), not scalloped.
 Ventral forewing androconial patch almost touching upper part of discal cell (Fig. 4a) male *hyacinthus*
 Inner edge of dorsal forewing marginal band scalloped (Fig. 2a). Ventral forewing androconial patch barely enters discal cell (Fig. 4c) male *immaculata*
3. Ventral hindwing with a white band between major brown transverse lines (Fig. 1d); hindwing with a tail female *hyacinthus*
 Ventral hindwing with a blue or blue-green (ground color) band between major brown transverse lines (Fig. 2d); hindwing without a tail female *immaculata*

TRICHONIS SYSTEMATICS

Nomenclature

Trichonis Hewitson (1865): Hewitson described *Trichonis* in the Lycaenidae with Cramer's *Papilio theanus* as the only species in the genus. It is the type species by monotypy (Hemming 1967). Lathy (1930) subsequently added *T. immaculata*.

Papilio hyacinthus Cramer (1775): Cramer described *Papilio hyacinthus* from the West Indies. He included a brief description and a figure of the underside, but did not mention its sex. Various authors (Fabricius 1782, Butler 1870, Draudt 1919–1920) discussed it, but their text paraphrased the original description, and illustrations were copies of Cramer's (sometimes poorly done, such as Seitz [Draudt 1919–1920]). No one has mentioned *P. hyacinthus* for more than half a century except to note that it is unknown from the West Indies (Comstock & Huntington 1943).

There is no other species with which the figure of *P. hyacinthus* can be confused; the white band sandwiched between two transverse brown lines on the ventral hindwing is distinctive. All known specimens are females.

There are no potential lectotypes in the Artis Collection, Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Universiteit van Amsterdam (Hogenes, pers. comm.), at the Rijksmuseum van Natuurlijke Historie in Leiden (de Jong, pers. comm.), or in the British Museum (Natural History) (BMNH). However, identification of Cramer's *P. hyacinthus* poses no problems, and a type is not needed. *Trichonis hyacinthus* is a **New Combination**.

Papilio theanus Cramer (1777): Cramer described *Papilio theanus* from Surinam with a brief description and a figure of the ventral surface, on which "androconial" patches are evident. Hewitson (1862–1878) illustrated the male and female, but Lathy (1930) noted that Hewitson's female is the male of a second species (which he named *Trichonis immaculata*). All known specimens are males.

Identification of *P. theanus* poses a problem. Males of both *Trichonis* species have extremely similar ventral wing patterns (Fig. 1b, 2b), and Cramer illustrated only the ventral surface. The species can be distinguished, however, by forewing shape and extent of the "polished spot" surrounding the forewing androconia. Unfortunately, the forewing shape in Cramer's illustration is inaccurate (the curvature at the forewing apex is too great for either species). The polished spot in the original illustration (in the BMNH library) extends almost to the radial vein, which is not the case in the few specimens of *T. immaculata* that I examined. However, considering the inaccuracy of other characters

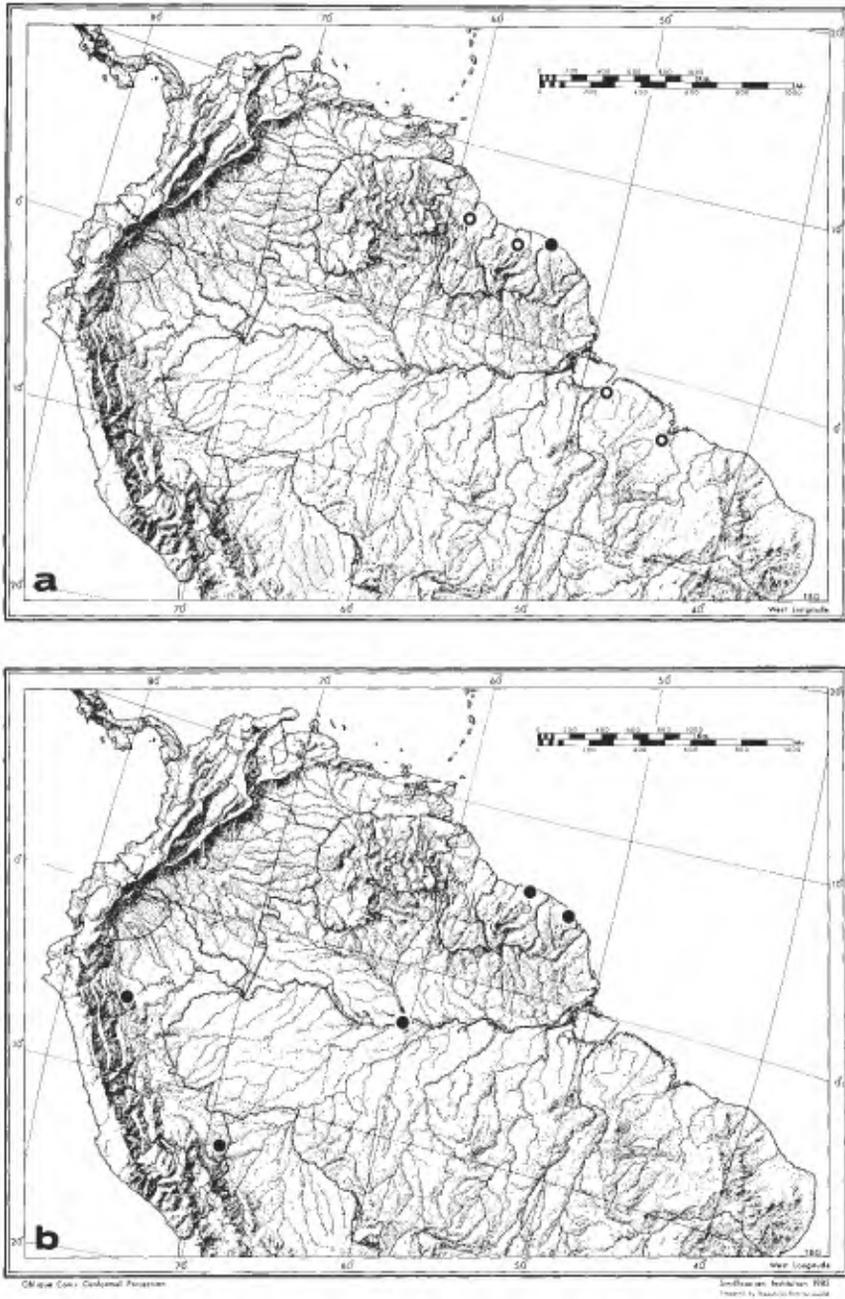


FIG. 3. Distribution of *Trichonis*. Solid dots designate exact localities, hollow dots represent generalized localities such as "Surinam" or "Maranh." (a) *T. hyacinthus*, (b) *T. immaculata*.

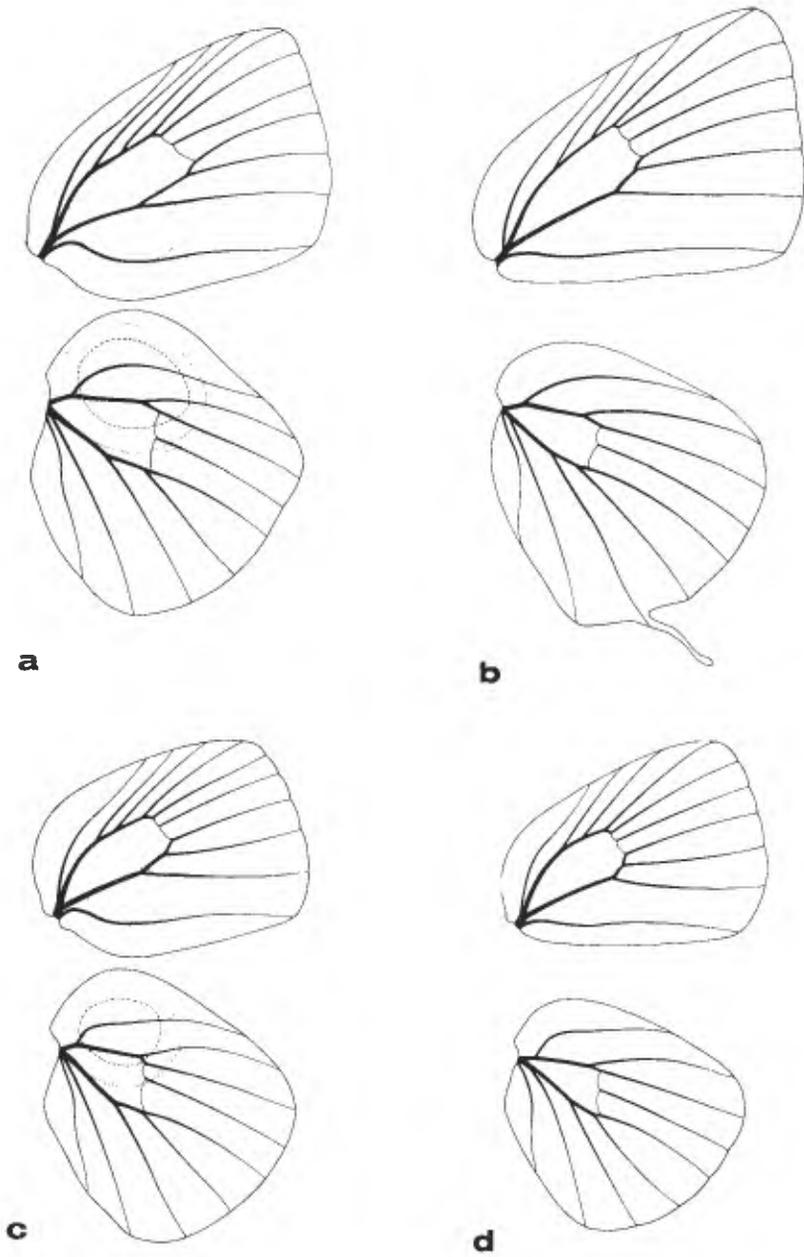


FIG. 4. *Trichonis* wing venation. (a) male *T. hyacinthus*, (b) female *T. hyacinthus*, (c) male *T. immaculata*, (d) female *T. immaculata*.

in the original figure, I hesitate to base a specific identification on so minute a detail. A type specimen is desirable.

I designate as lectotype of *P. theanus* a specimen in the Artis Collection (Zoölogisch Museum, Amsterdam). This specimen fits Cramer's original figure well, and was probably seen by Cramer even if it was not the model for his figure. There are no potential lectotypes in Leiden or London. The specimen bears two labels: one with the number "16" and one with the text "Trichonis Theanus Cram," written in the hand of Snellen, according to Willem Hogenes, Keeper of Lepidoptera at the Zoölogisch Museum. I have added a black-bordered label which reads: "Lectotype Papilio theanus Cramer, 1777; by R. Robbins." The words "Lectotype" and "by" are printed in red and the remainder of the label is hand-written in black ink. This lectotype designation will prevent confusion in the future, and maintain the previous identifications of *P. theanus* used by Hewitson (1862-1878), Staudinger (1884-1888), Schatz and Röber (1885-1892), and Lathy (1930).

I already outlined the evidence for considering *P. theanus* to be the male of *P. hyacinthus*, and now designate *P. theanus* Cramer a junior synonym of *P. hyacinthus* Cramer; **New Synonymy.**

Trichonis immaculata Lathy (1930): Lathy described *T. immaculata* from two males: one without locality data (presumably in the Museum National D'Histoire Naturelle) and one which was the model for Hewitson's (1862-1878) "female" illustration of *T. theanus* (BMNH). Either can eventually be designated a lectotype, but identification poses no problems. Male *T. immaculata* can be distinguished from male *T. hyacinthus* (= *T. theanus*) by the "smooth" dorsal forewing border, as noted in the above key.

Geographic Distribution

Trichonis occurs in the Guianas and throughout the lowland Amazon Valley from the mouth of the Amazon River at the Atlantic Ocean to the headwaters at the base of the eastern Andes (Fig. 3). The genus is unrecorded from the West Indies except for Cramer's unverified *T. hyacinthus* record.

I examined the following specimens of *T. hyacinthus* (Fig. 3a) in the BMNH except where noted. Guyana (formerly British Guiana)—5 males; Surinam—2 males; French Guiana (sometimes labelled Cayenne, which is thus inseparable from the present day city of that name)—5 males and 2 females, Maroni—1 female, Maroni R., St. Laurent—1 male; Brasil, Para—3 males and 1 female (1 male and 1 female in NMNH—National Museum of Natural History, Smithsonian Institution), Maranhão—1 female; No Data—2 males from the Felder

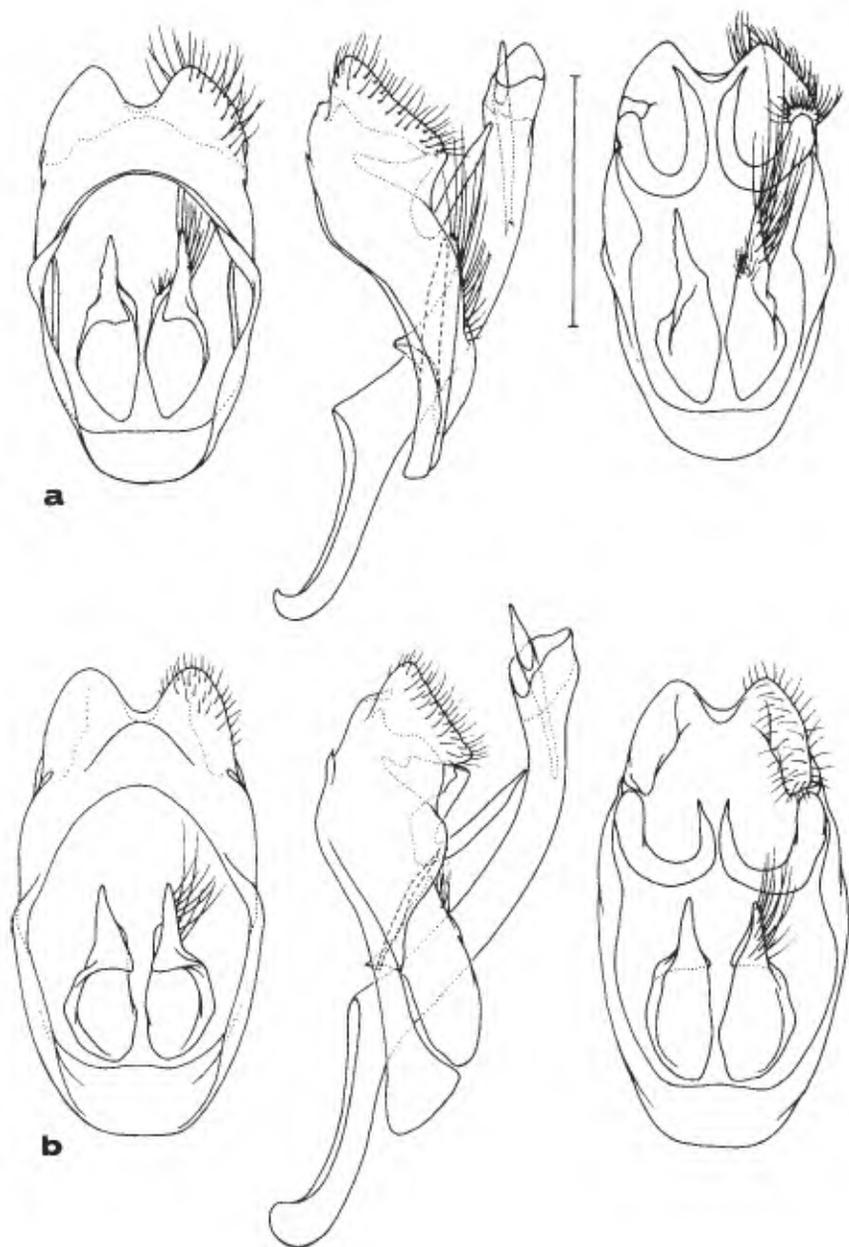


FIG. 5. *Trichonis* male genitalia. From left to right: dorsal, lateral, and ventral views. (a) *T. hyacinthus*, (b) *T. immaculata*. Scale line is 1 mm.

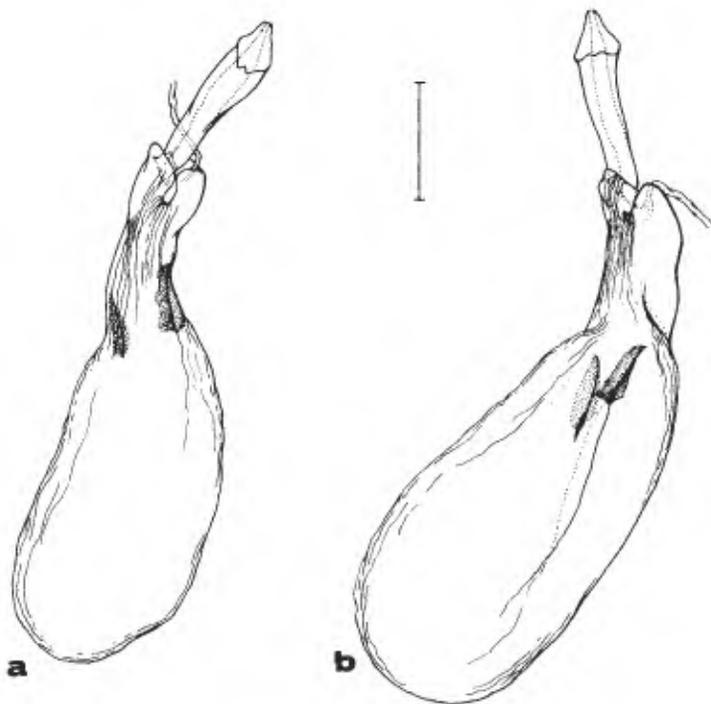


FIG. 6. *Trichonis* female genitalia, ventral view of bursa copulatrix. (a) *T. hyacinthus*, (b) *T. immaculata*. Scale line is 1 mm.

Collection, 1 male (lectotype) in Zoölogisch Museum. None of the specimens has a date of capture.

I saw the following specimens of *T. immaculata* (Fig. 3b) in the BMNH unless otherwise noted. Surinam—1 male, Paramaribo—1 male (NMNH); French Guiana—(labelled Cayenne, Hewitson's female figure)—1 male, Gourdonville, R. Kourou—1 male; Brasil, Amazonas, Manacapuru—1 male (Carnegie Museum of Natural History); Peru—Loreto, Iquitos, Rio Cachiyaca (usually spelled Cachiyacu)—1 male and 1 female, Madre de Dios, 30 km SW of Pto. Maldonado—1 male (private collection of Dan Bogar). The Paramaribo specimen was collected in September/October, the Manacapuru specimen in May 1926, and the Madre de Dios specimen on 22 October 1983 at 0930 h.

Morphology

Antennae: 40–44 segments. The beginning of the club is not clearly defined; rather, the segments gradually increase in size and become slightly flattened (dried specimens) on either side. As a result, the club

segments are elliptically shaped. The club is composed of 18 or 19 segments. The nudum (area without scales) is found on the 5 apical segments dorsally and on the 23–24 apical segments ventrally. There are incomplete white annulations around the segments on the stalk and the first few segments of the club, where the white scaling sometimes coalesces into a short line. The few specimens with intact antennae reveal no difference between the sexes or between the species.

Eyes: The eyes have short sparse hairs, and are slightly emarginate at the antennal bases. Hewitson (1862–1868) and Draudt (1919–1920) incorrectly reported the eyes as smooth, which, if true, would have made *Trichonis* unique among the Eumaeini (Eliot 1973). There is a ring of scales (some white and some blue) surrounding the eyes, but interrupted by the antennal scape and chaetosema.

Frons: The frons is covered with downward oriented blue scales lined laterally with white scales.

Labial Palps: I measured length of the third palpal segment (with an ocular scale) because it appeared to be sexually dimorphic and to differ interspecifically. The male *T. hyacinthus* third palpal segment (mean = 0.31 mm, SD = 0.026, N = 4) is significantly shorter than the female segment (mean = 0.83, SD = 0.193, N = 3; $P < 0.05$, *t*-test for unequal variances, Sokal & Rohlf 1969). Likewise, this length is significantly shorter in male *T. immaculata* (male: mean = 0.40, SD = 0.011, N = 3; female: mean = 0.78, N = 1; $P < 0.01$, *t*-test for one observation with mean of a sample). Although such sexual dimorphism has apparently not been reported for eumaeines, a quick survey of other genera indicated that it occurs frequently. Length of the third segment is also significantly longer in male *T. immaculata* than in male *T. hyacinthus* ($P < 0.01$, *t*-test), contrary to Hewitson's (1862–1878) claim that they are the same. There is no evidence that the females are different ($P > 0.05$, *t*-test).

Thorax: Thorax, legs, and wings are covered with blue or blue-green scales. The color varies individually, not seeming to be species specific, except that the dorsal wing color of male *T. hyacinthus* is consistently more greenish than that of male *T. immaculata*.

Legs: Discussed later in the section on phylogenetic affinities.

Wing Venation: Schatz and Röber (1885–1892) figured the venation of male *T. hyacinthus* (as male *T. theanus*). The venation of both species and sexes (Fig. 4) is typical of the Eumaeini with 10 forewing veins. The position of forewing veins R_3 and M_2 varies interspecifically among eumaeine species. In *Trichonis*, forewing vein R_3 arises from the discal cell, and forewing vein M_2 arises slightly nearer vein M_1 than M_3 .

Wing Shape: The forewing apex is strongly truncated in both

species—more so in males than in females and more so in *T. immaculata* than in *T. hyacinthus* (Fig. 4). To show this, I measured the angle between a line connecting the ends of veins R_1 and R_2 on the costa and a line connecting the ends of veins M_1 and M_3 on the outer margin. The angle of male *T. hyacinthus* was at or slightly more acute than 90° ($N = 4$) while male *T. immaculata* was always more than 100° ($N = 4$). Female *T. hyacinthus* ranged from 75° to 83° ($N = 3$). I measured the forewing angle of the single *T. immaculata* female at 87° .

Female *T. hyacinthus* is tailed at hindwing vein Cu_2 (Fig. 4b), but neither its male nor either sex of *T. immaculata* has an indication of a tail (Fig. 4a, c, d).

Size: I measured forewing length from the base of the radial vein to the forewing apex as follows: male *T. hyacinthus*, mean = 1.7 cm, SD = 0.17, $N = 4$; female *T. hyacinthus*, mean = 1.8 cm, SD = 0.416, $N = 3$; male *T. immaculata*, mean = 1.5 cm, SD = 0.05, $N = 4$; female *T. immaculata*, mean = 1.5 cm, $N = 1$.

Androconia: The venation drawings show the position and outline of the androconial patches on the ventral forewing and dorsal hindwing (Fig. 4). Each patch is composed of two or three parts. Forewing and hindwing inner patches of *T. hyacinthus* are dark brown while those of *T. immaculata* are beige. Around the inner patches, and contrasting with them, is an area of silver scales which give the impression of being a "polished spot." The extent of the polished area is poorly defined on some parts of the wings, as shown by the trailing dotted lines in the figures. The polished area immediately surrounding the inner patches has a greenish tint, but once again, this area is poorly defined. The extent of the polished area on the ventral forewing differs in the two species. In *T. hyacinthus* it extends through the discal cell, and touches or nearly touches the radial vein at the top of the cell. In *T. immaculata* the polished spot extends less than half way through the cell. (Figs. 1b, 2b do not show this difference clearly unless used in conjunction with Fig. 4.) Eliot (1973) published an outline drawing of a hindwing androconium in *T. hyacinthus*.

Male Genitalia (Fig. 5): Saccus almost lacking, vinculum thick ventrally, valvae small, penis thick with a single terminal cornutus. I found no consistent differences between the species. The specimens illustrated in Fig. 5 represent the extremes of individual genital variation in shape of the valvae and ventral vinculum, and in the position of the vinculum strut.

Female Genitalia (Fig. 6): Ductus bursae short and sclerotized, concave dorsally for its entire length and twisted dextrally (not evident from the figure). The corpus bursae is exceedingly long compared to the ductus bursae, and is posteriorly constricted and lightly sclerotized.

The ductus seminalis, which arises from the posterior end of the corpus bursae, is "off-center" to the right side of the female. There are a pair of signa as illustrated. As with the males, there are no evident differences between the species.

Biology

Almost nothing is known about the biology of *Trichonis*. Since most of the known specimens were collected long ago, I speculate that *Trichonis* species inhabit primary forest. Because of extensive deforestation, modern visitors to the Amazon Basin rarely collect in virgin jungle. Indeed, the one recent collection of *T. immaculata* was in the Tambopata Reserve (Madre de Dios, Peru), where the jungle is protected from cutting.

Similar Species

The wing pattern of male *Trichonis* is so distinctive that it cannot be confused with that of species in other genera. Female *Trichonis*, however, are superficially similar to, and might be confused with, "*Thecla*" *tagyra* Hewitson and "*Thecla*" *floralia* Druce (which I consider a senior synonym of "*Thecla*" *tagyroides* Lathy). "*Thecla*" *tagyra* and "*T.*" *floralia* have a light blue frons and ventral ground color that is similar to *Trichonis*, but of a different quality when compared side by side. They are most easily differentiated from *Trichonis* by two superficial characters: they possess a red anal lobe on the dorsal hindwing, and black transverse lines on the ventral hindwing. *Trichonis* females lack a red anal lobe and have brown transverse lines on the ventral hindwing. I tentatively place *tagyra* and *floralia* in *Evenus* Hübner, a genus I consider unrelated to *Trichonis* on the basis of androconial structure and genital morphology.

PHYLOGENETIC AFFINITIES

Eliot (1973) placed *Trichonis* in the Eumaeini because it shares the diagnostic characters of the tribe: 10 forewing veins, "greyhound-shaped" male genitalia lacking a juxta, a stubby-tipped male foretarsus (at least in *T. immaculata*), and hairy eyes. I address the question of its phylogenetic affinities within the Eumaeini by discussing leg morphology, genitalia, and wing structures.

Legs

The lycaenid male foretarsus is unique among the Lepidoptera. The tarsomeres are fused into one segment, lack tarsal claws, are used for walking, and possess on the ventral surface "smooth-walled sensilla" with an opening at the tip and "spines"—presumed sensilla with

longitudinal striations and no opening at the tip (Fig. 8). Although male Riodinidae, Libytheidae, and Nymphalidae also have clawless foretarsi, they lack spines and smooth-walled sensilla on the foretarsus, and do not use their forelegs for walking. Some male lycaenids have a segmented and clawed foretarsus (Eliot [1973] lists genera), but evidently this structure has been independently re-expressed a number of times within the Lycaenidae (Eliot 1973, Robbins, in prep.). The male lycaenid foretarsus may be stubby-tipped (characteristic of the Eumaeini) or tapered to a sharp point (Clench 1955, Eliot 1973).

The male foretarsus of *T. hyacinthus* is different from that of *T. immaculata*. The male of *T. immaculata* has a typical eumaeine foretarsus (Fig. 7c, d); it is cylindrical and stubby-tipped, and possesses spines and smooth-walled sensilla. Although Hewitson (1862–1878) claimed that it was a normal female foreleg, it lacks the claws and segmentation that occur in all lycaenid females. Unlike that of *T. immaculata*, the foretarsus of male *T. hyacinthus* (Figs. 7a, b, 8a, b), has a mid-ventral bulge (Hewitson 1862–1878), spines only at the tip (Eliot 1973), and smaller, somewhat flattened spinelike projections covering the ventral surface except for the tip. The spinelike projections, however, are striated like normal eumaeine spines (Fig. 8b), and there is a sharp transitional area of intermediate-sized spines (Fig. 8a). On the basis of this observation, I consider the spinelike projections to be small spines. Despite its unusual morphology, the male foretarsus of *T. hyacinthus* is technically lycaenid in that it is fused and possesses spines and smooth-walled sensilla (Fig. 8a).

Two other eumaeines besides *T. hyacinthus* have a stout, centrally swollen foretarsus spined only at the tip. The first is *Micandra platyptera* Felder & Felder (Figs. 7e, f, 8c, d), as Eliot (1973) noted. The foretarsus, however, lacks most of the mid-ventral bulge, and the transition in spine size is more gradual than in *T. hyacinthus*. The second species is "*Thecla*" *myrtusa* Hewitson (Figs. 7i, j, 8e, f). Its foretarsus is shaped differently than the other two, has fewer long spines at the tip, and, most notably, the small spines occur primarily on the inner face of foretarsus (not evident from the figures).

Micandra, like *Trichonis*, contains only one species with an atypical male foretarsus. Clench (1971) placed *platyptera* and *tongida* Clench in *Micandra* on the basis of venation, genitalia, and wing pattern, and listed eight other potential member species. I examined the male genitalia and venation of *ion* Druce, *comae* Druce, *cyda* Godman & Salvin, *aegides* Felder & Felder, and *amplitudo* Druce (probably a synonym of *aegides*), and all belong to *Micandra* as Clench characterized it. The "invaginated pocket" that Clench described on the male genital valvae is actually a process pointing caudally. Also, all species have

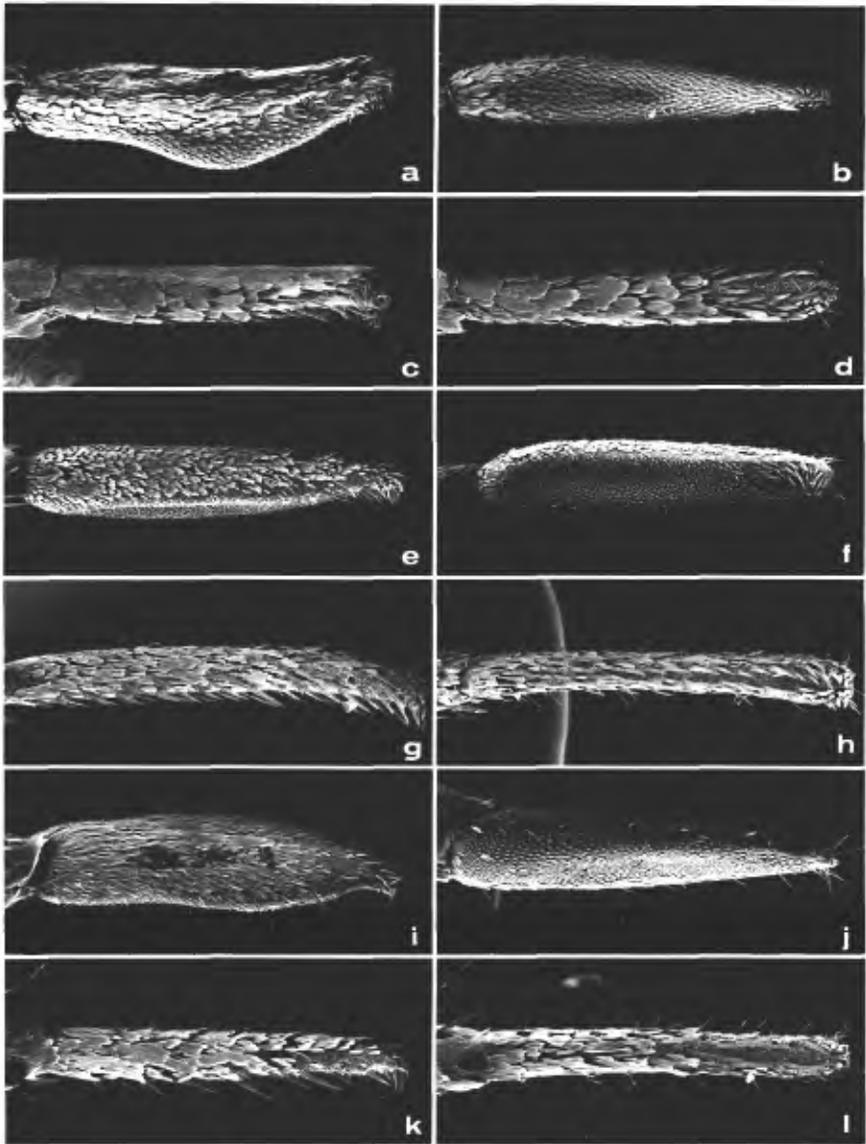


FIG. 7. Male forelegs. Lateral view on left and ventral view on right. (a & b) *T. hyacinthus*, 35 \times , (c & d) *T. immaculata*, 40 \times , (e & f) *Micandra platyptera*, 24 \times , (g & h) *M. comae*, 37 \times , (i & j) "*Thecla*" *myrtusa* — lateral view is of outer surface, two spines at tip of foretarsus are broken, 32 \times , (k & l) "*Thecla*" *myrtea*, 44 \times .

dorsal forewing androconia, contrary to Clench's key. Except for *M. platyptera*, however, these species have regularly spined male foretarsi lacking a ventral bulge (Fig. 7g, h).

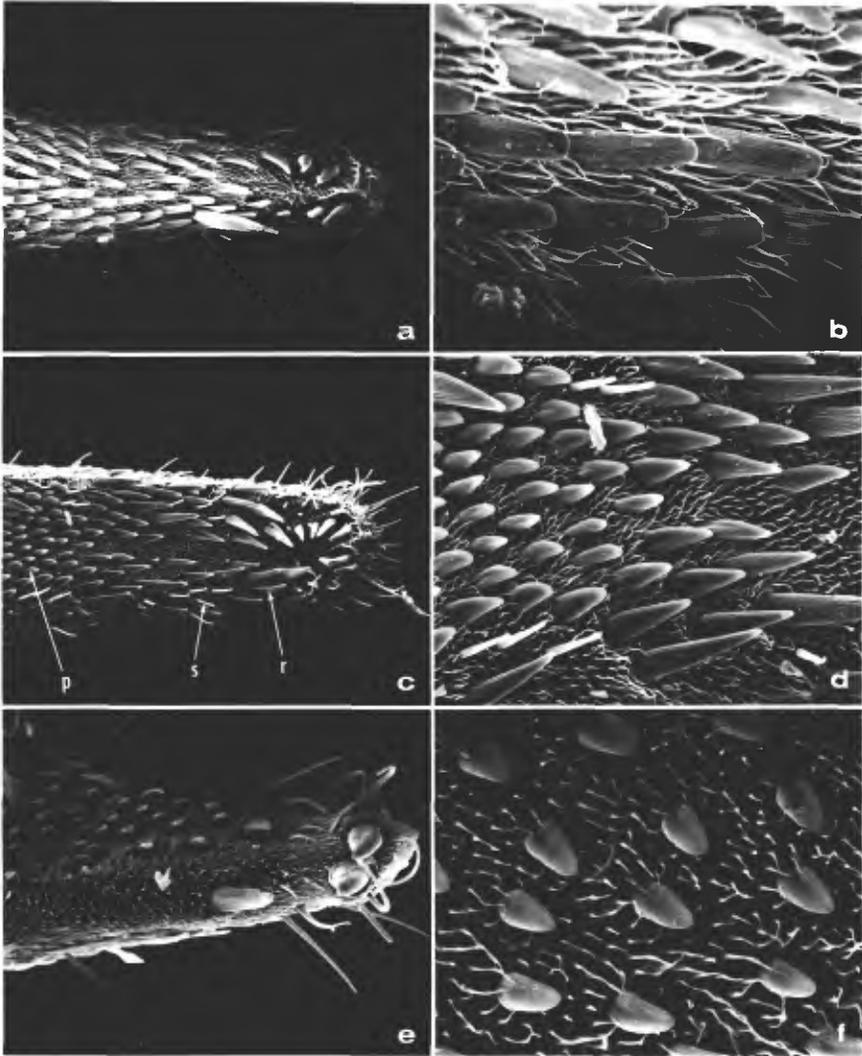


FIG. 8. Male forelegs. Ventral view. (a) *T. hyacinthus*, distal end, 110 \times , (b) *T. hyacinthus*, small flattened spines with striations, 525 \times , (c) *Micandra platyptera*, distal end, 85 \times , r—regular lycaenid "spine," p—small, flattened "spine," s—"smooth-walled sensillum," (d) *M. platyptera*, transition between small and regular spines, 210 \times , (e) "*Thecla*" *myrtusa*, distal end with inner face on top, 190 \times , (f) "*T.*" *myrtusa*, small spines, 530 \times .

The species most closely related to "*Thecla*" *myrtusa* also lack a centrally swollen foretarsus spined only at the tip. Although phylogenetic relations are not yet worked out, "*T.*" *myrtusa* appears to be most closely related to two groups of hairstreaks. The first group con-

tains "*Thecla*" *myrtea* Hewitson, "*T.*" *falerina* Hewitson, "*T.*" *eunus* Godman & Salvin, and "*T.*" *thara* Hewitson, and is defined by a unique dorsal hindwing "androconial" patch in which the scales have coalesced to form a thin foil-like lamination on the wing membrane. "*Thecla*" *myrtusa* shares with them a dark androconial patch at the base of the ventral forewing cubital vein, and shares a similar ventral wing pattern with "*T.*" *myrtea* and "*T.*" *falerina*. The second potential "closest relative" of "*T.*" *myrtusa* is *Allosmaitia* Clench. It shares with "*T.*" *myrtusa* beige (gray in some specimens) dorsal forewing androconia interspersed with regular wing scales, a character that Clench (1964) overlooked in *Allosmaitia*. The species in the "*T.*" *myrtea* group and in *Allosmaitia* have male foretarsi with regular rows of spines and without a central bulge (Fig. 7k, l).

"Short spines" are currently known only on the foretarsi of *T. hyacinthus*, *M. platyptera*, and "*T.*" *myrtusa*, but are difficult to see under a binocular microscope. Since I did not look at the male foretarsi of all their relatives under greater magnification, it is possible that some have short spines interspersed with regular ones.

Genitalia

The genitalia of *Trichonis* are quantitatively distinct from those of other eumaeines, and lack unusual qualitative characters that might be shared with other genera. Thus, in this case genital structures give, at best, an imprecise indication of relationship.

I found two major patterns of correlated genital structures among eumaeines. The first is characterized by a thick ventral vinculum, stout penis, taut manica (the membrane attaching the penis to the valvae) allowing little penial movement, no ventral processes on the lateral tegumen, and short ductus bursae with a simple cervix (the anterior ductus bursae ends abruptly with almost no change in structure). The second pattern is the antithesis of the first: a thin ventral vinculum, thin penis, loose manica, ventral processes of the tegumen present, and long ductus bursae (usually as long as the corpus bursae) with a "complex" cervix in which the shape of the anterior ductus bursae is different from the remainder of the ductus bursae. Examples of the first pattern are *Parrhasius* Hübner, *Iaspis* Kaye, *Erora* Scudder, and *Symbiopsis* Nicolay, and of the second, *Mithras* Hübner, *Evenus*, *Theritas* Hübner, and *Rekoa* Kaye. The two patterns represent extreme modes along a continuum of genital patterns, so that many species are intermediate and congeners may differ in one or two of these characters. However, *Trichonis* fits the first pattern while *Micandra* and "*T.*" *myrtusa* fit the second. In the absence of qualitative characters, this

evidence indicates that *Trichonis* is not phylogenetically close to *Micandra* and "*T.*" *myrtusa*.

Wing Venation, Shape, Pattern, and Androconia

Trichonis wing venation is commonplace, but the truncate forewing is unusual. Although various other eumaeine species, such as *Panthiades bitias* Cramer, have truncate forewings, there are no other shared characters to support a close relation with *Trichonis*. Species in the "*Thecla*" *rocena* Hewitson complex, however, share a relatively rectangular forewing shape and ventral forewing androconia with *Trichonis*, and have broadly similar genitalia (though with many points of difference). The coxa, femur, and tibia of "*T.*" *rocena* male forelegs are abnormal, but the tarsus, unlike *T. hyacinthus*, is normal. "*Thecla*" *rocena* and allies may be close relatives of *Trichonis*, but I did not find definitive evidence supporting this relation.

Wing venation may be a good indicator of *Micandra*'s relations. Both Schatz and Röber (1885–1892) and Eliot (1973) illustrated the unusual distal forewing discal cell venation, which is shared with minor variation by all species of *Micandra*. Species in other genera, such as "*Thecla*" *timaeus* Felder & Felder and relatives, also share this character, and are undoubtedly close relatives of *Micandra*.

Schatz and Röber (1885–1892) and Clench (1971) noted that *Micandra* forewing vein R_1 originates far basad of the other radials, and is situated next to Sc for most of its length. This distinctive venation is found in *Micandra*, "*Thecla*" *timaeus*, "*Thecla*" *eronos* Druce and relatives, "*Thecla*" *auda* Hewitson and relatives, and "*Thecla*" *busa* Godman & Salvin and relatives, but does not occur in either *Trichonis* or "*Thecla*" *myrtusa*. I consider it likely that this character state will eventually characterize a monophyletic assemblage of eumaeine genera, and if so, indicates that the closest relatives of *Micandra* are not *Trichonis* or "*T.*" *myrtusa*.

The ventral wing pattern of *Trichonis* is unique, and does not provide clues to its systematic position. I mentioned earlier that I consider the superficial similarity between the ventral wing patterns of female *Trichonis* and two species of *Evenus* to be convergence.

Male *Trichonis* androconia on the dorsal hindwing and ventral forewing, located where the wings overlap, are also of no help in working out phylogenetic position. Many species scattered throughout the Eumaeini, as well as the Deuodorigini, a close relative of the Eumaeini (Eliot 1973), have androconia where the wings overlap. The exact structure of *Trichonis* androconial patches, as detailed above, is unique, so far as I am aware.

Eliot (1973) supported his *Trichonis* Section with the observation

that *Trichonis* and *Micandra* androconia are the same size or larger than ordinary scales—in contrast to the “small” androconia of the *Eumaeus* Section. My results do not support this observation. I found that the dorsal forewing androconia of “*Thecla*” *mycon* Godman & Salvin average 2.8 times larger than adjacent iridescent blue scales (N = 10). Likewise, the dorsal forewing distal androconia of *Atlides halesus* Cramer average 1.5 times larger than dorsal forewing blue scales (N = 10). Further, Eliot (1973:402) listed other species with ventral forewing androconia that are larger than “ordinary” scales. A quick survey indicated that this character state is widespread in the tribe. Further, “ordinary” wing scales can vary in size by a factor of 7 (Gray 1962). I doubt that relative androconia size will be a useful character state.

Conclusions

There are three evolutionary hypotheses that might account for the information just presented. The first hypothesis is that *T. hyacinthus*, *M. platyptera*, and “*T.*” *myrtusa* form a monophyletic group defined by their male foretarsus. Consistent with this hypothesis is the observation that males of the first two species have round hindwings lacking tails while their females are tailed. However, wing pattern, genital, androconial, and venational characters are inconsistent with this hypothesis, and indicate that *T. hyacinthus* is congeneric with *T. immaculata*, *M. platyptera* with the species that Clench (1971) placed in *Micandra*, and “*T.*” *myrtusa* with the “*T.*” *myrtea* group and/or *Allosmaitia*. Further, sexual dimorphism in the tailed condition occurs in other eumaeines with typical eumaeine male foretarsi, such as *Erora phrosine* Druce and “*Thecla*” *timaeus*.

The second hypothesis is that *Trichonis*, *Micandra*, and the eventual generic assignment of “*Thecla*” *myrtusa* form a monophyletic group defined by the tendency to express the atypical male foretarsus. This group would approximately correspond to Eliot's (1973) *Trichonis* Section. However, there are no similarities in genitalia, venation, wing pattern, or androconia to support this hypothesis. Even the unusual tailed dimorphism mentioned in the previous paragraph occurs in only one species of *Trichonis* and one species of *Micandra*. Further, genital and venational structures, as discussed in the previous section, indicate that *Trichonis* belongs to a different group of eumaeine genera than *Micandra* and “*T.*” *myrtusa*.

The third hypothesis is that the atypical male foretarsus of *T. hyacinthus*, *M. platyptera*, and “*T.*” *myrtusa* has evolved independently three times. The distribution of other character states is consistent with this hypothesis, and indicates that Eliot's *Trichonis* Section is diphyletic.

An objection to this conclusion is that the repeated evolution of a qualitatively distinct foreleg is unlikely. However, the three atypical forelegs are not identical, casting doubt on their homology. Further, if a slight change during development of the male foreleg were responsible for the atypical foretarsus, then only a small genetic change, such as a mutation in a promoter or in the timing of transcription, is necessary to explain its repeated independent occurrence. Indeed, eukaryotic genes that regulate timing of development are now known (Ambros & Horvitz 1984). As the regulatory mechanisms determining development of insect leg structures are worked out, as they are being done for egg chorion structures (reviewed in Kafatos 1981) and wing pattern (Nijhout 1978, 1980a, b, 1981, 1984), it will be possible to test this idea.

ACKNOWLEDGMENTS

I thank R. I. Vane-Wright, P. Ackery, R. Smiles (British Museum [Natural History]), C. W. Young (Carnegie Museum of Natural History), and D. Bogar (Harrisburg, PA) for allowing me access to *Trichontis* specimens in collections under their care. I thank R. de Jong for good natured correspondence on Cramer types in Leiden, and particularly thank Willem Hogenes, Keeper of Lepidoptera at the Zoölogisch Museum, for loaning me the lectotype of *T. theanus*, and for sending me historical information on Cramer types in the Artis Collection. I thank S. S. Nicolay for providing me with unpublished information on eumaeine morphology. I thank J. M. Burns, J. N. Eliot, J. S. Glassberg, S. S. Nicolay, and R. W. Poole for reading and commenting on the manuscript.

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