PHYLOGENETIC STUDIES
IN THE PAPILIONINAE
(LEPIDOPTERA: PAPILIONIDAE)

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CONTENTS

ABSTRACT

Cladistic analyses of relationships among genera in the subfamily Papilioninae reveal that many taxonomic subgroups accepted by previous authors are not monophyletic. Four tribes are recognized: The Troidini and Papilionini are considered to be sister-groups; the genus *Teinopalpus* is given tribal status as the sister-group to the Troidini/Papilionini; the Graphiini is the sister-group of the other three tribes.

An analysis of relationships among the five genera recognized in the Graphiini suggests that *Eurytides* and *Protographium* are sister-taxa, and that *Iphiclides* is the sister-group of a clade which includes *Lamproptera* and *Graphium*. Four subgenera within *Graphium* are recognized: *Pazala, Pathysa, Arisbe,* and *Graphium*.

Meandrusa is placed in the Papilionini with *Papilio,* the latter being retained as a single genus.

Two subtribes are recognized in the Troidini, the Battiti, containing only *Battus,* and the Troiditi, containing six genera. *Parides* consists of two Old World groups, subgenera *Atrophaneura* and *Panosmia* (formerly in the genus *Atrophaneura*), and Neotropical species (subgenus *Parides*). Subgenus *Atrophaneura* is equivalent to the *nox* group of previous authors; *Panosmia* is equivalent to the *latreillei* group. *Parides* is hypothesized to be the sister-genus of *Troides,* which contains all the "birdwings." The genera *Ornithoptera, Ripponia,* and *Trogonoptera* are synonymized with *Troides. Pachliopta,* comprised of Munroe's *Pachliopta* plus species (subgenus *Losaria*) formerly in *Atrophaneura,* is the sister-group of a clade which includes *Cressida* and *Euryades.* A single species, *Pharmacophagus antenor*—removed from *Atrophaneura* and given generic status—is the sister-group of all other Troiditi.

Area cladograms for genera in the Graphiini and Troidini reveal few patterns, but suggest that some taxa are between 50 and 80 million years old. Available character information for the fossil genus *Praepapilio* is insufficient to determine its phylogenetic placement with respect to extant Papilionidae.

INTRODUCTION

Few insects have attracted more attention from biologists than have the swallowtail butterflies (Lepidoptera: Papilionidae). Being both large and colorful, they are prized by amateur collectors, and have been the subject of much basic biological research. They have been collected so extensively throughout the world that few species remain to be described. In addition, the host-plants and life histories of swallowtails are better known than those of most other lepidopteran groups. It is therefore likely that papilionids will continue to play a pivotal role as research organisms for biologists with interests in ecological and evolutionary questions.

Our knowledge of swallowtails remains critically inadequate in one important respect; the family has not been subjected to rigorous phylogenetic analysis. Until cladistic relationships are understood, biological studies will lack a well-founded historical component (Eldredge and Cracraft, 1980). For example, Ehrlich and Raven (1964) formulated the theory of coevolution largely on the basis of known relationships between butter-flies and their host-plants, and one of their most important examples was that of swallowtail host associations. Yet Ehrlich and Raven did not have cladistic hypotheses available to them. Parallel cladogenesis between butterflies and their host-plants would be a consequence of coevolution as defined by Ehrlich and Raven (Mitter and Brooks, 1983), and cladistic hypotheses are therefore a prerequisite to understanding whether or not these two groups have coevolved (Miller, 1987).

The goals of the research described here are two: The first is to identify monophyletic groups within the Papilioninae, the largest of the three swallowtail subfamilies, and specify phylogenetic relationships among genera. As a result of these findings, future researchers interested in "macroevolutionary" studies involving swallowtails will have a better framework on which to base evolutionary hypotheses such as those concerning the origins of host-plant associations. The second goal is to document as completely as possible the morphological data used in these phyloge-

TABLE 1
Species Dissected (arranged in accordance with the classification proposed in this study)

	No. spp. in gr.	Species dissected
Family **Papilionidae**	561	
Subfamily **Baroniinae**		
Genus *Baronia* Salvin	1	*brevicornis* Salvin[a]
Subfamily **Parnassiinae**	51	
Tribe Parnassiini	36	
Genus *Archon* Hübner	1	*apollinus* (Herbst)[a]
Genus *Hypermnestra* Menetries	1	*helios* (Nickerl)[b]
Genus *Parnassius* Latreillei	34	*phoebus* (Fabricius); *apollo* (L.); *mnemosyne* (L.); *clodius* Menetries; *hardwickei* Gray; *szechenyii* Frivaldszky[a]; *acco* Gray; *delphius* (Eversmann); *imperator* Oberthur; *charltonius* Gray; *tenedius* Eversmann; *simo* Gray.
Tribe Zerynthiini	15	
Genus *Sericinus* Westwood	1	*montela* Gray
Genus *Allancastria* Bryk	4	*cerisy* (Godart)
Genus *Parnalius* Rafinesque	3	*polyxena* (Denis and Schiffermuller)
Genus *Bhutanitis* Atkinson	4	*lidderdalii* Atkinson
Genus *Luehdorfia* Cruger	3	*japonica* Leech[a]
Subfamily **Papilioninae**	509	
Tribe Graphiini	147	
Genus *Eurytides* Hübner		
Subgenus *Protesilaus*	40	*marcellus* (Cramer); *epidaus* (Doubleday)[a]; *celadon* (Lucas); *bellerophon* (Dalman)[b]; *agesilaus* (Guérin-Méneville); *telesilaus* (C. and R. Felder)[a]; *asius* (Fabricius)[b]; *branchus* (Doubleday); *lysithous* (Hübner); *phaon* (Boisduval).
Subgenus *Eurytides*	13	*thyastes* (Drury)[b]; *dolicaon* (Cramer)[b].
Genus *Protographium* Munroe	1	*leosthenes* (Doubleday)[a]
Genus *Iphiclides* Hübner	2	*podalirius* (L.)[a]
Genus *Lamproptera* Gray	2	*meges* (Zinken-Sommer)[a]; *curius* (Fabricius)[b].
Genus *Graphium* Scopoli		
Subgenus *Pazala*	4	*eurous* (Leech)[a]; *mandarinus* (Oberthur).
Subgenus *Graphium*	27	*euryplus* (L.)[a]; *agamemnon* (L.); *weiskei* (Ribbe)[b]; *codrus* (Cramer); *sarpedon* (L.); *mendana* (Godman and Salvin)[b]; *hicetaon* (Mathew); *wallacei* (Hewitson)[b].
Subgenus *Pathysa*	22	*nomius* (Esper)[a]; *antiphates* (Cramer); *delessertii* (Guérin-Méneville)[b]; *macareus* (Godart)[b].
Subgenus *Arisbe*	36	*taboranus* (Oberthur); *ridleyanus* White; *philonoe* (Ward)[a]; *ucalegon* (Hewitson); *leonidas* (Fabricius); *tynderaeus* (Fabricius)[b]; *policenes* (Cramer); *porthaon* (Hewitson); *kirbyi* (Hewitson)[b]; *colonna* (Ward); *antheus* (Cramer).
Tribe Teinopalpini		
Genus *Teinopalpus* Hope	2	*imperialis* Hope
Tribe Papilionini		
Genus *Papilio* (L.)	222	*epicydes* (Hewitson); *clytia* (L.); *laglaizei* (Depuiset); *toboroi* (Ribbe)[a]; *anactus* (Macleay)[a]; *aegeus* (Donovan); *woodfordi* (Godman and Salvin); *fuscus* (Goeze); *castor* (Westwood); *polytes* (L.); *helenus* (L.); *memnon* (L.); *protenor* (Cramer)[a]; *bootes* (Westwood); *euchenor* (Guérin); *demoleus* (L.); *xuthus* (L.); *machaon* (L.); *paris* (L.); *blumei* (Boisduval); *peranthus* (Fabricius); *ulysses* (L.); *zalmoxis* (Hewitson)[b]; *antimachus* (Drury)[b]; *rex* (Oberthur); *phorcas* (Cramer); *cynorta* (Fabricius); *nireus* (L.); *leucotaenia* (Rothschild); *gallienus* (Aurivillius); *multicau-*

TABLE 1—(*Continued*)

	No. spp. in gr.	Species dissected
		datus (Kirby); *troilus* (L.)[a]; *thoas* (L.)[a]; *anchisiades* (Esper); *hectorides* (Esper); *zagreus* (Doubleday)[b]; *scamander* (Boisduval); *victorinus* (Doubldeay)[a].
Genus *Meandrusa* Moore	2	*sciron* (Leech)[a]; *payeni* (Boisduval)[a].
Tribe Troidini	138	
Subtribe Battiti		
Genus *Battus* Scopoli	14	*philenor* (L.); *zetides* (Munroe); *devilliers* (Godart); *polydamus* (L.)[a]; *belus* (Cramer)[a]; *crassus* (Cramer); *polystichtus* (Butler); *laodamus* (C. and R. Felder); *eracon* (Godman and Salvin).
Subtribe Troiditi		
Genus *Pharmacophagus* Haase	1	*antenor* (Drury)[a]
Genus *Cressida* Swainson	1	*cressida* (Fabricius)[a]
Genus *Euryades* C. and R. Felder	2	*corethrus* (Boisduval)[a]; *duponchelii* (Lucas).
Genus *Pachliopta* Munroe		
Subgenus *Losaria*	4	*neptunus* (Guérin-Méneville)[a]; *palu* (Martin)[a]; *coon* (Fabricius)[a]; *rhodifer* (Butler).
Subgenus *Pachliopta*	13	*hector* (L.)[a]; *polydorus* (L.); *aristolochiae* (Fabricius)[a]; *polyphontes* (Boisduval).
Genus *Troides* Hübner		
Subgenus *Trogonoptera*	2	*brookiana* (Wallace)[a]; *trojana* (Honrath).
Subgenus *Troides*	30	*hypolitus* (Cramer)[a]; *aeacus* (C. and R. Felder)[a]; *amphrysus* (Cramer); *helena* (L.); *priamus* (L.)[a]; *richmondia* (Gray).
Genus *Parides* Hübner		
Subgenus *Atrophaneura*	12	*nox* (Swainson); *varuna* (White)[a]; *horishanus* (Matsumura)[a]; *priapus* (Boisduval); *semperi* (C. and R. Felder).
Subgenus *Parides*	45	*gundlachianus* (C. and R. Felder); *photinus* (Doubleday)[a]; *proneus* (Hübner); *ascanius* (Cramer); *bunichus* (Hübner); *hahneli* (Staudinger); *nephalion* (Godart); *aeneus* (L.); *sesostris* (Cramer); *lysander* (Cramer)[a]; *neophilus* (Hübner); *agavus* (Drury)[a].
Subgenus *Panosmia*	14	*latreillei* (Donovan)[a]; *polyeuctes* (Doubleday)[a]; *dasarada* (Moore); *alcinous* (Klug).

[a] Male and female genitalia figured.
[b] Female unavailable for dissection.

netic analyses. The types of character complexes that have proven informative for papilionids may also be of value to other lepidopteran morphologists. Research in swallowtail systematics has been hindered because the taxonomic distribution of characters was not established rigorously, so that determinations of character polarity were often ambiguous. In addition, many currently recognized groups are not monophyletic (sensu Hennig, 1966), having been defined by symplesiomorphic characters. Experimental studies, on the other hand, have demonstrated that grouping by synapomorphy (cladistic analysis) produces the most stable classifications (Mickevich, 1978, 1980; Schuh and Farris, 1981; Schuh and Polhemus, 1980). Therefore, until all taxonomic groups in the Papilionidae are recognized on the basis of monophyly, the classification will remain unstable.

It is extremely important to state at the outset that the cladograms presented in this study should be considered hypotheses to be tested by future researchers, and not final results. I intend to point out instances where phylogenetic results are particularly ambiguous, as well as potentially fruitful areas of morphological, biogeographical, and biological research.

METHODS

MORPHOLOGY

Relationships among papilionid groups have previously been proposed chiefly on the basis of comparative analyses of wing venation and male genitalic morphology. In this study I supplemented these traditional characters with as many new characters as I could discover. A total of 152 of the 561 described species in the Papilionidae were examined in detail (table 1). I chose the species to represent all genera and species-groups recognized by Munroe (1961). Where possible, at least two species in each group were studied. I dissected a male and female of each species, except where morphological interpretation was particularly difficult. In these cases more than one specimen of each sex was studied.

A generalized set of male and female genitalia is illustrated in figure 17, showing the morphological terminology used in this paper. Nomenclature for the various parts of the male genitalia is from Klots (1970). However, my interpretation of the structures located medially on the tegumen (= male 9th tergite) in papilionids differs from that of previous authors. I have termed the socii of others (e.g., Munroe, 1961; Hancock, 1983) the uncus (see Character 9). Nomenclature for female genitalic morphology is also taken essentially unchanged from Klots (1970; see also Saigusa et al., 1977, 1982; Saigusa and Lee, 1982). I term the entire portion of the ductus, from the point at which it narrows behind the bursa to the ostial opening, the ductus bursae. I do not attempt to homologize and name the various structures located around the ostial opening in papilionids. This is a difficult problem requiring further study.

Terminology for other morphological features, including those in the thorax and head, is from Ehrlich's (1958a) work on *Danaus plexippus*. Wing veins are named in accordance with the scheme used by Ackery and Vane-Wright (1984), the only addition being the use of Forbes' (1923) nomenclature for the "discocellulars" (fig. 150).

Most investigations have considered a fairly small sample of the male genitalic characters for which there is variation. Historically, papilionid workers have limited their studies to the shape of the valve and modifications of the clasper or harpe (e.g., Gosse, 1882; Rothschild, 1895; Jordan, 1907, 1928; Zeuner, 1943; Talbot, 1949; Munroe, 1961). Hancock (1980, 1983) studied the pseuduncus in detail. The present study considers these structures in addition to others such as the juxta, tegumen, saccus, and vesica (see Saigusa and Lee, 1982). Several character complexes, superficially examined by previous authors, appeared to require more detailed study. One of these is the scent organ (Rothschild, 1895; Rothschild and Jordan, 1906) located on the anal margin of the male hind wing. No comprehensive analysis of female genitalia has as yet been undertaken. The works of Igarashi (1979, 1984) provided most of the data for immature stages used in this study.

Before examining the external and skeletal anatomy of a specimen, I removed both pairs of wings and soaked the entire body in 10 percent potassium hydroxide. Soft tissues and scales were then removed. The aedeagus and left valve were removed from males and the vesica of the aedeagus was everted. The female ostial region was also everted. Specimens were then placed in 70 percent ethanol and male and female genitalia drawn in lateral view using a camera lucida attached to a Wild M5 dissecting microscope. The aedeagus, juxta, and male 8th tergite were then further dissected from the genitalic preparations. These, as well as legs and antennae, were mounted on slides in Canada Balsam after being sequentially rinsed in 70 percent ethanol (15 min), absolute ethanol (15 min), clove oil (15 min), and xylene (5 min). The aedeagus, juxta, male 8th tergite, and labial palpus were then drawn from these slide mounts using a Bausch & Lomb Microprojector. Wings were bleached in Clorox and mounted on slides in euparal for study of venation. Drawings were prepared by projecting these through a photographic enlarger. Several structures were examined using a scanning electron microscope (courtesy of the American Museum of Natural History). Heads of dried specimens with the right palpus removed were sputter-coated with gold-palladium before electronmicrographs of labial palpi were taken. For the study of male scent scale organs, a small section of hind wing from the anal margin was removed and

coated. Micrographs of setae on the female ovipositor lobes were prepared from cleared material that had been removed from ethanol and dehydrated by critical point drying.

CLADISTIC METHODOLOGY

Morphological data (tables 2, 4, 6) were analyzed using the numerical cladistic computer program developed by D. L. Swofford (1984; "Phylogenetic Analysis Using Parsimony," Version 2.3). The program identifies nested sets of synapomorphies, the method pioneered by Hennig (1966). Furthermore, it employs the principle of parsimony (see Kluge and Farris, 1969; Farris, 1983), whereby the shortest possible tree for the data set is produced. Characters (scored as 0 for plesiomorphic and 1 for apomorphic) were polarized and the cladogram rooted using an outgroup comparison procedure (Lundberg, 1972; Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984) in which character states for the ingroup are determined by comparison with the character state in the outgroup. I have reported consistency indexes (equal to the "index of consistency" of Kluge and Farris, 1969), which measure the degree to which a tree is consistent with the original data, for all cladograms generated by the PAUP program. The consistency index is 1 if there is no homoplasy on the cladogram, and tends to 0 as the amount of homoplasy increases. During each PAUP run, the "Branch and Bound" command option was utilized. When this command is used the program tries all possible branching combinations in its search for the shortest tree. This procedure guarantees that the most parsimonious cladogram (or cladograms) will be generated for the data set. Of the possible optimization procedures available in PAUP, I used Farris Optimization. I tried MINF optimization (Swofford, 1984) as an alternative for each analysis, but obtained identical results.

The morphological data, totaling 170 characters, was analyzed in three stages: (1) Preliminary studies suggested that two of the three previously recognized papilionine tribes are not monophyletic. The first analysis was therefore designed to establish tribal boundaries in the Papilioninae and phylogenetic relationships among those tribes. (2) In the second analysis, I examined phylogenetic relationships among genera and subgenera in the tribe Graphiini. As a result of Analysis 1, the genera *Teinopalpus* and *Meandrusa,* placed by previous authors in the Graphiini, were excluded from the tribe. Five genera, *Eurytides, Protographium, Iphiclides, Lamproptera,* and *Graphium,* are recognized. Graphiine characters were polarized using a composite outgroup that included all other tribes in the Papilionidae. (3) In the final analysis, I examined relationships among genera and subgenera within the Troidini. Seven genera are recognized; *Battus, Pharmacophagus, Cressida, Euryades, Pachliopta, Troides,* and *Parides.* Analysis 1 suggested that the sister-tribe to the Troidini is the Papilionini. The latter was therefore used to polarize character states within the Troidini. The details of each analysis are discussed further in appropriate sections.

CLASSIFICATIONS

The names given in the classifications presented in tables 3 and 5 will be used throughout this paper. The classifications of Hancock (1980, 1983) and Munroe (1961) are also presented for comparison. I have not attempted to make the classifications and cladograms equivalent as Hennig (1966) originally suggested. Rather, in an attempt to promote nomenclatural stability in the Papilionidae [see Ehrlich and Murphy's (1982) defense of such a position], I largely followed the criteria of Robbins and Henson (1986) in choosing generic and tribal nomenclature: (1) If a genus is monophyletic, the name should not be changed. (2) If a genus is not monophyletic, one should choose the combination of monophyletic generic groupings that will create the fewest name changes. (3) Increase the number of names only if evidence for monophyly suggests that the classification will be more stable in the future. My classifications are therefore proposed with the hope that future systematics research can change the phylogenetic position of various swallowtail taxa without requiring additional changes in generic nomenclature. To the best of my knowledge, all generic and subgeneric groupings constitute monophyletic associations.

MONOPHYLY OF TRIBES IN THE PAPILIONIDAE: ANALYSIS 1

HISTORY OF THE CLASSIFICATION

Of the three papilionid subfamilies, the Papilioninae is by far the largest. The Baroniinae is monobasic, containing only *Baronia brevicornis,* the Parnassiinae includes 51 species in 8 genera (Hancock, 1983), and the Papilioninae contains the remaining swallowtails, currently 509 species. I classify the Papilioninae in 14 genera belonging to 4 tribes. This classification, presented in table 1, differs substantially from previous works on the Papilionidae. Before presenting the evidence that led to my tribal classification, it will be useful to discuss the tribal schemes of other authors.

Rothschild and Jordan (1906) were the first to offer a coherent classification of subgroupings within American Papilioninae. They retained a single generic name (*Papilio*), but broke the American species into three "sections": (1) The "Aristolochia Swallowtails," currently in the Troidini; (2) The "Fluted Swallowtails," Papilionini of modern workers; and (3) The "Kite Swallowtails," subsequently included in the Graphiini. Seitz (1906) also retained all Papilioninae in a single genus, but recognized three subgenera: *Ornithoptera* for the birdwings, *Pharmacophagus* for the *Aristolochia*-feeders, and *Papilio* for the rest. Jordan (1907), in his treatment of the American papilionids, accepted generic status for *Euryades* in addition to *Papilio,* but noted its close affinity with the other *Aristolochia*-feeding species.

Bryk (1923, 1929–1930) recognized family-level status for each of the modern swallowtail subfamilies. His Papilionidae is therefore equivalent to the Papilioninae of subsequent authors except that Bryk erected the Teinopalpidae for the genus *Teinopalpus.* Ford (1944b) presented a system of tribal groupings within the Papilioninae based largely on his studies of pigment chemistry in the Lepidoptera. He recognized five tribes, the Cressidini, Troidini, Graphiini, Papilionini, and Teinopalpini. The Cressidini and Troidini comprised all the *Aristolochia*-feeding species in the Papilioninae, and were subsequently united in a single tribe by Talbot

(1949) and Ehrlich (1958b), both of whom otherwise suggested tribal classifications identical to that of Ford. These authors also placed *Teinopalpus* in its own tribe.

Munroe (1961) investigated papilionid relationships in more detail than previous authors, basing his analysis largely on male genitalic dissections of a large sample of species. His classification remained essentially unchallenged for over 20 years. Munroe's tribal concepts differed from those of Ford. Within the Papilioninae he recognized three tribes; the Leptocircini (=Graphiini), Papilionini, and Troidini. Like Ehrlich, Munroe recognized a single *Aristolochia*-feeding tribe in the Papilioninae, but he considered *Teinopalpus* to be a member of the Graphiini. Munroe and Ehrlich (1960), in a paper attempting to resolve points of difference between their individual contributions, accepted the tribal arrangement of Munroe. They further subdivided the Troidini by erecting two subtribes, the Battiti and Troiditi. In addition, the Graphiini was classified into two subtribes; the Graphiiti contained all genera except for *Teinopalpus,* which was placed in its own subtribe, the Teinopalpiti. The most significant research on the Papilionidae since Munroe's work has been that of Hancock (1979a, 1979b, 1980, 1983, 1984). Like Munroe, most of Hancock's conclusions were based on a comparative study of male genitalic structure, although his analysis also considered characters that had been used by previous researchers. His tribal classification was similar to the one suggested by Munroe and Ehrlich. He accepted three papilionine tribes, the Graphiini, Papilionini, and Troidini, and retained *Teinopalpus* in the Graphiini. Igarashi (1979, 1984) published his views on papilionid classification in the first comprehensive attempt to include morphology of immature stages. Like Hancock, he recognized the tribes of Munroe and Ehrlich.

Genealogical relationships among these tribes have been poorly understood. Ford (1944b) considered the Cressidini to be the most primitive tribe, followed by the Troidini. He argued that the Papilionini and Graphiini were more closely related to each other than either was to the Troidini, and suggested that the Teinopalpini was "derived as an extreme specialization from the Papil-
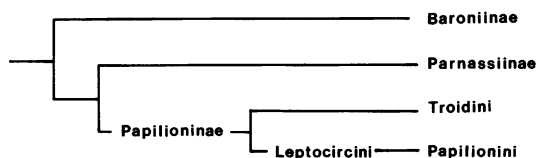
Fig. 1. Relationships among subfamilies in the Papilionidae and tribes in the Papilioninae according to the branching diagram of Munroe and Ehrlich (1960).

ionini" (p. 217), but gave no evidence for his belief. Ehrlich (1958b) did not specify tribal relationships, and Munroe (1961) was noncommital. However, according to the branching diagram published in their joint paper (fig. 1), these authors believed, following Ford, that the Graphiini and Papilionini are more closely related than either is to the Troidini. They stated that "the most probable origin [of the Papilionini] still appears to be from the higher Graphiini" (p. 175). Igarashi (1984) also placed the Graphiini and Papilionini as sister-tribes within the Papilioninae. Not until the first cladistic analysis of the Papilionidae, published by Hancock (1983, fig. 2), was there a significant change in these arrangements. On the basis of characters taken from the literature and reinterpreted by phylogenetic methods, Hancock argued that the Graphiini is the plesiomorphic tribe in the Papilioninae, and that the Troidini and Papilionini are sister-tribes.

CLADISTIC ANALYSIS

My phylogenetic analysis of relationships among tribes in the Papilioninae corroborates Hancock's hypothesis that the Troidini

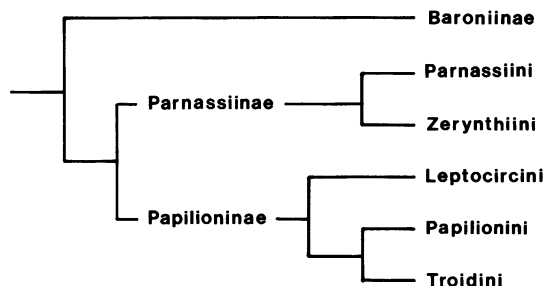Fig. 2. Cladistic relationships among subfamilies and tribes in the Papilionidae according to Hancock (1983).

and Papilionini together form a monophyletic group, and that the Graphiini is the plesiomorphic tribe in the subfamily. However, there is a significant difference between my results and those of Hancock. I conclude that he misinterpreted the phylogenetic positions of two papilionine genera, *Teinopalpus* and *Meandrusa*. In an attempt to elucidate the correct position of these genera I did a numerical cladistic analysis (PAUP) based on 44 morphological characters, using *Teinopalpus, Meandrusa,* and the papilionid tribes as terminal taxa.

Prior to resolving this problem, a decision had to be made concerning an appropriate outgroup for the analysis. Recent studies question the previously accepted hypothesis (see, e.g., Pierce and Beirne, 1941; Wilson, 1961) that the Pieridae are most closely related to the Papilionidae. Ehrlich and Ehrlich (1967) analyzed relationships among butterfly families using numerical phenetic methods (Sokal and Sneath, 1963). The technique gave different results when an analysis of internal morphological characters was compared with an analysis of external morphological characters. Ehrlich and Ehrlich concluded that "we must adjust to the existence of a multitude of 'valid' taxonomic arrangements of the butterflies" (1967: 315). Kristensen (1976) argued convincingly that this instability is a natural result of phenetic analysis. His cladistic interpretation of existing data contradicted Ehrlich's (1958b) suggestion that the Papilionidae and Pieridae are most closely related. Instead, Kristensen proposed that the Papilionidae are the plesiomorphic family in the superfamily Papilionoidea, which would mean their sister-group comprises the Pieridae, Lycaenidae, and Nymphalidae. According to him, the only potential synapomorphy for the Papilionidae and Pieridae (involving the configuration of the retinular sense cells in the compound eye; from Yagi and Koyama, 1963) requires further investigation. In accordance with Kristensen's hypothesis, it becomes difficult to determine character polarities for the Papilionidae by outgroup analysis. None of the characters I have used for the Papilionidae occur in a single state throughout the rest of the Papilionoidea. Assigning a particular character state to this "composite outgroup"

would therefore be a very rough approximation.

To avoid such problems, and because I was most interested in determining relationships within only one of the three subfamilies in the Papilionidae, I designated *Baronia brevicornis* (Baroniinae) as the outgroup for the rest of the Papilionidae. There is firm evidence that the Baroniinae is plesiomorphic relative to the rest of the Papilionidae. It belongs in the family (see justification of Clade 1; fig. 3), but the Parnassiinae and Papilioninae (Clade 3) share uniquely derived characters not present in *Baronia*.

Using character states in *Baronia* to infer the plesiomorphic condition, 44 morphological traits were scored (table 2) using the following terminal taxa: *Baronia brevicornis* (outgroup), *Teinopalpus, Meandrusa,* the Zerynthiini, Parnassiini, Graphiini, Papilionini, and Troidini. Both species of *Meandrusa* (*payeni* and *sciron*), and a single species of *Teinopalpus* (*imperialis*) were examined. I made judgements in certain cases to assign a single character state to an entire tribe. For example, presence of a pseuduncus (Character 17) is hypothesized in this study to represent a synapomorphy for all tribes in the Papilioninae, yet there are species within both the Graphiini and Troidini in which the pseuduncus is absent (see Characters 67, 111). In both of these tribes, loss of the pseuduncus is hypothesized to represent separately derived states. The Graphiini and Troidini are therefore scored as having the pseuduncus present. For the data set described above, the cladogram was rooted using *Baronia* as an outgroup.

CLASSIFICATION

The Branch and Bound procedure resulted in two equally parsimonious trees (figs. 3, 4), both having a consistency index of 0.70. I chose the one in figure 3, in which *Meandrusa* is a member of the Papilionini, rather than the one in figure 4, in which it is the sister-group to the Papilionini/Troidini. The rationale for this decision is twofold. First, *Meandrusa* remains one of the few swallowtail genera for which the immatures are incompletely known. Future findings may provide evidence that will change its position. In the

TABLE 2
Data Matrix for Analysis 1; Monophyly of Tribes in the Papilionidae
0 indicates the plesiomorphic state, 1 the apomorphic state

	Character number																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Baroniinae	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Parnassiinae																			
Parnassiini	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0
Zerynthiini	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0
Papilioninae																			
Graphiini	1	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1
Teinopalpus	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	0	1	1	1
Meandrusa	1	1	1	1	0	0	1	1	1	0	0	0	1	0	1	0	1	1	1
Papilio	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1
Troidini	1	1	1	1	0	0	1	1	1	0	0	0	0	1	0	1	1	1	1
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Baroniinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parnassiinae																			
Parnassiini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zerynthiini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Papilioninae																			
Graphiini	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Teinopalpus	1	?	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Meandrusa	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0
Papilio	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Troidini	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0
	39	40	41	42	43	44													
Baroniinae	0	0	0	0	0	0													
Parnassiinae																			
Parnassiini	0	0	0	0	0	0													
Zerynthiini	0	0	0	0	0	0													
Papilioninae																			
Graphiini	0	0	0	0	0	0													
Teinopalpus	0	0	0	0	0	0													
Meandrusa	1	1	1	1	1	1													
Papilio	0	0	0	0	0	0													
Troidini	0	0	0	0	0	0													

meantime I take a conservative approach and adopt the proposal of Igarashi (1984) that *Meandrusa* be placed in the Papilionini. Another potentially controversial position is recognition of tribal status for the genus *Teinopalpus*. However, the data suggest that such status will result in a more stable classification (see discussion of Clade 10).

I use the name Graphiini in place of Leptocircini. Keith Brown (personal commun.) has submitted a recommendation to the ICZN that the name Graphiini be accepted rather than Leptocircini. He argues that, when a ge-

nus which forms the base of an accepted family-group name is shown to be a synonym or homonym and falls from common usage, then the family-group name should be replaced with a more recent synonym based on a genus still in wide usage. The name *Leptocircus* (Swainson) is an objective synonym of *Lamproptera* (G. R. Gray).

CHARACTERS

The following is a list of descriptions for the characters used. Where a character has been discussed by previous authors, their in-
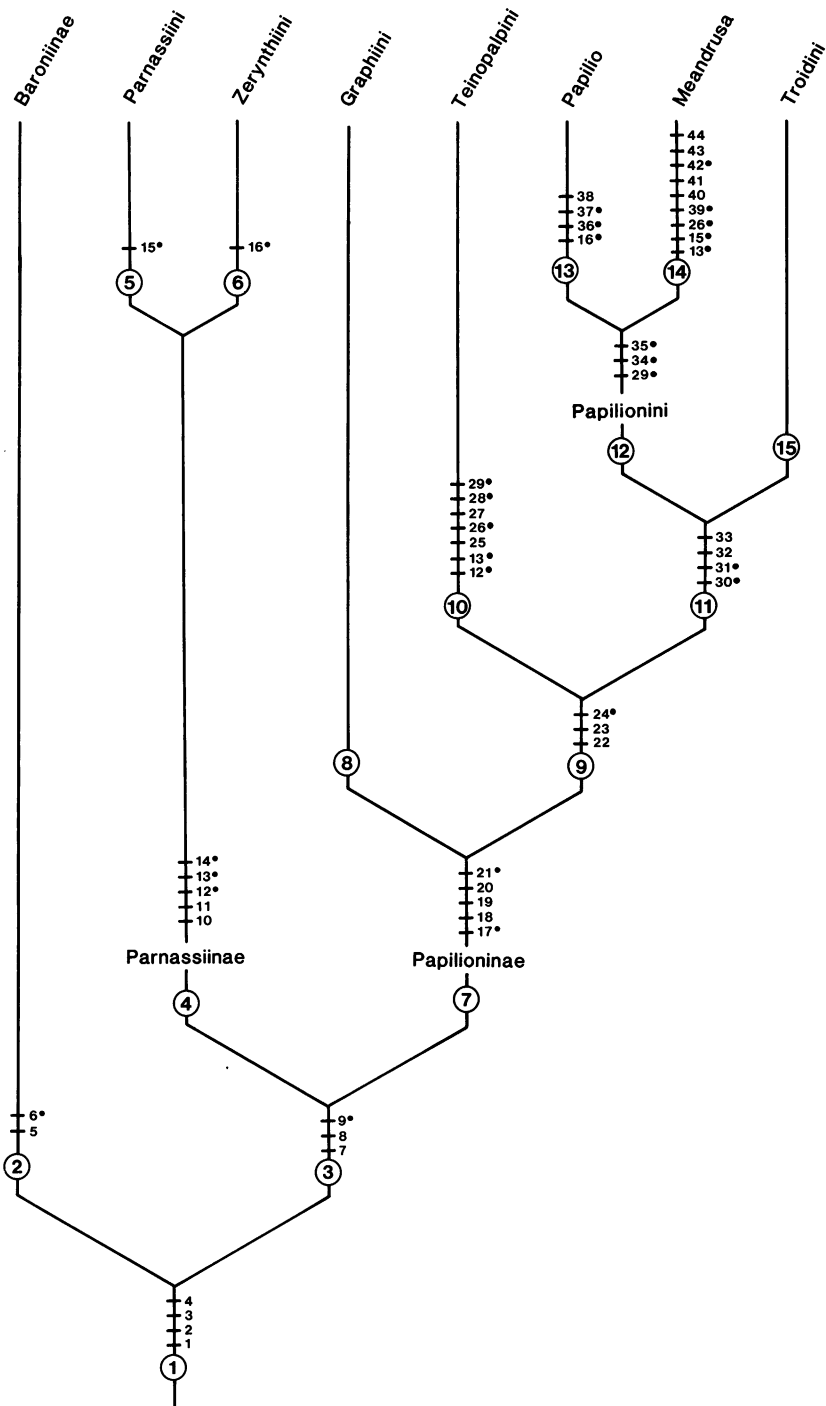
Fig. 3.   Hypothesis of cladistic relationships among tribes in the Papilionidae (Analysis 1). Closed circles designate homoplasious characters.

terpretation is given. The list is arranged phylogenetically and corresponds with the cladogram (fig. 3). The data matrix is shown in table 2. Homoplasious characters are indicated by brackets following Ackery and Vane-Wright (1984).
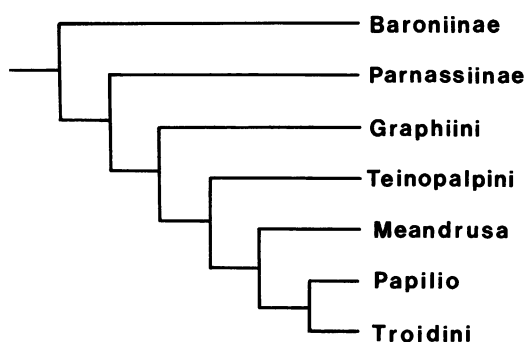
Fig. 4. Equally parsimonious solution for the data set in Analysis 1.

CLADE 1—FAMILY PAPILIONIDAE

Kristensen (1976; see also Ackery, 1984) summarized the known autapomorphies for the Papilionidae. In addition to the characters listed below, he included four internal morphological characters. Two involve configurations of the pterothoracic musculature (from Ehrlich and Ehrlich, 1963), characters not examined in this study. Two others involve the structure of the dorsal vessel (=aorta) in adult butterflies. In the Papilionidae the mesothoracic portion of the aorta lacks ostia, and the mesothoracic aorta does not have a "horizontal chamber." Hessel (1966, 1969) discovered and figured these characters, but did not examine specimens of *Baronia brevicornis*. The character state distributions are therefore insufficiently known.

1. Larvae with osmeteria. The larvae of *Baronia brevicornis* possess osmeteria (Vazquez and Perez, 1961). Since 1961 all papilionid workers have considered the presence of these glands to be an autapomorphy for the family. Osmeterial secretions have been shown to act as defenses against predators (Eisner and Meinwald, 1965; Honda, 1983; Brower, 1984; Damman, 1986). Crossley and Waterhouse (1969) studied the ultrastructure of osmeterial glands, and Tanaka et al. (1983) have described their embryonic development. The chemical components of osmeterial secretions have been described for 27 swallowtail species, 19 of these being in the genus *Papilio*. The compounds appear to be synthesized de novo rather than being dietary derivatives of host-plant chemicals (Eisner et al., 1970, 1971).

It is tempting to speculate concerning the phylogenetic significance of osmeterial chemistry in the Papilionidae, but existing data are inconclusive. The osmeterial secretions of species in three groups, the Baroniinae, Graphiini, and Papilionini, consist largely of a mixture of two aliphatic compounds, isobutyric and 2-methylbutyric acids (Eisner and Meinwald, 1965; Eisner et al., 1970; Crossley and Waterhouse, 1969; Lopez and Quesnel, 1970; Honda, 1980a, 1980b, 1981), but species in *Papilio* exhibit a dramatic change in chemical composition during larval development (Seligman and Doy, 1972; Burger et al., 1978; Honda, 1980a). Only final instar larvae produce aliphatic acids whereas the osmeteria in preceding instars contain monoterpenes, characteristic of secretions in *Luehdorfia* (Parnassiinae) (Suzuki et al., 1979; Honda, 1980a), and sesquiterpenes, shown to occur in members of the Troidini (Eisner et al., 1971; Honda, 1980a). Osmeterial secretions require additional study before they can be used as taxonomic characters in the Papilionidae.

2. Pretarsal aroliar pads and pulvilli reduced. I have not verified this character, originally described by Ehrlich (1958b) and listed by Kristensen (1976). Ehrlich noted, however, that pretarsal aroliar pads and pulvilli are reduced or absent in some pierid and nymphalid genera as well as in papilionids, so the trait requires further study.

3. Vein 2A of forewing present as a free vein to wing margin. In the Papilionidae veins 1A and 2A in the forewing diverge from the wing base; 2A is free to the wing margin (figs. 150–184). In other butterfly families vein 2A converges with 1A and does not reach the wing margin. Common (1979) considered that a free second anal in the forewing is an archaic condition whereas Kristensen (1976), following Hennig (1981), asserted that fusion is plesiomorphic at the level of the Amphiesmenoptera (= Lepidoptera plus Trichoptera). I accept the latter hypothesis because the first requires the fused condition to have evolved independently numerous times. Having vein 2A free to the wing margin therefore represents an autapomorphy for the Papilionidae.

4. Cervical sclerites joined ventromedially. In all Papilionidae, the cervical sclerites are joined beneath the neck by a "narrow sclerotic band," a condition which does not

occur in other butterflies (Ehrlich, 1958b). It has also been reported in the fossil genus *Praepapilio* (Durden and Rose, 1978; see "Biogeography and Age of the Papilionine Genera").

CLADE 2—SUBFAMILY BARONIINAE

Baronia brevicornis is the only member of this subfamily, and possesses the following apomorphic characters:

5. Male valve with lateral lobe. The only autapomorphic trait I have been able to identify concerning the genitalia is the membranous lobe located on the lateral surface of the valve (fig. 22). I did not observe this structure elsewhere in the swallowtails.

[6]. Forewing vein R_4 absent. Two features of the forewing radial venation in *Baronia* have been interpreted as specializations by past authors, and both are homoplasious. First is fusion of R_1 with Sc (fig. 151). Within the Papilionidae R_1 is fused with Sc in the genus *Graphium* and the *dolicaon* group of *Eurytides* (Character 79). The second is loss of R_4. This loss appears to have occurred in two parnassiine genera, *Hypermnestra* and *Parnassius,* as well as in *Baronia* (see figures in Ackery, 1975). Ford (1944b) correctly argued that neither of these venational characters, loss of R_4 or fusion of R_1 and Sc, is homologous in *Baronia* and the other groups in which they occur. Regarding the first trait he argued (p. 221): "If we suppose that the loss of [R_4] is homologous in the two groups, we should be driven to consider that *Baronia* had evolved between *Archon* (with all 12 veins) and *Parnassius,* in which [R_4] is lost. It seems scarcely credible that a distinct subfamily should have arisen within so homogeneous a group as the existing Parnassiinae." He similarly rejected the argument based on fusion of R_1 with Sc, suggesting that it reflected an "entirely impossible affinity."

CLADE 3

The Parnassiinae and Papilioninae have been considered sister-groups by all authors since Ford (1944b). Three characters support this relationship:

7. Third anal vein of hind wing lacking. There has been much confusion in the Lepidoptera literature concerning the primitive number and appropriate nomenclature for the anal veins of the hind wing. In this work I have followed the nomenclature of Ackery and Vane-Wright (1984). According to their interpretation, members of the subfamilies Parnassiinae and Papilioninae are unique among butterflies in lacking the third anal vein of the hind wing, their only anal vein being 1A+2A (figs. 151–184).

8. Cervical membrane with ventral sclerite. Ehrlich (1958b) discovered a small "ventral sclerite" in the cervical membrane close to the head, and described it as occurring in species belonging to the subfamilies Parnassiinae and Papilioninae, as well as in a few genera within the Nymphalidae. He did not find it in *Baronia* and recognized it as a trait uniting the Parnassiinae and Papilioninae. Kristensen (1976) suggested that this character requires further study.

[9]. Uncus of male bifid. Throughout the Lepidoptera two structures (sometimes more in certain groups) are generally associated with the tegumen, the socii and uncus (Klots, 1970). In most Lepidoptera the uncus is a single projection narrowed distally, and the socii are paired with one socius located on either side of the uncus. Within the Papilionidae there has been much confusion concerning these structures. They were collectively termed the scaphium by early authors (Gosse, 1882; and subsequently van Son, 1949; Talbot, 1949). In *Baronia brevicornis* (fig. 66A), there is a single pointed projection on the tegumen. Authors since Munroe (1961) have termed it the uncus, the assumption being that socii are absent in this species. Throughout the Parnassiinae paired structures (uncul processes of Saigusa and Lee, 1982) are present (e.g., *Luehdorfia japonica,* fig. 66B), the uncus thus being bifid within this subfamily. When one looks at the Papilioninae, however, the terminology seems to break down. In several graphiine genera, such as *Iphiclides* (fig. 66F) and *Graphium* (fig. 66H), the structure is again bifid, and in two taxa (*Eurytides celadon,* fig. 66D; and *Protographium leosthenes,* fig. 66E) it is a single projection quite similar in shape to that of *Baronia*. *Eurytides* (fig. 66E) and *Teinopalpus* (fig. 66I) exhibit an apparently trifid structure, though the three parts are very closely apposed and only clearly separated for

a short distance distally. Munroe (1961) suggested that in groups with this trifid arrangement both the uncus and socii are present, and in addition, that graphiines with a bifid structure have lost the uncus, leaving only the socii. Others have subsequently agreed with these interpretations (e.g., Common and Waterhouse, 1981; Hancock, 1983). In both the Papilionini and Troidini the structure is universally bifid (fig. 66J–M) but has been termed socii (e.g., Munroe, 1961; Hancock, 1983). This state of confusion can be resolved most simply by hypothesizing the following: In *Baronia* the single structure on the tegumen is indeed the uncus and is homologous with the uncus of other butterflies. The bifid structure present in the Parnassiinae should also be termed the uncus, as it has been in the past. I here suggest that the bifid structure in the Papilionini, Graphiini, and Troidini is homologous with the bifid uncus of the Parnassiines and should therefore be called the uncus. Cases in the Papilioninae where it is trifid or single (e.g., *Eurytides, Protographium,* and *Teinopalpus*) should be considered derived.

CLADE 4—SUBFAMILY PARNASSIINAE

I examined parnassiines only superficially in this study. Male and female specimens representing all the genera and species-groups recognized by Munroe (1961) were dissected (table 1), but a phylogenetic analysis of these taxa was not undertaken.

Bryk (1923) recognized family-level status for the Parnassiinae, in which he included all the currently recognized genera. Subsequent authors (e.g., Ford, 1944b; Talbot, 1949) considered the Parnassiini and Zerynthiini to be separate subfamilies. All authors since Munroe (1961) have recognized these as sister-tribes. Hancock (1983) discussed phylogenetic relationships among genera, and Igarashi (1979, 1984) discussed some of the uniquely derived larval and pupal traits that corroborate the monophyly of this subfamily. Ackery (1975) figured the male genitalia and wing venation of all 14 parnassiine genera, and all my references to wing venational characters for this subfamily are taken from his work. In addition, Hiura (1980) presented a cladistic analysis of the genera, and his re-

sults can be compared with those of Hancock. The following characters were included in my analysis. The first two corroborate the monophyly of the subfamily, and the others are significant because they occur in other papilionid taxa, leading to confusion about their interpretation.

10. Aedeagus thin and heavily sclerotized. The aedeagus of species in the Parnassiinae (figs. 23C–26C) is very thin and usually heavily sclerotized, especially distally. This trait appears to represent a synapomorphy for the Parnassiinae, but there are species in the genus *Pachliopta* (Troidini) with a thin, heavily sclerotized aedeagus (*P. coon,* fig. 52C). Such a configuration is hypothesized to have arisen separately in these groups.

11. Ostial region of female heavily sclerotized. The parnassiine species examined have a unique ostial configuration observed nowhere else in the Papilionidae. There is a large platelike region surrounding the opening of the ductus bursae (figs. 23A–26A; Saigusa and Lee, 1982). This structure is sclerotized to an unusual degree in almost all species, and, unlike the ostium of many papilionines, carries little ornamentation. In many species there are small, paired lobes immediately behind the opening, but this is unlikely to represent a derived character state; the ostium of *Baronia brevicornis* (fig. 22A) has paired lobes as do the ostial regions of species in the Papilioninae such as *Teinopalpus, Papilio* sp., and many graphiines (see figures). As previously mentioned, homology of the female swallowtail ostium presents an extremely difficult problem.

[12]. Third segment of labial palpus elongate. The labial palpi of species in the Papilionidae and four species in the Pieridae are shown in figures 68–71. The third (terminal) palpal segment of all troidines, all papilionines, and all graphiines is characteristically a small round segment with a distal invagination that is found in all Lepidoptera (Kuznetsov, 1967). The basal segment in these species is the longest one, and the middle segment intermediate in length. The palpus of *Baronia* (fig. 68E) is similar in shape. In the Parnassiinae the palpi are unusually long (fig. 68F–I). This appears to be due largely to elongation of the third segment. Elongation of the terminal segment is not unique to

members of this subfamily however. The palpi of some species in the Pieridae (e.g., fig. 68A–D) are almost identical with those of parnassiines, as is the labial palpus of *Teinopalpus* (fig. 69A). According to my character analysis, however, all three of these cases have arisen independently.

[13]. Middle discocellular vein (mdc) of forewing incurved. An incurved forewing mdc was described by Hancock (1983) as a synapomorphy for his subtribe Teinopalpiti (Papilioninae). Examination of the wing venation of parnassiine species (see figures in Ackery, 1975) shows that the same is true of the mdc in all genera within this subfamily. According to the present analysis, an incurved mdc is homoplasious, having arisen separately in the Parnassiinae, *Teinopalpus*, and *Meandrusa*.

[14]. Female with a sphragis. The sphragis is an accessory gland secretion produced by male butterflies during copulation. After deposition in the female ductus bursae (fig. 17A), it hardens and acts as a mating plug (Drummond, 1984; Ehrlich and Ehrlich, 1978). A sphragis has been reported in the parnassiine genera *Parnassius, Hypermnestra, Luehdorfia,* and *Bhutanitis* (Munroe, 1961; Saigusa and Lee, 1982), and occurs in many troidines as well. It was a character that led Ford (1944b) to suggest a close relationship between the Troidini and Parnassiinae. Its taxonomic distribution within both of these groups is considered in the present study to be incompletely known. The argument for this conclusion is given in the discussion of the sphragis of *Cressida* and *Euryades* (Troidini; Character 121). Comparison of physiological processes involved in production of the parnassiine sphragis with those of the troidine sphragis would be very interesting in view of the hypothesis suggested here that a sphragis has arisen separately in these butterflies. Perhaps there is a fundamental difference between the two.

CLADE 5—TRIBE PARNASSIINI

[15]. Antennae with scales. This character is difficult to polarize. All previous workers have suggested that the presence of scales on the antennae is primitive for the Papilionidae. Munroe (1961) relied heavily on such an interpretation for his phylogenetic conclusions. Workers have based this hypothesis on the observation that the Pieridae, considered by them to represent the closest relatives of the Papilionidae, have scales on the antennae. The majority of species in the other butterfly families exhibit scales as well, but a cursory examination showed that some members of the Pieridae (e.g., *Pseudopontia*) and Nymphalidae (e.g., species in *Heliconius* and the Apaturinae) lack scales on the antennae. The Baroniinae were chosen to polarize character states for the rest of the Papilionidae, and they have scaleless antennae. For the sake of consistency, scaled antennae are therefore suggested to be a derived character state in the Papilionidae, although it should be recognized that this interpretation may be inaccurate. The trait shows homoplasy no matter how it is interpreted. Scaled antennae occur in the tribes Parnassiini and Graphiini, as well as in the genus *Meandrusa*.

CLADE 6—TRIBE ZERYNTHIINI

A small group, including 15 species in five genera, the Zerynthiini has been considered the sister-tribe to the Parnassiini by all swallowtail researchers since Munroe (1961). Bryk (1923) included them in the "Parnassiidae." Other authors (e.g., Ford, 1944b; Talbot, 1949) recognized subfamily status for this tribe. For characters of the group, see Munroe (1961), Hiura (1980), and Hancock (1983). Saigusa and Lee (1982) detailed the morphology of *Bhutanitis mansfieldi* (Riley), offering an excellent morphological reference for the tribe.

[16]. Tibiae and tarsi lacking scales. Munroe (1961) and all subsequent authors suggested that the presence of tibial and tarsal scales is "primitive" within the Papilionidae. *Baronia,* the outgroup used in this analysis, has scales on the tibia and tarsus and it was therefore scored as plesiomorphic here as well. The tibiae and tarsi of all species in the Parnassiini and Graphiini as well as the genera *Teinopalpus* and *Meandrusa* are scaled, whereas those in the Zerynthiini, Troidini, and the genus *Papilio* are not. Loss of scales is here hypothesized to have occurred three times.

CLADE 7—SUBFAMILY PAPILIONINAE

The Papilioninae has been recognized as monophyletic by almost all previous swallowtail researchers. In my study, the genus *Teinopalpus* is removed from the Graphiini and is instead placed in its own tribe, the Teinopalpini, as the sister-group to the Papilionini/Troidini. In addition, I follow Igarashi's (1984) recent suggestion based on larval characters, that the genus *Meandrusa* be removed from the Graphiini and placed as the sister-genus to *Papilio* in the Papilionini. Justification for these changes is presented in the discussions of Clades 9–12. Five characters are suggested to corroborate monophyly of the Papilioninae:

[17]. Pseuduncus present on male tergite VIII. At first mistakenly described as the lepidopteran uncus (Gosse, 1882; and subsequently Rothschild, 1895; Pierce and Beirne, 1941; van Son, 1949; Talbot, 1949), the pseuduncus of swallowtails is actually a projection on the posterior margin of the 8th tergite rather than being associated with the tegumen, as is the true uncus. The presence of a pseuduncus is hypothesized to represent a synapomorphy for the subfamily Papilioninae. It is not found in other swallowtail subfamilies nor generally in other butterflies. However, I observed a structure of similar appearance in *Colias philodice* (Pieridae, fig. 21B, E), but not in the other pierids (figs. 18B–20B). This species belongs to a relatively derived group within the Pieridae (Klots, 1933) and the structure is likely to have evolved independently within that family. I examined too few species to know whether projections on the 8th tergite are present in additional butterfly groups. Given the evidence at hand, it is hypothesized that the pseuduncus is a synapomorphy for the Papilioninae.

18. "Anal brushes" present along vein 2A on ventral surface of male hind wing. Male-specific scale patches on the hind wing occur throughout the subfamily Papilioninae. They can be found in the Graphiini (Characters 49, 57, 58), and are quite elaborate in various groups within the Troidini (see Characters 105, 118, 143). Although the Papilionini have always been characterized as lacking androconia on the hind wing (e.g., Jordan, 1907;

Munroe, 1961; Hancock, 1983), I found examples of apparently homologous structures in this tribe. Members of Munroe's Section V possess well-developed dorsal bristles (in addition to the ventral bristles described below) on the anal margin of the male hind wing. Such scales are also found in males of *Meandrusa* (Corbet and Pendlebury, 1978).

Zeuner (1943) noted "anal brushes" on the ventral surface of the male hind wing in *Ornithoptera*. These consist of a dense row of hairlike scales, usually most numerous along vein 1A+2A. However, such an arrangement occurs in all groups within the Papilioninae. For example, males of other troidines such as those in *Battus* and *Panosmia* have long, bristlelike scales on the underside of the hind wing anal region. Close examination of other troidines confirmed their presence in all groups, though they are not as obvious as in the genera noted above. Some *Papilio* males also possess a large mass of bristlelike scales superficially identical to those of *Battus* and other troidines. These can be seen most clearly in members of Munroe's (1961) Section V, such as *Papilio zagreus, P. scamander*, and *P. victorinus*. Males of *Teinopalpus* and both *Meandrusa* species have such scales as do all graphiines examined. This trait is here hypothesized to represent a synapomorphy for the Papilioninae. Presence of androconia on the hind wing margin is possibly related to mating behavior basic for the Papilioninae. Chemical analyses of male hind wing scales would be extremely valuable and would perhaps more accurately define the androconial system in this group. Species that superficially lack androconia may produce male-specific compounds. In addition, groups might produce different chemicals that would be useful as taxonomic characters.

19. Forewing with basal spur. Munroe and Ehrlich (1960) pointed out that the cubitovannal vein of the forewing (= basal spur, fig. 150) is found only in species belonging to the Papilioninae and not outside the Papilionidae. They concluded that this condition "indicates with great probability that [the Papilioninae] is a natural and monophyletic group." I agree. As these authors observed, the basal spur of *Teinopalpus* (fig. 163) is relatively short, but is present. Forewings of papilionines are shown in figures 152–184.

20. Metathorax with a distinct meral suture. Ehrlich (1958b) first discovered a transverse suture "represented internally by a lamella" on the metameron of papilionids. This suture is absent or indistinct in other butterflies according to him. Furthermore, my own investigation has found it only in members of the Papilioninae including the genera *Teinopalpus* and *Meandrusa*. The suture is absent in *Baronia* and members of the Parnassiini. In some Zerynthiini a faint indentation occurs on the metameron but there is no sign of the internal lamella. I scored both tribes of the Parnassiinae as lacking the meral suture.

[21]. Larvae with white saddle on abdominal segments. The white saddle, so often seen on abdominal segments 3 and 4 in troidine larvae (e.g., Igarashi, 1979), is here suggested to be homologous with the white saddle observed in many larvae of the Papilionini, those with the "bird-dropping" pattern (Seitz, 1906). In addition, the fourth instar larva of *Meandrusa*, figured by Igarashi (1979), exhibits a white saddle. Although the majority of species in the Graphiini show no such pattern, a white saddle is clearly visible in the larvae of many *Eurytides* species (DeVries, 1987). If, as I here propose, the presence of a white saddle is a synapomorphy for the Papilioninae, then it was lost in many groups such as the troidine genera *Battus* and *Euryades,* and in graphiines other than *Eurytides.* The white patch is located laterally on abdominal segment 3 and meets dorsally on abdominal segment 4. It will be interesting to discover whether such a pattern occurs on the larvae of *Teinopalpus.*

Character Not Used in the Analysis: The relative length of the upper and middle discocellular veins (udc and mdc, fig. 150) in the forewing is a trait for which enormous variation occurs within the Papilionidae. In *Baronia* the udc is shorter than the mdc (fig. 151) as it is in members of the Parnassiinae (see figures in Ackery, 1975). It results from having M_1 arise close to the base of R_{4+5} on the discal cell. A short udc appears to be typical of butterflies in the Nymphalidae, Lycaenidae, and Hesperiidae (e.g., see figures in Clench, 1975; Common, 1979). In many species representing these groups M_1 arises directly from the base of the radials, and in

Pierids it is stalked with R_2–R_5. A short udc is thus likely to be plesiomorphic for the Papilionidae. However, there is so much inconsistency within tribes of the Papilioninae that it was impossible to score each. The udc is clearly shorter than the mdc in *Teinopalpus* and *Meandrusa* (figs. 163, 164), whereas it is as long as or longer than the mdc in graphiines (figs. 152–162). Within both the Troidini and Papilionini there are species exhibiting either of these character states. In *Papilio* the plesiomorphic condition (udc < mdc) is observed in members of the *zagreus, glaucus,* and *troilus* groups (e.g., fig. 165), but these veins are of equal length in others (e.g., *P. thoas*, fig. 150). The same is true of the Troidini. In most species the udc is shorter than the mdc (e.g., *Pachliopta aristolochiae*, fig. 171) and in others it is as long or longer (e.g., *Battus* species, fig. 166). No solution to this inconsistency could be found so the trait was not used in the tribal-level analysis. Having the udc clearly longer than the mdc was treated as derived within the Graphiini and Troidini (Character 71).

CLADE 8 — TRIBE GRAPHIINI

The monophyly of the Graphiini and phylogenetic relationships among genera are treated in Analysis 2.

CLADE 9

Three characters suggest that *Teinopalpus* is the sister-group to the Papilionini/Troidini, and it has been placed in its own tribe, the Teinopalpini, for that reason. This is not without precedent since Ford (1944b), Talbot (1949), and Ehrlich (1958b) recognized the Teinopalpini as a tribe. I suggest tribal recognition here because this genus does not share uniquely derived characters with existing papilionine tribes. It does show synapomorphies with the members of Clade 11.

22. Patagia membranous. The patagia are sclerotized in almost all Lepidoptera but are membranous in several groups within the Papilionidae. The Baroniinae, Parnassiinae, and Graphiini have sclerotized patagia (the plesiomorphic character state), while the Teinopalpini, Troidini, *Papilio,* and *Meandrusa* have membranous patagia (Ehrlich, 1958b). Though the degree of desclerotization varies

slightly within these groups, the patagium is never heavily sclerotized and melanized as in species outside Clade 9.

23. Female with sclerotized invagination dorsal to opening of ductus bursae. This character state is present in all members of Clade 9. Presumably the uncus or pseuduncus fits into the invagination during copulation, but its function is speculative because I have been unable to study the mechanics of copulation in papilionids. In the Troidini it is usually a sclerotized pocket opening dorsally (see for example *Battus polydamus,* fig. 45A). It is membranous in some members of the Papilionini, but is sclerotized in others such as *Papilio thoas* and *Papilio victorinus* (figs. 41A, 42A). The invagination is quite deep and is oriented horizontally in *Meandrusa sciron* (fig. 43A), whereas it is more shallow in *Teinopalpus imperialis* (fig. 36A).

[24]. Pattern between longitudinal cuticular thickenings of wing scales reticulate. Ghiradella (1985) discovered a unique configuration of transverse crossribs between the longitudinal ridges on the dorsal surface of wing scales in papilionids. She noted that in most lepidopteran families and in some papilionids, the crossribs form a "rectangular, rectilinear arrangement." These she termed "windows." Micrographs of scales representing other lepidopteran families show such an arrangement (see Eliot, 1973; Davis, 1978, 1986; Rutowski, 1980; De Jong, 1982; Ackery and Vane-Wright, 1984). In most papilionids, however, Ghiradella found that the crossribs "form instead a coarse network" between the longitudinal ridges. I discovered this trait independently and studied its taxonomic distribution within the family. I term the plesiomorphic state "ladderlike" and the derived state "reticulate." The ladderlike configuration occurs in *Dismorphia* (Pieridae, fig. 72), in *Pieris* (Pieridae, fig. 73), throughout the Parnassiinae, in *Baronia brevicornis* (Baroniinae), and in all members of the Graphiini examined, including *Graphium* (fig. 74), *Eurytides* (fig. 75), *Iphiclides,* and *Protographium.* The derived state (reticulate) is restricted to *Papilio* (fig. 76), *Meandrusa* (fig. 77), the Troidini—*Pachliopta* (figs. 78, 79), *Cressida,* and all subgenera of *Parides* (e.g., fig. 80)—and *Teinopalpus* (fig. 81). I therefore propose that the presence of a reticulate crossrib pattern between the longitudinal ridges of wing scales is a synapomorphy for members of Clade 9.

CLADE 10—TRIBE TEINOPALPINI

The phylogenetic position of *Teinopalpus* has been one of the most perplexing issues in the study of swallowtail systematics. Bryk (1923) placed it in its own family, the Teinopalpidae. Ford (1944b) erected the tribe Teinopalpini to include only this genus. He appeared to have made that decision because he recognized the many autapomorphies of the genus, and felt that it was sufficiently different phenetically to warrant its own tribe. Talbot (1949) and Ehrlich (1958b) followed Ford's judgment, Ehrlich further emphasizing the phenetic differences between this genus and other papilionids. Munroe (1961) included it in the Graphiini because it "has genitalia closely similar to those of primitive [Graphiini]," possibly referring to the broad pseuduncus, freely telescoping tegumen and 8th male tergite, and trifid uncus. The first trait is considered in the present study to represent a synapomorphy for the entire Papilioninae (Character 17). The second was discussed by Munroe in contrast to the sclerotized 8th and 9th intersegmental membrane of the Troidini/Papilionini, a uniquely derived trait for those tribes (Character 30). The third trait is here considered to have been derived independently in *Teinopalpus* and the genus *Eurytides* (Character 27). Munroe and Ehrlich (1960) considered *Teinopalpus* the sister-group to the rest of the Graphiini, in its own subtribe, the Teinopalpiti (fig. 5). They recognized it as separate from other graphiines on the basis of uniquely derived characters—"inflation of the frons and associated hypertrophy of the palpus, ... sexual dimorphism and specialization of the pattern and wing shape, atypical wing venation"—as well as characters found in other papilionine groups, "smaller tentorial crests, lacking sclerotized patagia, reduced antennal scaling." Of these latter traits, the first is plesiomorphic (see Character 45), the second is shared with members of Clade 11 (Character 21), and the third is also considered to be plesiomorphic in swallowtails (Character 15). Igarashi (1984) noted that the position of *Tei-*

nopalpus is "rather difficult to determine" because of the lack of information on early stages. He added that adult morphology "suggests remote association with the Graphiini."

Hancock (1983), like Munroe and Ehrlich, recognized the subtribe Teinopalpiti within the Graphiini, but included the genera *Meandrusa* and *Iphiclides* in it as well as *Teinopalpus*. I argue that *Meandrusa* is more closely related to the genus *Papilio* (see discussion of Clade 12). Eight synapomorphies, none of which are found in *Teinopalpus*, unite *Iphiclides* with other graphiine genera. Hancock listed a single synapomorphy for the Graphiini, "tentorial crests very high," and on that basis included *Teinopalpus*.

I have been unable to find a single synapomorphy that would suggest placing *Teinopalpus* in the Graphiini. The tentorial crests of *T. imperialis*, graphiines, and members of other papilionid groups are shown in figure 66. It is clearly inaccurate to characterize the crests of *Teinopalpus* as very high. Instead, they are not higher than in species belonging to the Parnassiinae, Papilionini, or Troidini. The inclusion of this genus in the Graphiini by past authors therefore appears to be a result either of grouping on the basis of shared plesiomorphic traits, or of inaccurate morphological interpretation. There are two described species, *T. imperialis* and *T. aureus*. Traits characterizing the genus are listed below. Note that five of the seven are homoplasious.

[12]. Distal segment of labial palpus elongate. Most previous authors regarded the long labial palpi of *Teinopalpus* (fig. 69A) as an autapomorphic character. The palpi are very long relative to other species in the Papilioninae (see figs. 69–71), but they are not long when compared to the palpi of species in the Parnassiinae (fig. 68F–I). There, as well as in *Teinopalpus*, the palpi are unusual in having the third segment elongate. As was described earlier, an elongate third palpal segment is suggested to be homoplasious, having arisen twice within the Papilionidae.

[13]. Middle discocellular vein (mdc) of forewing incurved. Hancock (1983) argued that the presence of a strongly concave or incurved mdc was a synapomorphy for his subtribe Teinopalpiti, in which he included the genera *Teinopalpus*, *Meandrusa*, and

Iphiclides. The mdc of *Iphiclides* (fig. 157) cannot be characterized as strongly concave. The mdc vein of both *Teinopalpus* and *Meandrusa* is strongly concave, and vein M_2 of the forewing is strongly arched as well (figs. 163, 164). However, both of these traits occur in exactly the same state in members of both the Parnassiini and Zerynthiini as well (figures in Ackery, 1975). The forewing venation of *Sericinus montela* (Zerynthiini) is identical in almost every respect with that of *T. imperialis*, except that the discal cell is not shortened (Character 25). The most parsimonious cladogram for the data presented here suggests that an incurved mdc (and arched M_2) arose three times in the Papilionidae; in the Parnassiinae, in *Teinopalpus*, and in *Meandrusa*. The possibility exists that future research will support a sister-group relationship between *Teinopalpus* and *Meandrusa*, in which case Character 11 would be redefined as a synapomorphy for these genera.

25. Frons protruding. The frontal region of the adult head in *Teinopalpus* protrudes markedly, giving it a configuration unique among papilionids (Ehrlich, 1958b; Munroe and Ehrlich, 1960). Munroe and Ehrlich (1960) also suggested, without supporting evidence, that this was associated with "hypertrophy of the palpus," a trait treated as unassociated in the present analysis (Character 12).

[26]. Forewing discal cell less than half the length of the wing. Hancock (1983) described the forewing discal cells of *Teinopalpus* and *Meandrusa* as shortened. There are species in the Parnassiinae (e.g., *Hypermnestra helios*; figures in Ackery, 1975) in which the discal cell is somewhat shorter than it is in other papilionids, but only in these two genera is it less than half the length of the wing (figs. 162, 163). The cladistic analysis suggests that a short discal cell arose independently in *Teinopalpus* and *Meandrusa*, but because the phylogenetic positions of these taxa are tentative, future research may show that it is actually a synapomorphy uniting them.

27. Forewing with vein R_3 short-stalked with R_{4+5}. *Teinopalpus* is the only genus in the subfamily Papilioninae in which R_3 is stalked with R_{4+5} (fig. 163). Genera in both

tribes of the Parnassiinae, such as *Archon* (Parnassiini), *Luehdorfia* (Zerynthiini), and *Bhutanitis* (Zerynthiini), show this condition (figures in Ackery, 1975), but in these taxa it is stalked for a much longer distance. I suggest that the trait in the Parnassiinae is not homologous with that in *Teinopalpus*.

[28]. Distal portion of uncus trilobed. Homology of the structures associated with the tegumen in male papilionids was discussed previously (Character 9). A bifid uncus is a synapomorphy for members of Clade 3, and socii are absent in all members of the Papilionidae. This means that the single-structure uncus (*Protographium leosthenes,* fig. 66E), and trilobed uncus (*Teinopalpus* and *Eurytides*), are each derived character states.

Both *Eurytides* and *Teinopalpus* have been characterized as having socii present because of their unusual morphology (Munroe, 1961; Hancock, 1983). However, the three lobes are formed from two short slits at the distal end of the uncus, which is a single piece for almost its entire length (fig. 66C, I). I suggest that the typically bifid uncus is fused in these two genera, and that the slits in its tip represent a derived character state that has arisen separately.

[29]. Ductus bursae of female elbowed. In *Teinopalpus imperialis* (fig. 36A) there is a distinct elbow-shaped kink in the ductus bursae distal to the region of sclerotization. The ductus seminalis arises beyond the elbow. This configuration was also found in the genus *Meandrusa*. It can be observed in *M. payeni* (fig. 44A) but not in *M. sciron* (fig. 43A). The ductus bursae of several *Papilio* species exhibits the same shape, as can be seen in *Papilio protenor* (fig. 38A) and *Papilio troilus* (fig. 39A). According to my analysis, an elbow-shaped ductus bursae arose independently in *Teinopalpus* and in members of Clade 12, and was lost in *Papilio* species such as *P. anactus* (fig. 38A). Future research may show that Character 29 is in fact a synapomorphy for *Teinopalpus* and the Papilionini, and that these are sister-groups.

Clade 11

Hancock (1983) first suggested that the Troidini and Papilionini are sister-tribes. My research corroborates his hypothesis. Of the five characters listed below, #30 and #32 were recognized by Hancock as supporting the monophyly of the Troidini/Papilionini. The most significant difference between my results and those of Hancock is the addition of *Meandrusa* to this clade.

[30]. Pseuduncus slender. Of the species with a pseuduncus, only in the Troidini and Papilionini are there species in which it is long and slender. Usually it is quite heavily sclerotized as well (figs. 37–65). In both the Graphiini and Teinopalpini the pseuduncus is flat and broad (figs. 27E–29E, 32E, 36E). I note that some troidines have a small and broad pseuduncus (Character 111), and that some Graphiini lack a pseuduncus altogether (Character 67).

[31]. Tegumen and 8th tergite fused. Nowhere but in the Troidini and Papilionini is the intersegmental membrane between the tegumen and 8th tergite sclerotized. In both groups the tegumen, usually positioned somewhat further inside segment 8 than in other papilionids, is thus immovable. Munroe (1961) noted that within the Papilioninae only the Graphiini have an unsclerotized membrane so that their genitalia can "telescope freely" within the 8th segment. This is true of *Teinopalpus* as well (fig. 36B). Hancock (1983) recognized sclerotization of the membrane as a synapomorphy for the Troidini/Papilionini. It occurs universally in *Papilio* (figs. 37B–42B), *Meandrusa* (figs. 43B, 44B), and the Troidini (figs. 45B–65B) except the subgenus *Pachliopta*, in which the tegumen is widely separated from tergite 8 (Character 138).

32. Prodiscrimen with a spine. Ehrlich (1958b) noted that several papilionid groups have a prodiscrimen—equivalent to the prosternum of other insects—with a small internal spinelike apodeme located near its anterior edge. This spine is unique to the Papilionidae (Ehrlich, 1958b). Munroe and Ehrlich (1960) found it only in the Troidini, *Papilio,* and *Meandrusa,* but nowhere else in the Papilionidae. It thus represents a synapomorphy for members of Clade 11.

33. Lamella of metadiscrimen connecting high on furca. Ehrlich (1958b) noted variation in the configuration of the metadiscrimen within the Papilionidae. The metadiscrimen, an internal support rising dorsally

from the sternum, consists of a transparent cuticular sheet (termed the "lamella" by Ehrlich, 1958a, 1958b) bounded by thicker, pigmented cuticle (figures in Ehrlich's work). In two subfamilies, the Baroniinae and Parnassiinae, the posterior margin of the lamella curves ventrally and connects at the base of the furca. Within the Papilioninae it can have one of two configurations, the one described above (considered plesiomorphic in this study), or alternatively, the lamella can connect high up on the furca, its posterior margin being essentially absent in these cases. I examined additional papilionid species not studied by Ehrlich and found the latter condition in all members of both the Papilionini and Troidini.

CLADE 12—TRIBE PAPILIONINI

Munroe (1961) listed over 15 characters in his description of the Papilionini. Of those, most are actually either plesiomorphic at the family level (e.g., "antennae with sense organs not sunk in pits"; Character 106) or are synapomorphies for the Papilionini/Troidini (e.g., "male with 8th tergite uncus-like"; Character 29).

Hancock (1983: 30) listed 20 characters in his diagnosis for the Papilionini, none of which are autapomorphies for the tribe. The branch on his cladogram for which the Papilionini is the terminal taxon is supported by 4 "apomorphic" characters: (1) tentorial arms not crested; (2) male hind wing without a scent organ or shiny streak; (3) precosta simple; and (4) larval food plants Rutaceae. The first is plesiomorphic at the family level, crested tentorial arms (Ehrlich, 1958b) being an autapomorphy for the Graphiini (Character 45). The second is inaccurate (see Character 18). Hancock's third character is plesiomorphic at the family level, and the fourth is true of only some Papilio species; many feed solely on plants other than those in the Rutaceae such as members of the Umbelliferae and plants in families belonging to the subclass Magnoliidae (Scriber, 1984).

I consider only three character states apomorphic for the Papilionini and all are homoplasious.

[29]. Ductus bursae elbow-shaped. This trait was described for *Teinopalpus,* but the most parsimonious cladogram suggests that it is not homologous in that genus and the Papilionini. As was mentioned, such a configuration occurs in *Meandrusa* (fig. 44A) and some *Papilio* species. It is present in *P. protenor* (fig. 39A) and *Papilio troilus* (fig. 40A), but not in *P. anactus* (fig. 38A). Character 28 should be studied in detail to define it more precisely morphologically, and to clarify its distribution within *Papilio.*

[34]. Fourth instar larvae glossy. As described for Character 31, the white saddle in the Papilionini is homologous with the pale patch in the Troidini. The fourth instar larvae of *Meandrusa payeni* and some members of *Papilio* are very similar in appearance. They lack tubercles, and are smooth and glossy in appearance. In addition, the pigmentation pattern of the fourth instar *Meandrusa* larva closely resembles that of *Papilio glaucus,* especially the browner color form. This superficial similarity between *Meandrusa* and *Papilio* is most strikingly observed in those groups that both Munroe (1961) and Forbes (1932) suggested are primitive within the Papilionini, Sections III and V. Much more detailed comparisons are clearly needed, and *Meandrusa* pupae as well as final instar larvae need to be described.

[35]. "Basal fleck" of labial palpus forming a large medial flap. The labial palpi of representative papilionines are shown in figures 68–70. Nowhere but within this tribe does one find the "basal fleck" of Reuter (1896) enlarged to form a flap that projects medially (scanning electron micrographs in figs. 85–89). This trait is not found throughout the Papilionini but is hypothesized to have been lost in several groups (see fig. 70D–G). It is most clearly seen in the same groups having green larvae with a white saddle (Character 34) as well as in the genus *Meandrusa* (fig. 70A).

CLADE 13—GENUS *PAPILIO*

Species in the Papilionini have previously been recognized as a single genus, *Papilio.* Recent attempts to subdivide *Papilio* into genera (Miller and Brown, 1981; Hancock, 1983; Igarashi, 1979, 1984) are unconvincing. None of these authors have adequately demonstrated that the subgroups proposed

are monophyletic. Neither Miller and Brown nor Igarashi give characters to justify their suggestions. Hancock's assertions are equally questionable. The only generic apomorphies he lists for adults are based upon subjective assessments of wing pattern (e.g., "*Chilasa* ... mimetic of Danainae, Uraniidae or Epicopeiidae"; or "*Princeps* [with] wing pattern slightly modified or specialized, often mimetic"). Most of Hancock's larval characters are also inadequate for delimiting monophyletic genera.

Two subgroups within the genus do appear to show synapomorphies supporting their monophyly. Larvae of Sections III plus V (Munroe, 1961; approximately equivalent to *Pterourus* of Hancock, 1983) exhibit thoracic eye-spots, a condition not observed in other species (Munroe, 1961), and larvae in the *machaon* group of Section II (Munroe, 1961; approximately equivalent to the genus *Papilio* of Hancock, 1983) have a unique pigmentation pattern. The relationships of Sections III plus V (comprising 26 species) and the *machaon* group (14 species) to the other 182 species in the genus are completely unknown; these two clades arise from somewhere within *Papilio*. I therefore concur with Ehrlich and Murphy (1982); at present there is no justification for subdividing *Papilio*.

I suggest four synapomorphies for the genus:

[16]. Tibiae and tarsi lacking scales. Hancock (1983) and Munroe (1961) noted unscaled tibiae and tarsi in the Troidini and Papilionini and scaled ones in the Graphiini. This dichotomy has subsequently become one of the most commonly mentioned characters in tribal-level keys for the Papilionidae (e.g., Corbet and Pendlebury, 1978). However, I place *Meandrusa* (Clade 13), which has scaled tibiae and tarsi, within the Papilionini. According to this hypothesis, tibial and tarsal scales have been lost separately in *Papilio*, the Troidini, and Zerynthiini. If future research shows that *Meandrusa* is the sistergroup to the Papilionini/Troidini (fig. 4), scales on the tibiae and tarsi would be reinterpreted as having been lost only twice.

[36]. Female with prominent ostial armature. Munroe (1961) discussed this character in some detail and it appears to be a fairly consistent feature of species in *Papilio*.

He described the ostial armature as "consisting typically of a large anterior and a smaller posterior plate or boss, and a pair of lateral plates, but often greatly elaborated by the development of flanges and teeth." I dissected females of 35 *Papilio* species but have been unable to homologize the various parts of the ostial armature described by Munroe. Several species (e.g., *Papilio anactus,* fig. 38A) appear to lack the lateral plates. Further study of *Papilio* female genitalia may reveal homologies, thus making this character complex valuable for understanding relationships within the genus.

[37]. Vesica with a lateral process. Males of 38 *Papilio* species were dissected, and most had a consistent configuration of the aedeagus and vesica. The aedeagus is characteristically somewhat S-shaped, but sometimes strongly curved (figs. 37C–42C). In addition, the vesica always opens ventrally and in many species a lateral process, observed nowhere else in the Papilionidae, is located at its base (figs. 39C–42C). Dissection of additional *Papilio* species would document more completely the distribution of this thumb. It is possible that its presence defines a monophyletic group within the genus.

38. Signum zipperlike. Munroe (1961) noted that in *Papilio* the signum is "long, strap-like, and medially seamed." In addition, the signum in those *Papilio* species that I dissected has a characteristic pattern of sclerotization exemplified by *Papilio thoas* (fig. 41A). It is usually zipperlike, being long, thin, and oriented longitudinally on the bursa. In only a few species (e.g., *Papilio toboroi* and *P. anactus,* figs. 37A, 38A), the signum is very small, the zipperlike configuration being less apparent. Examination of females representing 35 *Papilio* species showed the trait to be extremely consistent.

Character Not Used in the Analysis: A fifth potential synapomorphy for the genus is the unique change in chemical composition of osmeterial secretions during larval development (see Character 1). Honda (1981) noted that the change from production of mono- and sesquiterpenes during the first four instars to the production of aliphatic acids by fifth instar larvae coincides with a dramatic change in pigmentation pattern; the first four instars are usually "bird dropping" mimics,

while the last is green in color, sometimes with eyespots. This developmental change in osmeterial chemistry appears to be unique to *Papilio,* but the larvae of *Meandrusa* have not been studied.

CLADE 14—GENUS *MEANDRUSA*

There has been considerable controversy concerning the correct phylogenetic placement of *Meandrusa.* It has been placed in the Graphiini by almost all researchers, but some have hinted at an affinity between *Meandrusa* and *Papilio.* Munroe (1961) suggested that it was a higher graphiine genus from which the Papilionini possibly arose. Munroe and Ehrlich (1960) placed it on their diagram (fig. 5) as the graphiine genus closest to the Papilionini, and argued that *Meandrusa* "arose close to the point of separation of Papilionini from Graphiini." Hancock (1983) did not agree with these ideas, however, claiming that "although *Meandrusa* is usually placed with the higher [Graphiini], in characters of pattern, venation and male genitalia it appears to be closely allied to *Teinopalpus.*" He thus placed these two genera, along with *Iphiclides,* in a separate subtribe of the Graphiini, the Teinopalpiti (fig. 7).

I tentatively suggest that *Meandrusa* be placed in the Papilionini, provisionally as the sister-group to *Papilio.* This conclusion was reached independently by Igarashi (1979, 1984; see also Tsukada and Nishiyama, 1980) on the basis of larval morphology. Igarashi (1979), who reared a single larva of *M. payeni* to the fourth instar on *Lindera umbellata* (Lauraceae), published the first descriptions of *Meandrusa* immatures. His illustration of this specimen (Plate 195) shows a smooth larva with pattern and coloration very similar to that of a penultimate instar larva of *Papilio glaucus.* On the basis of his findings he argued that "*Meandrusa* should be regarded as belonging to the Papilionini rather than Graphiini."

Meandrusa has been placed in the Graphiini largely on the basis of two characters: (1) tibiae and tarsi scaled; and (2) antennae scaled (Munroe, 1961). Both of these are problematical. The antennae of *Meandrusa* are sparsely scaled dorsally (apomorphic in this study) as is true of species in the Graphiini

and Parnassiini. My cladistic analysis suggests that all three of these are cases of homoplasy and not synapomorphy (Character 15). Tibial and tarsal scaling I consider plesiomorphic (Character 16) and therefore not grounds for indicating immediate common ancestry. Munroe (1961) and Munroe and Ehrlich (1960) also interpreted both of these characters as being plesiomorphic for the Papilionidae. They therefore included *Meandrusa* in the Graphiini on the basis of symplesiomorphy.

According to Hancock's cladogram (1983: 14), *Meandrusa* should have a high tentorial crest as is characteristic of the Graphiini. I found, however, that its tentorial crest (fig. 67F) is not higher than many members of either the Papilionini or Troidini and is much lower than that of graphiines (Character 45, Analysis 2). Hancock (1983) listed four apomorphic characters on his cladogram to support placement of *Meandrusa* with the Teinopalpiti. Of those, two are actually synapomorphies for the Troidini/Papilionini ("[male] tergites 9 and 10 fused with 8th"; and "prodiscrimen with a spine"), one is found in the Parnassiinae, Papilionini, and Troidini as well as the Graphiini ("precosta simple"), and the fourth I argued is an incorrect morphological interpretation ("uncus absent," Character 9).

The genus exhibits all three synapomorphies of Clade 9. In addition, five synapomorphies unite *Meandrusa* with the Papilionini/Troidini. Two synapomorphies are found in *Meandrusa* and the Papilionini; the larval pattern (Character 34) was described above, and the basal fleck on the labial palpus of *Meandrusa* is very large, projecting medially as in several *Papilio* species (Character 35). The genus, whose geographical distribution and nomenclature are covered by Igarashi (1979) and Hemming (1934, 1967), respectively, comprises only two species, *M. sciron* and *M. payeni.*

[13]. Middle discocellular (mdc) incurved. According to my analysis, an incurved mdc arose three separate times in the Papilionidae; in *Meandrusa,* in *Teinopalpus,* and in the Parnassiinae.

[15]. Antennae with scales. It was argued earlier that presence of scales on the antennae is a derived state within the Papilionidae.

This is the opposite polarity decision of all previous authors. According to my interpretation, antennal scales evolved separately in three groups, the Parnassiini, Graphiini, and *Meandrusa*.

[26]. Forewing discal cell less than half the length of wing. In both *Meandrusa* (fig. 164) and *Teinopalpus* (fig. 163) the forewing discal cell is less than half as long as the wing. The trait was previously described for the latter genus, but the current analysis suggests that it is homoplasious.

[39]. Tarsal claws bifid. Both species of *Meandrusa* have a distinct tooth on the tarsal claws. This condition is also observed in one of the two *Lamproptera* species (*L. curius*) and in many pierids. All three of these occurrences are here hypothesized to represent cases of homoplasy.

40. Blue scales on underside of wing opalescent. Hancock (1983) listed this trait as characteristic of the genus but it has not been closely examined in the present study.

41. Uncus shoe-shaped. Munroe (1961) described the socii, structures that I consider to be a bifid uncus (Character 9), as "shoe-shaped" in *Meandrusa*. Though a somewhat inaccurate description (see figs. 43B, 44B), the characteristic shape of the *Meandrusa* uncus was found in no other papilionids examined.

[42]. Juxta with strong lateral flaps. Another trait described by Munroe (1961; see fig. 43D), it again appears to be uniquely derived within the genus, but occurs in only one of the two species, being absent in *M. payeni* (fig. 44D).

43. Aedeagus with a toothed flange on the distal portion. The aedeagus of both *M. sciron* and *M. payeni* have such a flange (figs. 43C, 44C) though its precise orientation differs between species.

44. Ductus bursae funnel-shaped at base. Both *Meandrusa* species have a unique ostial configuration (figs. 43A, 44A). In addition to having a funnel-shaped ductus, there is a smooth dorsal plate posterior to the ostial opening of *M. sciron*. Further comparative study of female genitalic morphology in *Meandrusa* and other papilionines may enable future workers to homologize the various structures, especially in the ostial region, and would subsequently allow polarization

of such characters within the genus *Papilio*.

Hancock described the valvae of both *Meandrusa* species as "broad, deeply emarginate dorsally" (1983: 18) and figured both with a large lobe at the base of the valve's dorsal margin (p. 18, figs. 6 and 7). I dissected several specimens of both species and found no emarginate valvae. Instead, the dorsal margin is smooth (figs. 43B, 44B) as is typical of papilionine valvae.

CLADE 15—TRIBE TROIDINI

Characters corroborating monophyly of the Troidini and generic relationships among the tribe are presented in Analysis 3.

DISCUSSION

There can be little doubt that the Troidini and Papilionini are sister-tribes, and that the Graphiini are plesiomorphic relative to all other groups in the Papilioninae. Hancock (1983) reached this conclusion independently, and the research described here corroborates his hypothesis. A single purported synapomorphy for the Graphiini and Papilionini, "tibiae and tarsi with ventral row of spines separated from dorsal row by an impressed spineless space" was discussed by Munroe (1961; originally described by Jordan, 1907). This character has been subsequently included in almost every diagnosis of the Papilionidae (e.g., Emmel, 1975; Tyler, 1975; Hancock, 1983). I have been completely unable to observe the impressed spineless space with any degree of confidence. A sister-group relationship between the Graphiini and Papilionini, implied by the writings of Munroe (1961) and Munroe and Ehrlich (1960), results from failure to recognize derived character states that unite the Troidini and Papilionini. A sister-group relationship between the latter tribes argues strongly against the theory that "red, tuberculate, *Aristolochia*-feeding larvae" (Munroe, 1961) in the Troidini and Parnassiinae are in any way homologous, as was suggested by Ehrlich and Raven (1964). Careful study of papilionid larvae is likely to reveal that these are convergent similarities. According to my results, *Aristolochia*-feeding would likewise not be a homologous trait in these two groups.

The tribal analysis shows conclusively that

neither *Meandrusa* nor *Teinopalpus* belong in the Graphiini. Their placement in that tribe by previous authors has resulted from grouping by symplesiomorphy, and from failure to recognize derived traits shared with members of the Papilionini/Troidini. The exact phylogenetic position of these two genera is much less certain, however. Neither of the synapomorphies uniting *Meandrusa* and *Papilio* occur throughout these groups. Presence of scales on the tibiae and tarsi suggests that *Meandrusa* may in fact be the sister-group to a clade including the Papilionini and Troidini (fig. 4), and this hypothesis should be tested further. In addition, two wing venational characters (#13 and #26) suggest a sister-group

relationship between *Meandrusa* and *Teinopalpus*.

The position of *Teinopalpus* is equally tenuous. Many adult morphological traits are plesiomorphic or autapomorphic. Few are informative regarding the relationship of this genus to other papilionids. The immature stages of *Teinopalpus* are not known. Larval and pupal characters often provide important information regarding higher-level relationships in the Papilionidae. It is therefore extremely important that field workers concentrate their efforts on studying the biology and life histories of both *Meandrusa* and *Teinopalpus*.

CLADISTIC RELATIONSHIPS AMONG GRAPHIINE GENERA: ANALYSIS 2

HISTORY OF THE CLASSIFICATION

The tribe Graphiini includes 147 species, 53 of which belong to *Eurytides,* and 89 to *Graphium* (table 1). All are tropical except for the Palearctic *Iphiclides podalirius* and the Nearctic *Eurytides marcellus.* The larvae feed primarily on the Annonaceae ("paw paw" family; superorder Magnoliidae), an association found nowhere else in the swallowtails. They also use other families in the Magnoliidae such as the Magnoliaceae, Lauraceae, and Hernandiaceae [see Scriber (1984) for a complete list of swallowtail host-plant families], overlapping some food plants of the Papilionini.

The Graphiini has been characterized in the past by what I regard as plesiomorphic traits. As a result, genera of doubtful affinity have been placed in the tribe, and the tribal boundaries of the Graphiini have been controversial.

Bryk (1929–1930) recognized the genus *Lamproptera,* but retained all other graphiine species in *Papilio.* *Lamproptera* appears to have been given generic status on the basis of its unusual appearance. Both species (*L. curius* and *L. meges*) are small papilionids, and the hind wing tail on vein M_3 is extremely long relative to the size of the insect. In ad-

dition, *Lamproptera* exhibits several wing venational characters found nowhere else in the Papilionidae. All of these traits are autapomorphic for the genus. Ford (1944b), Talbot (1949), and Ehrlich (1958b) placed *Graphium* and *Lamproptera* in the Graphiini. Ehrlich (1958b) united *Lamproptera* and *Graphium* because their tentorial crests are high compared to those of other butterflies (Character 45).

Munroe (1961) significantly changed the classification of the Graphiini (table 3). He included *Teinopalpus,* though I dispute this placement (Analysis 1). In addition, he noted that two "graphiine" species, *Graphium payeni* and *G. sciron* (=*gyas*) were markedly different from other members of the tribe. However, he retained them in the tribe, noting that "they belong to the very distinctive genus *Dabasa* Moore 1887" (= *Meandrusa* Moore 1887). Munroe accepted generic status for *Lamproptera,* but subdivided *Graphium* (sensu Ford and Ehrlich); he erected the genus *Protographium* for an Australian species, *leosthenes,* and recognized *Iphiclides,* a genus with two Palearctic species, *podalirius* and *podalirinus.* Munroe placed all the American graphiines (the "Kite Swallowtails" of Rothschild and Jordan, 1906) in the genus *Eurytides,* and divided them into sub-

TABLE 3
Graphiine Classifications

A. Present classification:

    Tribe Graphiini
        Genus *Eurytides* Hübner
           Subgenus *Protesilaus* Swainson
           Subgenus *Eurytides* Hübner
        Genus *Protographium* Munroe
        Genus *Iphiclides* Hübner
        Genus *Lamproptera* Gray
        Genus *Graphium* Scopoli
           Subgenus *Pazala* Moore
           Subgenus *Pathysa* Reakirt
           Subgenus *Arisbe* Hübner
           Subgenus *Graphium* Scopoli

B. Classification of Hancock (1983):

    Tribe Leptocircini (=Graphiini)
        Subtribe Teinopalpiti
           Genus *Iphiclides* Hübner
           Genus *Teinopalpus* Hope
           Genus *Meandrusa* Moore
        Subtribe Leptocirciti
           Genus *Protesilaus* Swainson
           Genus *Eurytides* Hübner
           Genus *Protographium* Munroe
           Genus *Lamproptera* Gray
           Genus *Graphium* Scopoli
               Subgenus *Pazala* Moore
               Subgenus *Pathysa* Reakirt
               Subgenus *Arisbe* Hübner
               Subgenus *Graphium* Scopoli

C. Classification of Munroe (1961):

    Tribe Leptocircini
        Genus *Lamproptera* Gray
        Genus *Teinopalpus* Hope
        Genus *Eurytides* Hübner
        Genus *Protographium* Munroe
        Genus *Iphiclides* Hübner
        Genus *Graphium* Scopoli
           Subgenus *Graphium* Scopoli
           Subgenus *Arisbe* Hübner
           Subgenus *Pathysa* Reakirt
        Genus *Meandrusa* Moore

Fig. 5. Relationships among genera and subgenera in the Graphiini according to the branching diagram of Munroe and Ehrlich (1960).

genera *Protesilaus* and *Eurytides*. The remaining graphiines were classified in three *Graphium* subgenera, *Pathysa, Arisbe,* and *Graphium.*

Munroe and Ehrlich (1960) made no substantive changes in either the tribal or generic classifications proposed by Munroe (1961). Their diagram showing the "order of the bifurcations" of graphiine lineages is repro-

duced in figure 5. They retained *Teinopalpus* in the tribe because it "appears to have real affinities with the most primitive Graphiini" and erected the subtribe Teinopalpiti. They further suggested that *Meandrusa* "arose close to the point of separation of Papilionini and Graphiini" but left it in the latter tribe. They upheld the other generic separations advocated by Munroe (1961), though noting that *Iphiclides* and *Graphium* were very closely related, and that future researchers might choose to synonymize them.

Igarashi's (1979, 1984) studies of immature stages provided important new information for understanding relationships within the Papilionidae. His work was regional, and for that reason his phylogenetic hypothesis was incomplete. He studied eggs, larvae, and pupae representing all the important Old World graphiine genera with the exception of *Teinopalpus,* for which no immatures were collected. Igarashi did not figure or discuss any New World species, however, and *Eurytides* was not placed on his diagram of phylogenetic relationships (fig. 6). His ideas concerning phylogeny and classification differed substantially from those of previous workers. He recognized generic status for three of the four subgenera of *Graphium* proposed by Munroe, retaining *Pazala* and *Pathysa,* but sinking *Arisbe* within *Graphium.* Further-
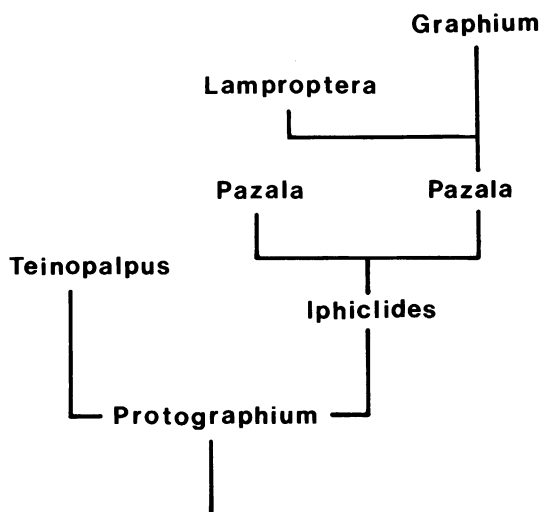
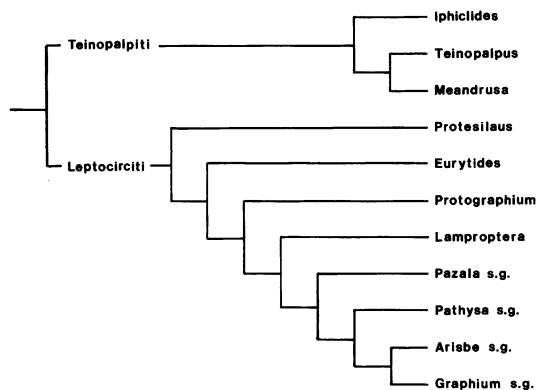Fig. 6.   Relationships among genera in the Graphiini according to the branching diagram of Igarashi (1984).

Fig. 7.   Cladistic relationships among genera in the Graphiini and subgenera in *Graphium* according to Hancock (1983).

more, he argued that *Lamproptera* is more closely related to *Graphium* (= subgenus *Graphium* of Munroe) than to either *Pazala* or *Pathysa*, therefore implying that *Graphium* of previous workers was paraphyletic with respect to *Lamproptera*.

Hancock (1983) published a cladogram for the graphiine genera (fig. 7), and his ideas also differed markedly from those of Munroe and Ehrlich. He agreed that *Teinopalpus* was a plesiomorphic member of the tribe, but placed *Meandrusa* and *Iphiclides* with it in the subtribe Teinopalpiti. All other genera were retained in the subtribe Graphiiti. Hancock's cladogram differs from the diagram published by Munroe and Ehrlich in almost every other respect. He used Munroe's generic names, except he resurrected *Protesilaus* Swainson [1832]—considered a subgenus of *Eurytides* by Munroe—and regarded it as the sister-group to the rest of the Graphiiti. Hancock recognized four *Graphium* subgenera, the three proposed by Munroe as well as *Pazala*, treated previously as a species-group within *Pathysa*.

As this discussion demonstrates, there have been few points of agreement among previous researchers concerning graphiine relationships. There are two likely explanations

for this instability. First of all, larval and pupal characters have been pivotal in all previous discussion of the group. Unfortunately, important information concerning the morphology of immature stages was not available to these authors. For example, Munroe had almost no data on three critical genera, *Teinopalpus, Meandrusa,* and *Lamproptera*. Igarashi's (1979) important discovery of the larva of *Meandrusa payeni* led him to remove this genus from the Graphiini. He also relied on larval and pupal morphology to propose a close relationship between *Lamproptera* and *Graphium*. Unfortunately, Igarashi was unable to obtain larvae or pupae of *Teinopalpus*.

The second reason for the controversy is that uniquely derived traits have rarely been used to establish monophyletic groups; the tribe itself has usually been described on the basis of plesiomorphic characters (e.g., Ford, 1944b; Munroe and Ehrlich, 1960; Munroe, 1961). Hancock (1983) published the only study to date that attempted to identify monophyletic groups in the Graphiini. His study was based on available characters in the literature, but these were too few and too poorly documented. For example, Hancock listed a single synapomorphy for the Graphiini on his cladogram of generic relationships in the Papilioninae: the presence of "very high" tentorial crests. I show that Hancock erred in this assessment because neither he nor Ehrlich had documented the character

TABLE 4
Data Matrix for Analysis 2; Cladistic Relationships Among Graphiine Genera
0 indicates the plesiomorphic state, 1 the apomorphic state

	Character number																		
	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Eurytides epidaus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
telesilaus	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0
Protographium leosthenes	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0
Iphiclides podalirius	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1
Lamproptera meges	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Graphium																			
(Pazala) eurous	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1
(Graphium) nomius	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1
(Pathysa) nomius	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1
(Arisbe) philonoe	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1

	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
Eurytides epidaus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
telesilaus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protographium leosthenes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iphiclides podalirius	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lamproptera meges	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Graphium																			
(Pazala) eurous	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
(Graphium) nomius	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
(Pathysa) nomius	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
(Arisbe) philonoe	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1

	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98
Eurytides epidaus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
telesilaus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protographium leosthenes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iphiclides podalirius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lamproptera meges	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Graphium																
(Pazala) eurous	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
(Graphium) nomius	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0
(Pathysa) nomius	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0
(Arisbe) philonoe	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1

state for tentorial crests in all graphiine genera and other members of the Papilionidae.

CLADISTIC ANALYSIS

Nine species were chosen as representative of the graphiine genera (listed in the data matrix, table 4), and were used as terminal taxa in the phylogenetic analysis. Four *Graphium* species were chosen to represent the four subgenera defined by Hancock (1983). Females in the subgenus *Eurytides* (= genus *Eurytides* of Hancock, 1983) are exceedingly rare in collections, and were unavailable for dissec-

tion. Because so many of the morphological characters employed involve female genitalia, this subgenus was not represented in the analysis. Examination of males from both species-groups in the subgenus *Eurytides* indicated that the genus itself is monophyletic (Character 60). Future study of females will almost certainly not necessitate fundamental changes in the phylogenetic hypotheses presented.

The outgroup chosen to root the cladogram was a composite of species belonging to all other papilionid tribes. Using the "Branch
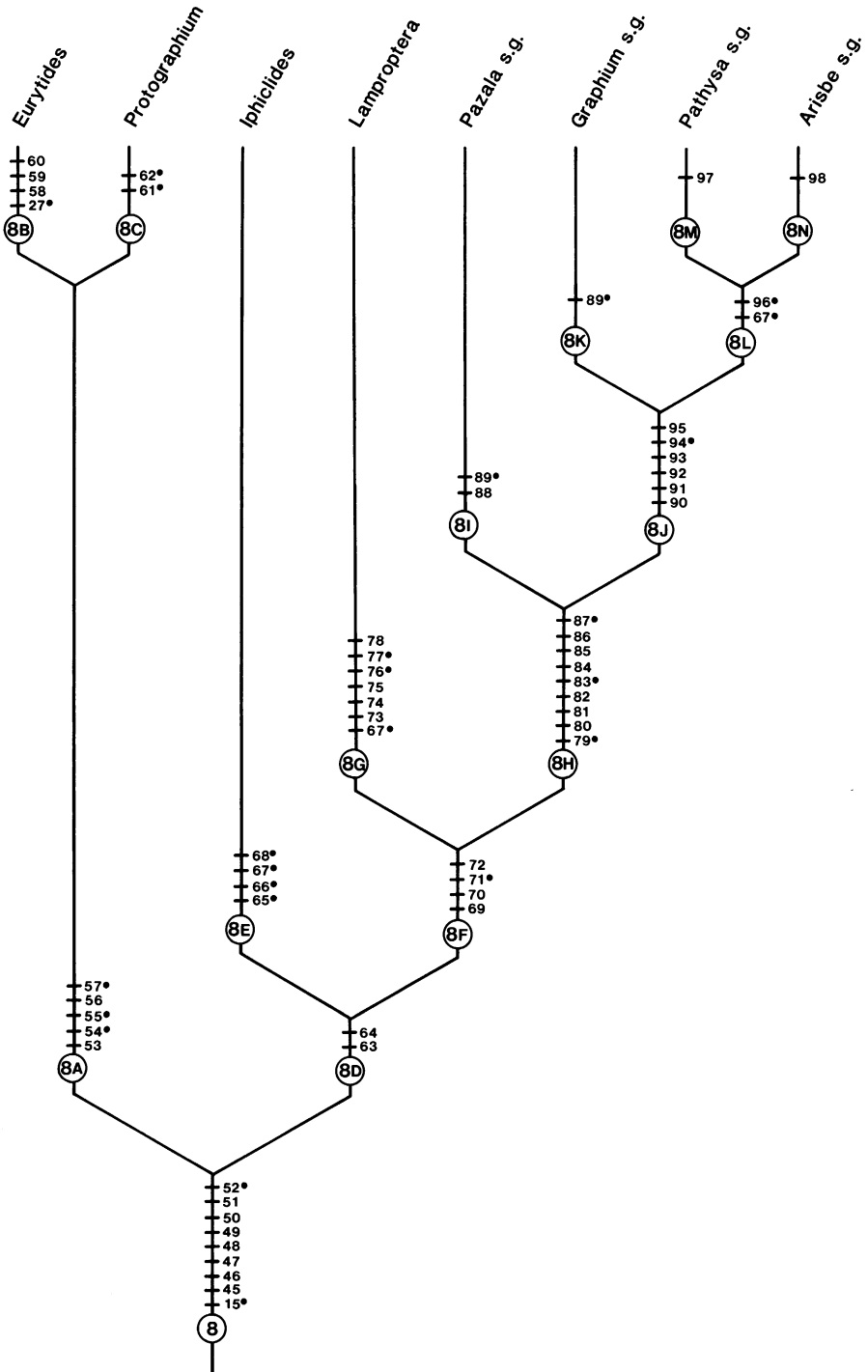
Fig. 8.   Hypothesis of cladistic relationships among genera in the Graphiini and subgenera in *Graphium* (Analysis 2). Closed circles designate homoplasious characters.

and Bound" option, the PAUP program found a single tree (fig. 8) with a consistency index of 0.887.

CLASSIFICATION

Though this research has resulted in a hypothesis of generic relationships very different from those of past authors, the classification accepted is similar to that of Munroe (1961). The major difference is the removal of two genera, *Meandrusa* and *Teinopalpus,* from the tribe. The taxa treated here as belonging to the Graphiini include five genera: *Eurytides* Hübner, *Protographium* Munroe, *Iphiclides* Hübner, *Lamproptera* Gray, and *Graphium* Scopoli. Because these groups are so closely related, and because their phylogenetic positions remain quite tentative, I chose not to erect subtribal groupings. The classifications of Munroe (1961) and Hancock (1983) are presented for comparison in Table 3.

CHARACTERS

CLADE 8—TRIBE GRAPHIINI

The Graphiini was determined in Analysis 1 to be the plesiomorphic tribe in the subfamily Papilioninae. Its monophyly is the most strongly supported of any papilionid tribe. On the other hand, relatively few characters were found that clarify relationships within the group. Areas for future research are pointed out below. The following synapomorphies corroborate the monophyly of the Graphiini:

[15]. Antennae scaled. Scaled antennae were regarded by Munroe and all subsequent researchers as a primitive papilionid character state. This assumption was based on the presence of scaled antennae in the Pieridae. Within the Papilionidae the antennae are bare in *Baronia,* the Zerynthiini, Teinopalpini, Troidini, and *Papilio,* whereas they are scaled in the Parnassiini and Graphiini. I suggest that the papilionid stem species had bare antennae, and that scaled antennae arose separately in three swallowtail lineages. Using Munroe's polarity hypothesis, scaling was lost in five lineages.

45. Tentorial crests high. Kristensen (1976) argued that the presence of dorsal tentorial

arms (=crests) is a synapomorphy for the Hesperioidea and Papilionoidea. High tentorial crests were suggested by Ehrlich (1958b) to be characteristic of the Graphiini. Comparison of the tentorial crests of graphiines with those of species belonging to other papilionid groups (fig. 67) indicates that they are unusually high in the genera *Eurytides, Protographium, Iphiclides, Lamproptera,* and *Graphium.* In *Teinopalpus, Meandrusa,* and other members of the Papilionidae the crests are represented by a smoothly rounded hump. There is variation in the height and amount of dorsal narrowing in species within the Graphiini. The trait is further discussed in relation to Character 95.

46. Cross-vein between Rs and M_1 of hind wing sinuate. Rothschild and Jordan (1906) noted that the cross-vein in the "third cellule" of the hind wing is "more or less strongly incurved" in *Eurytides* (their "Kite Swallowtails"). The cross-vein between Rs and M_1 curves inward toward the center of the discal cell. I found this character state in all five graphiine genera. The vein in *Iphiclides* (fig. 157) is less markedly curved. The discal cell of *Lamproptera* (fig. 158) is very small, making this trait hard to see. However the cross-vein does appear to be incurved here as well. The trait is very clearly observed in species within the genus *Graphium* such as *G. (Pathysa) macareus* (fig. 162).

47. Aedeagus bell-shaped at base. All graphiine genera have the base of the aedeagus funnel- or bell-shaped. In *Iphiclides podalirius* (fig. 30C) it is huge, whereas in *Lamproptera* (fig. 31C) and several *Graphium* species, such as *G. (Graphium) euryplus* (fig. 33C), it is less markedly developed. Some members of the Parnassiinae, Papilionini, and Troidini have the base of the aedeagus somewhat flared (e.g., *Pachliopta* species, figs. 50C–54C), but not as strongly as graphiines. The aedeagus of *Teinopalpus* (fig. 36C) widens slightly at the base and has a medial notch unlike members of the Graphiini. The aedeagus of *Baronia* (fig. 22C) is not flared.

48. Dorsolateral sclerite of valve articulated. Throughout the Papilioninae and in some parnassiine species I observed a previously undescribed sclerite of the male genitalia. It is usually a small structure located

in the membrane between the dorsobasal attachment of the valve and the tegumen (see generalized genitalia, fig. 17). In members of the Teinopalpini, Papilionini, and Troidini it is set apart from the valve, tegumen, and uncus, appearing to be free-floating in the membrane. Among these tribes it is always small and lightly sclerotized (e.g., *Papilio* sp., figs. 37B–42B). Within the Graphiini this sclerite is larger and is quite heavily sclerotized. Furthermore, it is firmly attached to the valve at the dorsal junction of the valve and tegumen, and the point of attachment is even more heavily sclerotized. The sclerite therefore appears to form a hinge at the base of the valve (figs. 27B–35B). The complex association of the sclerite and valve was observed in no other butterflies examined.

49. Dorsal bristlelike scales present basally on ventral anal margin of male hind wing. Graphiines have bristlelike scales on the dorsal surface of the anal margin. They are typically very long, most numerous toward the base of wing, and often lie horizontally, pointing distally along the anal vein (vein 1A+2A). I observed these scales in *Eurytides, Protographium,* and *Graphium.* They occur in male *Lamproptera curius,* but not *L. meges.* Males of *Iphiclides podalirius* lack such scales, but they have what appear to be modified scales on the hind wing margin (fig. 95). According to this cladistic analysis, lack of bristlelike scales in *Iphiclides podalirius* is secondarily derived within the tribe.

50. First instar larvae with bifid setae on thoracic and abdominal segments. Igarashi (1979) figured bifid setae on the thorax and abdomen of first instar larvae of nine *Graphium* species as well as those of *Iphiclides podalirius* and *Protographium leosthenes,* and mentioned that they also occur on first instar *Lamproptera.* I examined *Eurytides marcellus* larvae, and found that they are present in that species as well. They appear to be a synapomorphy for the Graphiini. The only other papilionid species in which bifid setae are known is *Baronia brevicornis,* but they occur on the larval head, rather than on the body (Igarashi, 1979, 1984; and see Character 66). A detailed study of the distribution of bifid setae on particular body segments and tubercles might provide important phylogenetic information concerning relationships within the Graphiini.

51. Pupa with lateral ridges extending from cremaster to head. Pupal morphology of graphiines is distinctive and has been used by all past authors to characterize the tribe. Munroe (1961) and Hancock (1983) noted a raised ridge located laterally on each side of the body and extending from the cremaster to the pupal head of graphiines (figured in Igarashi, 1979, 1984).

[52]. Papillae anales with peglike setae. Short, hooklike setae are found on the medial surfaces of the ovipositor lobes in almost all Papilionidae (fig. 103). Such setae may be a synapomorphy for Clade 3 because I did not see them on the papillae anales of *Baronia.* Their distribution outside the swallowtails is unknown.

One type of setal configuration is restricted to the Graphiini. A series of very short, peglike setae occurs along the lateroposterior edge of each lobe (figs. 90, 91). Scanning electron micrographs reveal more setal types. Short, hairlike setae cover the surface of the papillae anales in all papilionids examined (e.g., figs. 107, 108). I recorded peglike setae in *Eurytides, Graphium,* and *Iphiclides,* but not in *Lamproptera.* In *Protographium,* the setae are not as short and peglike, but are distinctly thickened. I suggest that peglike setae are a synapomorphy for the Graphiini but were lost in *Lamproptera.*

The function of these structures is open to speculation. Klijnstra (1985) found that setae on the ovipositor lobes of *Pieris rapae* (Pieridae) detect "oviposition deterrent pheromone," and Eaton (1986) suggested that similar setae in *Manduca* (Sphingidae) detect host plant chemicals. Four distinct types of setae were observed on the lobes of *Iphiclides* and other graphiines, and each may serve a different function, possibly as chemosensors during the final phases of oviposition.

CLADE 8A

My results indicate that *Protographium* and *Eurytides* are sister-genera. Munroe (1961) mentioned that *Protographium* is "separated by very slight characters from *Eurytides,*" but that "detailed resemblance of pattern and the occurrence in the same geographic region" indicate a close relationship between *Protographium* and *Graphium.* Munroe and Ehrlich (1960) accepted the latter interpretation.

Hancock too decided that *Protographium* is more closely related to *Graphium* than to *Eurytides*. The monophyly of Clade 8A is quite firmly established.

53. Pupa squat. Igarashi (1979) figured the pupa of *Protographium leosthenes,* which is squat in appearance, unlike the elongate pupa of *Iphiclides, Lamproptera,* or *Graphium.* He did not show the pupae of species in the genus *Eurytides.* I found that the pupa of *E. marcellus* is squat like that of *Protographium.*

[54]. Clasper triangular with a serrate margin. The clasper of *Protographium leosthenes* is relatively broad and triangular (fig. 29B) with many short teeth along its margin. Within *Eurytides* there is variation in the shape of the clasper. However, in those characterized by Munroe (1961) as being primitive within the genus, the clasper is also triangular and marginal teeth are present. These species include members of both the *E. dolicaon* and *E. thyastes* groups. The claspers of these species are much less complex than those of the *E. protesilaus* and *E. marcellus* groups (e.g., fig. 27B). This trait is not well-substantiated; the clasper of *E. telesilaus* (fig. 28B) is not triangular, though its margins are serrate. Of the species dissected, the valve of *E. telesilaus* is unusual among members of this genus.

[55]. Uncus fused. The uncus is fused for almost its entire length in *Eurytides* species (fig. 66C) and is entirely fused in *Protographium leosthenes* (fig. 66E). The uncus of *Eurytides* has been termed "trilobed" (Munroe, 1961) because of the two short slits at its distal end. These lobes have been interpreted to represent paired lateral socii and a medial uncus (Character 9). One species, *E. celadon* (Lucas), has an uncus fused for its entire length (fig. 66D) exactly as in *P. leosthenes.* I have termed fusion of the uncus a synapomorphy for Clade 8A. Other graphiines (fig. 66F–H) exhibit a bilobed uncus, the plesiomorphic state.

56. Dorsolateral sclerite of valve triangular and fused to tegumen. In most graphiines the sclerite described in Character 48 as the dorsolateral sclerite is somewhat concave and elongate (see figs. 30B–35B). In *Lamproptera* (fig. 31B) the sclerite is huge and is only lightly melanized. In *Protographium* and *Eurytides* this sclerite is firmly attached to the tegumen and articulates at the base of the uncus

(figs. 27B–29B). In addition, these two groups have a sclerite that is triangular and sharply elbowed anteriorly. The configuration of the dorsolateral sclerite in *Protographium* and *Eurytides* is suggested to be a derived state.

[57]. Anal margin of male hind wing with deciduous scales. Within the Graphiini there are groups in which deciduous androconia occur in addition to the more commonly observed bristlelike scales (Character 49). If androzonia stuck to a probe as it was gently dragged over the anal margin, deciduous scales were scored as present. Typically, large masses of scales did so. Species belonging to the following groups were found to have deciduous scales: some members of *Eurytides,* all subgenera of *Graphium* except *Pazala,* and *Protographium leosthenes.* Similar scales are described for species in the Troidini (Character 143), but they are not considered homologous with such scales in the Graphiini. Furthermore, it is hypothesized that deciduous scales arose in Clade 8A separately from their derivation in *Graphium* (Character 91).

CLADE 8B—Genus *Eurytides*

Hancock (1983) separated the subgenus *Protesilaus* (as defined by Munroe) from the rest of *Eurytides* and suggested that it was the sister-group to the rest of the Leptocirciti (table 3 and fig. 7). A single synapomorphy was listed on Hancock's cladogram to corroborate monophyly of the lineage for which *Protesilaus* was the sister-group; "of Gondwanan origin" was the derived state whereas "of Nearctic origin" was the plesiomorphic state. This is not a heritable character and does not constitute grounds for identifying a monophyletic group. I argue that Munroe's original formulation was correct, and that *Eurytides* is a monophyletic genus. The two subgenera of Munroe, *Eurytides* and *Protesilaus,* are tentatively accepted. Precise relationships within the genus were not examined because females in the subgenus *Eurytides* are rare in collections and were not available for dissection. Without such data there is little hope of producing a cladogram for the genus. The following characters corroborate the monophyly of *Eurytides:*

[27]. Uncus trilobed. All species in *Eurytides* have the tip of the uncus trilobed or trifid (fig. 66C). This state occurs in *Teino-*

palpus imperialis as well (fig. 66I), and perhaps led Munroe (1961) to include the latter in the Graphiini. The present study suggests that a trifid uncus was independently derived in these two genera and therefore represents a synapomorphy for *Eurytides*.

[58]. Deciduous scales curly. Most species in the genus *Eurytides* have three types of androconia on the ventral surface of the male hind wing: (1) bristlelike scales characteristic of graphiines (Character 49), (2) scales somewhat like typical hind wing scales but longer and thinner, and (3) deciduous scales. The deciduous scales of *Eurytides* species are unlike those of other graphiines. As the scales of *E. epidaus* illustrate (fig. 96), they are quite short and occur in a tangled mat. The bases of these scales are thin (fig. 97) and the scales themselves appear to have broken off at the scale socket in several cases. This may be a mechanism whereby they are transferred to the female during courtship (see discussion of Character 143, Analysis 3).

Deciduous scales do not occur in all *Eurytides* species. Presumed mimetic species, such as *E. phaon, E. pausanius,* and *E. branchus,* possess only bristlelike scales as well as a small patch of scales similar to the second type described above. Whether presence of deciduous scales defines a monophyletic group within *Eurytides* or whether it represents a plesiomorphic state is impossible to determine in the absence of additional character information.

59. Ostium of female a series of folds. There is much variation in the configuration of the ostium throughout the Papilionidae. Within the genus *Eurytides,* the ostium is unique in that it consists of a set of membranous folds and is only lightly sclerotized compared to other species in the Papilioninae (figs. 27A, 28A). Further study of the ostium within this genus may help elucidate species relationships.

60. Clasper of male with a dorsal flange and central process. Elaborations of the clasper in *Eurytides* species are much easier to homologize than those in other swallowtail genera, and many species exhibit remarkably similar configurations, as was noted by Munroe (1961). There is always a large, toothed, dorsal flange that either lies flat against the valve (e.g., *E. dolicaon,* and *E. marcellus,* not

figured) or projects medially (e.g., *E. epidaus,* fig. 27B). There is also a central process (Hancock, 1983) in all species examined that projects medially. It is either thin as in *E. epidaus,* or stout and toothed as in *E. dolicaon* and *E. thyastes* (not figured). One structure, a ventrally located thumblike process, is found on the claspers of only some species (e.g., *E. epidaus,* fig. 27B; *E. branchus, E. agesilaus,* and others). In some species it is very small (e.g., *E. asius*) or absent (e.g., *E. dolicaon*). The fundamentally similar clasper morphology of *Eurytides* species supports the contention that the group is monophyletic and argues against the assertion of Hancock (1983) that *Eurytides* is polyphyletic with respect to the subgenus *Protesilaus.* The clasper of *E. telesilaus* (fig. 28B) is unusual among the species examined, but the parts can be homologized with those described above.

CLADE 8C—Genus *Protographium*

Munroe's *Protographium* possesses few autapomorphies. I identify two derived traits, both of which occur in other taxa.

[61]. Uncus a single projection. In *Protographium* the uncus is a single narrow structure (fig. 66E). Munroe (1961) and Hancock (1983) suggested that this is an instance where socii are secondarily aborted and only the uncus remains (see also Common and Waterhouse, 1981). Instead, I suggest that socii never occur in the Papilionidae and that the presence of a bifid uncus is a synapomorphy for members of Clade 3 (Character 9). The uncus of *Protographium* is derived independently from the single uncus of either *Baronia* (fig. 66A) or *Eurytides celadon* (fig. 66D).

[62]. Vesica with cornuti. The vesica of *P. leosthenes* (fig. 29C) is covered with short cornuti. Similar cornuti were observed in *Graphium* species (Character 97). Their taxonomic distribution in the latter is extremely scattered and it is unlikely that their presence delimits a monophyletic group. The cornuti of *Protographium* and *Graphium* are not considered homologous.

CLADE 8D

I propose that *Iphiclides, Lamproptera,* and *Graphium* together form a monophyletic

group. Igarashi (1984) also seemed to indicate such a relationship (fig. 6).

63. Aedeagus pointed distally. In the members of Clade 8D the aedeagus is strongly pointed distally and the point is more heavily sclerotized than the rest of the aedeagus. *Iphiclides podalirius* (fig. 30C) has a pointed aedeagus as does *Lamproptera meges* (fig. 31C). The aedeagus of *Graphium nomius* (fig. 34C) is not sharply pointed, but is atypical of the *antiphates* group in which *G. nomius* had been placed. All other *Graphium* species examined have a strongly pointed aedeagus (figs. 32C, 33C, 35C).

64. Tegumen narrowed dorsolaterally. The dorsolateral portion of the tegumen is broad and robust in most swallowtails. This is especially true of *Baronia* (fig. 22B), most parnassiines (figs. 23B–26B), and *Teinopalpus* (fig. 36B). Within the Graphiini the tegumen is relatively broad dorsolaterally in *Eurytides* and *Protographium* (figs. 27B–29B), but is narrow in *Iphiclides, Lamproptera,* and *Graphium* (figs. 30B–35B).

Clade 8E—Genus *Iphiclides*

The following characters are based on examination of *I. podalirius*. Specimens of *I. podalirinus* were unavailable for study.

[65]. Valve with a point on distal margin. The valve of *I. podalirius* is uniquely shaped (fig. 30B), possessing a point on the posterior margin. A projection on the valve is characteristic of species in the genus *Troides* (Troidini), but is not homologous with that of *Iphiclides*.

[66]. First instar larva with bifid setae on head. Igarashi (1984) described *Iphiclides podalirius* as the only papilionid species other than *Baronia* to have bifid setae on the head of the first instar larva. *Iphiclides* also exhibits bifid setae on the thorax and abdomen (Character 50), a synapomorphy for the Graphiini. Bifid setae on the larval head of both *Baronia* and *Iphiclides* are unlikely to indicate immediate common ancestry for these genera.

[67]. Pseuduncus absent. The presence of a projection on the posterior margin of tergite VIII in male swallowtails was earlier termed a synapomorphy for the subfamily Papilioninae (see Analysis 1, Character 17). Within the Graphiini there is no sign of this structure in members of three genera: *Iphiclides* (fig. 30E), *Lamproptera* (fig. 31E), and *Graphium*. Within *Graphium* it is absent in two of four subgenera.

[68]. Aedeagus curved. Hancock (1983) included "aedeagus curved" in his list of characters supporting monophyly of the graphiine subtribe Teinopalpiti, in which he placed *Iphiclides, Meandrusa,* and *Teinopalpus*. This trait is poorly defined. The aedeagus of *Meandrusa* (figs. 43C, 44C) is not more strongly curved than that of some species within *Papilio* (e.g., *P. toboroi,* fig. 37C), and there are species within the Troidini with a strongly curved aedeagus (e.g., *Troides priamus,* fig. 58C). Members of the *wallacei* group (subgenus *Graphium*) have an almost corkscrew shaped aedeagus (figures in Saigusa et al., 1977). The curved aedeagi of *Iphiclides* (fig. 30C), *Teinopalpus* (fig. 36C), and the cases described above are suggested to be independently derived traits.

Clade 8F

A sister-group relationship between *Lamproptera* and *Graphium* was proposed by Hancock (1983). He supported this hypothesis with two derived traits: (1) "uncus emarginate"; and (2) "Pupal dorsal horn large, pointed," further noting that "the immature stages provide the best evidence of a close relationship" between these two genera. I argue that "uncus emarginate," referring to the bifid condition, is plesiomorphic at the level of Clade 3. I accept Hancock's second character as a synapomorphy. Howarth (1976) and Igarashi (1979) described the immature stages of *Lamproptera*.

69. Pupa with long dorsal horn. The pupae of most *Graphium* species have a long dorsal horn, often extending anteriorly well beyond the head. Such a horn occurs only in these species and in *Lamproptera* (figures in Igarashi, 1979).

70. Long setose tubercles on thoracic segments 3 and 4 and on abdominal segment 10 of first instar larvae. Among graphiines, long tubercles on thoracic segments 3 and 4 and on abdominal segment 10 of first instar larvae occur only in *Graphium* and *Lamproptera*. A detailed study of tubercle and setal

arrangements in first instar larvae of all papilionids is warranted. This character requires more careful definition and more complete taxonomic documentation.

[71]. Forewing upper discocellular (udc) longer than middle discocellular (mdc). Rothschild (1895) first noted that in *Graphium* the udc is longer than the mdc (figs. 159–162). Other than these species, the udc is longer than the mdc only in *Lamproptera* (fig. 158), though the orientation of the discocellulars is unique in this genus. A short udc is recognized as the plesiomorphic state. A long udc also occurs in *Battus* (Troidini).

72. Tentorial crests sharply narrowed. The tentorial crests of species in the Graphiini are higher than those of other papilionids, and this trait is a synapomorphy for the tribe (Character 45). Ehrlich (1958b) described the high tentorial crest of *Lamproptera*, and my study of tentoria representing all graphiine groups has further revealed that a sharply narrowed crest is found only in *Lamproptera* (fig. 67L) and *Graphium*. Tentorial crests of species in the subgenus *Pazala* (fig. 67M), here proposed as the plesiomorphic group in *Graphium*, are most similar in shape to those of *Lamproptera*.

CLADE 8G—Genus *Lamproptera*

Lamproptera has been considered distinctive from other graphiines by previous swallowtail workers largely because of its unique habitus. It also exhibits many autapomorphous traits, the majority of them involving wing venation. Although *L. meges* and *L. curius* are superficially very similar, they are morphologically quite different. *Lamproptera curius* has a highly developed androconial region lacking in *L. meges*. It may have been secondarily lost in *L. meges*. The male genitalia of *L. curius* appear more similar to other graphiines than do the genitalia of *L. meges*. There were no females of *L. curius* available for examination.

[67]. Pseuduncus absent. I discussed this trait previously, and proposed that it has been lost in *Iphiclides, Lamproptera,* and Clade 8L of the genus *Graphium*.

73. Hind wing discal cell small. Munroe (1961) described the hind wing precostal cell of *Lamproptera* as being large and the discal

cell as being "very small, hardly larger than the precostal cell." The discal cell is very small in this genus (fig. 158) and represents an autapomorphy, being found nowhere else in the Papilionidae. The precostal cell is not unusually large relative to that in other papilionids. A large precostal cell is termed an autapomorphy for *Cressida cressida* (Troidini; Character 127).

74. Upper angle of forewing cell acute. An autapomorphy for *Lamproptera,* this trait was described by Munroe (1961). It results from having the upper discocellular vein angle sharply downward from the base of R_{4+5} (fig. 158).

75. Forewing with "R_3 and R_4 long-stalked, R_5 arising from R_{3+4} just beyond cell." Another character originally discussed by Munroe (1961), that is unique to *Lamproptera* (fig. 158).

[76]. Ductus bursae membranous. Among graphiines the ductus bursae is membranous only in *Lamproptera* (fig. 31A). Usually the region of sclerotization extends from the ostial opening to about the point at which the ductus seminalis exits. Within both *Eurytides* and *Graphium*, species exist in which the ductus bursae is only slightly sclerotized (e.g., *Eurytides epidaus,* fig. 27A; *Graphium nomius,* fig. 34A). However, even in these species some degree of sclerotization can be observed. A membranous ductus bursae also occurs in Clade 15L of the Troidini.

[77]. Anterior apophysis absent. The female anterior apophysis, located on the posteroventral corner of tergite 8, is present in all graphiines and almost all papilionids. It is very long in some species within the subgenus *Graphium* (e.g., *G. hicetaon,* not figured). In *Lamproptera meges* (fig. 31A) there is no anterior apophysis. The only other group in which it appears to have been lost is the Troidini (Clade 15D).

78. Peglike setae on papillae anales absent. *Lamproptera meges* is the only graphiine examined in which there are no peglike setae on the ovipositor lobes (Character 52). The papillae anales were not studied with SEM in this species.

CLADE 8H—Genus *Graphium*

Igarashi (1979, 1984) and other workers (e.g., D'Abrera, 1982) recognized generic sta-

tus for the *Graphium* subgenera. I recognize the four subgenera proposed by Hancock (1983), *Pazala, Pathysa, Arisbe,* and *Graphium,* except that the species included in *Arisbe* follow Munroe (1961). Nine synapomorphies corroborate the monophyly of this genus.

[79]. Vein R_1 of forewing anastomosed with Sc. Members of two graphiine groups have R_1 fused with Sc; the *dolicaon* group of *Eurytides* (fig. 154; Jordan, 1907) and the genus *Graphium* (figs. 159–162). In other papilionines, including the *thyastes* species-group, subgenus *Eurytides,* R_1 and Sc are free (fig. 153). In *Graphium* R_1 anastomoses with Sc a short distance from the point at which it leaves the discal cell while in *Eurytides dolicaon* R_1 fuses with Sc much further away from the discal cell (fig. 154). I interpret fusion of R_1 and Sc to be a derived character state for the genus *Graphium* and to be independently evolved in the *dolicaon* group. In the *wallacei* subgroup (genus *Graphium;* Saigusa et al., 1982), both R_2 and R_1 are anastomosed with Sc.

80. Juxta with setae. The juxta is setose in *Graphium.* Saigusa et al. (1982) noted this trait in the subgenus *Graphium.* In most species the setae are more numerous toward the dorsal portion of the juxta, giving that region a furry appearance (figs. 32D–35D). Numerous setae occur on the membrane dorsal to the opening through which the aedeagus passes. In *Pathysa* the juxta appears to be absent (fig. 34B); the region where it would occur is totally membranous. Several species in this subgenus have the area dorsal to the aedeagal opening sclerotized. Even in *Pathysa,* however, the membrane surrounding the aedeagal opening is covered with a dense mat of setae. I observed such setae nowhere else in the Papilionidae.

81. Clasper composed of three parts. Determining homology of the various elaborations of the clasper is difficult in the Papilionidae. In *Graphium* the clasper is usually composed of three parts (e..g, *G. nomius,* fig. 34B; *G. eurous,* fig. 32B). There is a basal projection, a medial flangelike process with a serrate edge, and a similarly shaped distal process. In *G. (Arisbe) philonoe* (fig. 35B) the basal projection is a small bump, the medial process is somewhat cup-shaped, and the dis-

tal piece is long and twisted, projecting above the dorsal margin of the valve. The configurations described above are typical of the subgenera *Pazala, Pathysa,* and *Arisbe.* In members of the subgenus *Graphium* the clasper is usually more broad and the three flangelike parts cannot be identified. In subgenus *Graphium* (e.g., *G. euryplus,* fig. 33B) there is a central process, a spiny process lateral to that, and a ventral spine. Whether these processes are homologous to the claspers of other *Graphium* subgenera is difficult to determine. Some species in the *agamemnon* group (subgenus *Graphium*) have a broad clasper with no elaborations. This structure is either a reduction or a plesiomorphic state within the genus. I tentatively suggest that a three-part clasper is a synapomorphy for the genus *Graphium,* but further study of this complex character is clearly necessary.

82. Tegumen with lateral horns. Munroe (1961) and Hancock (1983) suggested that in the genus *Graphium* the socii are membranous lobes. I homologize these "lobes" with the bifid uncus of the Parnassiinae, Papilionini, and Troidini (Character 9). *Graphium* has additional lateral projections at the base of each uncus lobe. Their configuration varies within the genus. They are typically setose as in *G. (Graphium) euryplus* (fig. 33B), *G. (Pathysa) nomius* (fig. 34B), and *G. (Arisbe) philonoe* (fig. 35B). In many species they project laterally as thornlike structures, as in *G. (Pazala) eurous* (figs. 32B, 66H).

[83]. Distal opening of aedeagus dorsal in position. This character is difficult to interpret. In *Baronia brevicornis* (fig. 22C) and Pieridae (e.g., *Dismorphia amphione,* fig. 18C; and *Pieris rapae,* fig. 20C) the distal opening of the aedeagus is ventral and the everted vesica expands downward. Within the Parnassiinae it opens either dorsally (e.g., *Luehdorfia japonica,* Zerynthiini; fig. 26C) or ventrally (e.g., *Parnassius szechenyii,* Parnassiini; fig. 24C). The opening is ventral in the Papilionini but dorsal in most members of the Troidini (see figs. 37C–65C). In *Teinopalpus imperialis* (Teinopalpini) the opening does not appear to be either dorsal or ventral, but is more lateral (fig. 36C).

Within the Graphiini the distal opening of the vesica is ventral in *Eurytides, Protographium,* and *Lamproptera* (figs. 27C–29C, 31C),

is approximately ventral in *Iphiclides podalirius* (fig. 30C), and is dorsal in *Graphium* (figs. 32C–35C).

84. Female genitalia with cuplike process. Saigusa et al. (1977) figured a "cup-like process" on the female genitalia of subgenus *Graphium*. The sclerotized pleural region of the female 8th segment forms a posterior apron, creating a deep cavity dorsal to the ostial opening (*G. (Graphium) euryplus*, fig. 33A). I found the cuplike structure in all members of *Graphium*, but not in other papilionids. Though not as clearly developed in *G. (Pathysa) nomius* (fig. 34A), other species in *Pathysa* exhibit a structure similar in shape to that of *G. (Arisbe) philonoe* (fig. 35A) and *G. (Graphium) euryplus*. In *Pazala* (e.g., *G. eurous*, fig. 32A) the cuplike configuration is not as regular in shape, but a large concavity is clearly present dorsal to the opening of the ductus bursae.

85. Ostium with ventral central structure and paired lateral lobes. It is difficult to determine homology of the various structures around the ostium in swallowtails. In some *Graphium* species there are three distinct projections around the ostial opening: a ventral one apparently contiguous with the ductus bursae, and two lateral projections. These lateral lobes were described for members of the subgenus *Graphium* by Saigusa et al. (1982). The ventral projection is often grooved medially and is sometimes clearly bifid (e.g., in *G. (Pazala) eurous*, fig. 32A). The lateral processes can be pointed (e.g., *G. (Graphium) euryplus*, fig. 33A) or broad and setose (e.g., *G. (Arisbe) philonoe*, fig. 35A and Character 98). The lateral lobes are not as apparent in subgenera *Pazala* and *Pathysa*, but the short, sclerotized lateral processes of *G. (Pazala) eurous* (fig. 32A) and *G. (Pathysa) nomius* (fig. 34A) are here suggested to be homologous structures. *Graphium* species in which no lateral lobes were found are the *angolanus* and *ridleyanus* groups of subgenus *Arisbe*. I tentatively conclude that presence of three ostial processes is a synapomorphy for *Graphium* that was lost in two species-groups. Further study of this difficult character complex may clarify these ideas and further resolve relationships within the genus.

86. Short tubercles present on 2nd and 3rd thoracic segments and 10th abdominal segment of final instar larvae. Presence of long tubercles on these body segments of first instar larvae was previously suggested to be a synapomorphy for the genera *Lamproptera* and *Graphium* (Character 70). In all species of *Graphium* figured by Igarashi (1979), short setose tubercles are present on thoracic segments 2 and 3 and on abdominal segment 10 of the last instar larvae. I did not observe these tubercles in last instar larvae of *Eurytides marcellus*, and they do not occur outside the genus *Graphium* as far as is known.

[87]. Valve with teeth on distal margin. The margin of the valve is smooth in all graphiine genera except *Graphium*. Within this genus the trait is extremely variable. Species possessing teeth (apparently not derived from setae) on the margin of the valve occur within the subgenera *Graphium*, *Pazala*, and *Arisbe*. In *Pazala* they are located distally on a projection of the valve (fig. 32B), as they do elsewhere in the genus (e.g., *G. (Arisbe) philonoe*, fig. 35B). Though there are no teeth on the valve of *G. (Graphium) euryplus* (fig. 33B), they are present in most other species in the subgenus *Graphium*. They were not observed in *Pathysa* (e.g., *G. nomius*, fig. 34B). Whether presence of teeth on the valve defines a monophyletic group within this genus cannot be determined without a more detailed analysis than that presented here.

CLADE 8I—Subgenus *Pazala*

Munroe (1961) argued that the *eurous* group, placed by later authors in the subgenus *Pazala*, belongs to *Pathysa*. Hancock (1983) disputed his proposal, suggesting that *Pazala* is the plesiomorphic sister-group to the rest of *Graphium* (fig. 7). My findings support Hancock's view. Seven synapomorphies support the monophyly of a clade including the subgenera *Graphium*, *Pathysa*, and *Arisbe* (Clade 8J; Characters 90–95). None of these traits occur in the derived state in *Pazala*. However, I do not recognize generic status for this group as did Igarashi (1984), because *Graphium* is monophyletic and splitting it needlessly promotes instability.

Male and female genitalic morphology of the two *Pazala* species examined is identical in almost every respect. Adults of all four

species are figured in Igarashi (1979), and they too are similar. I found the following apomorphies for this subgenus:

88. Ventral lobe of ostium strongly forked. The ventral lobe (Character 85) is bifurcate in *Pazala* and the two points are extremely long. This is true of both species examined, *G. (Pazala) eurous* (fig. 32A), and *G. (Pazala) mandarinus*. In addition, the lateral lobes of the ostium in both species are blunt and heavily sclerotized.

[89]. Vesica with a kink. In *Pazala* and *Graphium* the vesica of the aedeagus expands dorsally and then kinks, with the distal portion expanding ventrally (e.g., *G. (Graphium) euryplus,* fig. 33C; *G. (Pazala) eurous,* fig. 32C). This trait would therefore by a synapomorphy for these two subgenera. An alternative explanation is that a kinked vesica is plesiomorphic within the genus *Graphium*, and that a vesica in which the distal portion opens dorsally (Character 83) is a synapomorphy for the subgenera *Arisbe* and *Nomius*. The most parsimonious cladogram suggests that a kinked vesica arose separately in these groups.

CLADE 8J

Saigusa et al. (1982) published a cladogram for species in the subgenus *Graphium*. They delimited the subgenus following Munroe (1961), but redefined species-group boundaries. My examination of representative species suggests that the three species-groups of Saigusa et al., the *agamemnon, sarpedon,* and *euryplus* groups, are each monophyletic. However, these workers appear to have accepted monophyly of the subgenus without question. They report no synapomorphies for the group, and I also have uncovered no evidence of them. In addition, several important character polarity decisions made by these authors differ from the ones presented here. For example, they argue that the presence of a pseuduncus is apomorphic within the subgenus. On the other hand, I term its absence apomorphic (see Character 67). Saigusa et al. have improved our understanding of species relationships, but detailed examination of the entire genus will be necessary before further advances can be made. Until then, relationships among species in Clade 8J should be considered unresolved.

Of the hypotheses discussed below, Clades 8K and 8L are conjectural because I examined too few species and character information is currently too scant. However, the monophyly of Clade 8J is strongly supported by the following synapomorphies:

90. Signum hornlike. The hornlike signum of *Graphium* species was noted by Munroe (1961) and all subsequent researchers. It occurs as a long, narrow invagination into the bursa (fig. 35A). The signum of *G. (Pathysa) nomius* (fig. 34A) is not as deeply invaginated into the bursa, but the signum of *G. (Pathysa) antiphates* (not figured) is long and hornlike as in other members of this clade. Within *Graphium* only members of the subgenus *Pazala* do not have a hornlike signum. The signum of *G. (Pazala) eurous* (fig. 32A) is long and bandlike and very slightly invaginated into the bursa. That of *G. (Pazala) mandarinus* (not figured) is a narrow band not invaginated into the bursa. Members of *Pazala* are the only *Graphium* species here scored as lacking a hornlike signum. Munroe (1961) mistakenly described the signum of *Eurytides* as being hornlike. Within that genus the signum is either a small group of spicules (e.g., *Eurytides epidaus,* fig. 27A) or is small with a medial seam (e.g., *E. telesilaus,* fig. 28A). The female genitalia of additional African *Graphium* species are illustrated in van Son (1949).

91. Androconia in bundles. I described deciduous scales in other graphiines (Character 57), and suggest that they were independently derived in Clades 8A and 8J. There are at least three types of modified wing scales in the hind wing of most *Graphium* species. The first are long, bristlelike scales that are most numerous toward the base of the wing. These were termed a synapomorphy for the Graphiini (Character 49). They are stout in all *Graphium* species except members of the subgenus *Pazala,* and are almost always a distinctive tan color. The second type is sparsely distributed, usually on the outer part of the androconial region (fig. 99). These are not highly modified, and may be common to species outside *Graphium*. They are similar to the androconia of *Lamproptera curius.* Similar scales appear in *Pazala* species.

A third scale type was observed only in the members of Clade 8J. These occur in a dense

layer beneath the stout, bristlelike scales. They are unique in that they appear to be grouped in bundles. As figures 100 and 101 illustrate, they are thin, slightly curved strands that seem to occur in packets. It is difficult to determine whether each of these packets is homologous with a single wing scale or if each strand is a separate wing scale. There appears to be a single socket for each bundle (fig. 101), so the former is probably true. They have been termed deciduous because they readily stick to a probe when touched (Character 57). However, if it is true that each packet is a single scale composed of a bundle of filaments, then it is scale fragments that are deciduous. Scale fragments that transfer male scent to the female during courtship have been termed particles (Boppré, 1984), and these would fit that definition. Bundlelike androconia were observed in all species belonging to the subgenera *Graphium, Pathysa,* and *Arisbe,* except that such scales appear to be absent in *G. (Graphium) ridleyanus,* probably a derived loss. Bundlelike scales were not found in the *Pazala* species examined. In these, the androconial region consists of bristlelike scales as well as a patch of sparsely arranged narrow scales. The latter are likely homologous with the second type described above.

92. Pterobilins present in wings. Rothschild and Mummery (1985) and Allyn et al. (1981, 1982) described an unusual form of wing pigmentation in *Graphium* species. These workers discovered that, unlike other butterflies where coloring is a result of wing scale pigmentation, areas of coloration in *G. (Graphium) agamemnon* and *G. (Graphium) sarpedon* result from bile pigments, pterobilins, within the wing membranes. These pigments are externally visible because scales on portions of the wing are small and hairlike (see figures in Rothschild and Mummery, 1985; Allyn et al., 1981, 1982). This combination of traits, hairlike wing scales and wing colors resulting from pterobilins, appears to be unique to the genus *Graphium.* Pterobilins in danaid species (Rothschild and Mummery, 1985) are not homologus with those of *Graphium.*

Presence of pterobilin pigments can be determined in many cases through examination with a dissecting microscope. They can produce colors that are bright green (e.g., *G.*

(*Graphium*) *agamemnon*), blue-green (e.g., *G. (Graphium) sarpedon*), yellow (e.g., *G. (Arisbe) tyndaereus*), purple (e.g., *G. (Graphium) weiskei*), or white (e.g., *G. (Graphium) euryplus*). Whether each of these colors is due to different pterobilins or combinations of pterobilins is unknown.

The taxonomic distribution of this type of pigmentation is somewhat unclear. My superficial examination of graphiines indicates that hairlike scales cover portions of the wing in species representing all *Graphium* subgenera. Transparent regions of the wing in *Eurytides* species appear to result from complete loss of scales, and transparent portions of the wing in *Lamproptera* are covered with thin fork-shaped scales that were observed nowhere else in the Papilionidae. Brightly pigmented wing membranes were observed in a single species of the subgenus *Pathysa (G. (Pathysa) antiphates).* They seem to occur only in some species within *Arisbe* such as *G. leonidas, G. tyndaereus,* and *G. policenes.* Pterobilins are characteristic of all species in the subgenus *Graphium.* Though pigmented wing membranes have not been reported in papilionids other than *Graphium* species, the light green regions of the wing in *Lamproptera meges* appear superficially to result from internal pigmentation, but this could not be confirmed. This area of research deserves further attention. Complete documentation of the taxonomic distribution of pterobilins and other pigments, such as the carotenoids (Valadon and Mummery, 1978), may provide valuable phylogenetic information.

93. Thickened setae on inner rim of valve. Almost all *Graphium* species have thickened setae on the inner face of the valve. They are found in two distinct locations. There is a dorsal group located on a projection of the valve, and a ventral group along the inner edge of the valve. In the subgenus *Graphium* the setae are only slightly enlarged (e.g., *G. (Graphium) euryplus,* fig. 33B). In other groups, the setae are markedly thickened (*G. (Pathysa) nomius,* fig. 34B; and *G. (Arisbe) philonoe,* fig. 35B), and in the *macareus* group (subgenus *Pathysa,* not figured), they are extremely stout and blunt, forming a dense mass of spines. Thickened setae on the valve were not found in members of the subgenus *Pazala.*

[94]. Valve with dorsal process. Munroe

(1961) described the dorsal process of the valve in *Graphium*. This process always bears thickened setae (Character 93). In both species-groups within *Pathysa* the dorsal process is broad and located toward the distal end of the valve (*G. (Pathysa) nomius,* fig. 34B). In members of *Arisbe* the dorsal process is very narrow, is located approximately halfway out on the margin of the valve, and usually projects medially. Munroe (1961) noted that the subgenus *Graphium* lacks the dorsal process, but I found that the *G. euryplus* group is an exception. In *G. (Graphium) euryplus* the process is small and located basally (fig. 33B). This character may define a monophyletic group within Clade 8J exclusive of the *euryplus* group. More species must be studied, and the homology of all structures on the valve better understood.

95. Tentorial crest with a membranous lamina along posterior margin. This structure was figured for *G. (Graphium) sarpedon* by Ehrlich (1958b) but not discussed. I found it only in the subgenera *Graphium, Pathysa,* and *Arisbe,* but not in *Pazala* (fig. 67M–P). I consider it to be a synapomorphy for those three subgenera.

CLADE 8K—Subgenus *Graphium*

I have discovered no autapomorphies for the subgenus *Graphium*. Character 89 is homoplasious according to my analysis, but more detailed study may change its interpretation.

[89]. Vesica with a kink. As previously discussed, all species in the subgenus *Graphium* have a kinked vesica, but such a condition also occurs in both *Pazala* species examined.

CLADE 8L

Two traits support the hypothesis that the subgenera *Arisbe* and *Pathysa* are sistergroups:

[67]. Pseuduncus absent. The presence of a pseuduncus is plesiomorphic for the Graphiini. Within *Graphium* there are species in which it is either present or absent. There is a projection on the male 8th tergite in *Pazala* (*G. (Pazala) eurous,* fig. 32E) and in the subgenus *Graphium*. In *G. euryplus,* it is only a small bump (fig. 33E), whereas in the *sarpedon* and *agamemnon* groups it is long and

spatulate. The pseuduncus is bifurcate and heavily sclerotized in the *wallacei* subgroup. No species in the subgenera *Arisbe* or *Pathysa* have a pseuduncus (e.g., *G. (Pathysa) nomius,* fig. 34E; and *G. (Arisbe) philonoe,* fig. 35E). The complete distribution of this trait is unclear. Saigusa et al. (1982) dissected more species in the subgenus *Graphium* than were studied here. They report the absence of a pseuduncus in *G. (Graphium) stresemanni* in the *sarpedon* group and imply the absence of a pseuduncus in members of the *euryplus* group, though I found one present in *G. euryplus*. In the absence of evidence to the contrary, lack of a pseuduncus is suggested to represent a synapomorphy for *Arisbe* and *Pathysa*.

[96]. Vesica expanding dorsally. As with Character 83 this trait shows homoplasy within the Papilionidae. It is here proposed that presence of a ventrally expanding vesica is plesiomorphic in the Graphiini. All graphiines have a vesica that expands ventrally except *Arisbe* and *Pathysa* (e.g., *G. (Pathysa) nomius,* fig. 34C; and *G. (Arisbe) philonoe,* fig. 35C) in which the distal opening of the aedeagus is dorsal in position but the entire vesica expands dorsally. While Hancock (1983) placed the *policenes, porthaon, illyris, colonna,* and *antheus* groups in subgenus *Graphium,* Munroe put them in subgenus *Arisbe*. My interpretation of this character suggests that Munroe's *Arisbe* is monophyletic; all species possess a dorsally opening vesica, not the kinked vesica characteristic of the subgenera *Graphium* and *Pazala*.

CLADE 8M—Subgenus *Pathysa*

Hancock's (1983) subgenus *Pathysa* includes two species-groups, the *macareus* and *antiphates* groups, which are united by the following synapomorphy:

97. Cornuti on vesica and base of aedeagus. *Pathysa* species have numerous cornuti covering the aedeagus and basal portion of the vesica. In addition, the opening of the aedeagus through which the vesica everts is very long. The vesica of *G. (Pathysa) nomius* (fig. 34C) is unusual; it is the only species in which I did not find cornuti on the vesica and aedeagus. I do not consider the cornuti on the aedeagus of *Teinopalpus imperialis* (fig. 36C), *Protographium leosthenes* (fig. 29C,
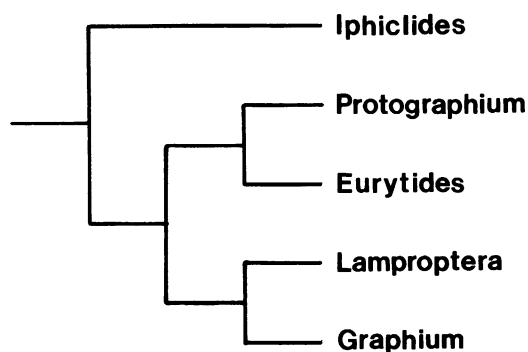
Fig. 9. A possible alternative hypothesis for the phylogenetic placement of *Iphiclides* (see Discussion, Analysis 2).

Character 62), and *Eurytides telesilaus* (fig. 28C) homologous with those of *Pathysa* species.

CLADE 8N—Subgenus *Arisbe*

Munroe (1961) put the *policenes, porthaon, illyris, colonna,* and *antheus* groups in *Arisbe,* while Hancock (1983) included them in subgenus *Graphium.* A single trait corroborates the monophyly of Munroe's *Arisbe:*

98. Lateral lobes of female setose. The lateral lobes of the female ostium, discussed in Character 85, often appear somewhat rugose in the genus *Graphium.* In subgenus *Arisbe* they are covered with a mat of short setae and have a fuzzy appearance (*G. (Arisbe) philonoe,* fig. 35A). Setose structures associated with the female ostium occur in other butterflies, such as pierids (e.g., figs. 19A, 20A; figures in Pierce and Beirne, 1941; van Son, 1949) and in the troidine genus *Battus* (Analysis 3, Character 107). The setose lobes in these latter groups are not homologous with those in *Arisbe.*

DISCUSSION

Monophyly of the Graphiini (as defined in this study) is strongly supported. It is also quite certain that the genus *Graphium* is monophyletic and that *Pazala* is the plesiomorphic subgenus within it. Other nodes on the graphiine cladogram are proposed with less confidence, and monophyly of the subgenus *Graphium* is unsubstantiated.

Of the intergeneric relationships I am quite certain that *Lamproptera* and *Graphium* are

sister-groups. On the other hand, the hypothesis that *Protographium* and *Eurytides* are sister-genera requires further testing, and relationships within *Eurytides* are unresolved. As was previously discussed, dissection of female specimens representing as many *Eurytides* species as possible is essential.

Perhaps the most poorly substantiated node on the graphiine cladogram is Clade 8D; inclusion of *Iphiclides* with *Lamproptera* and *Graphium.* In particular, the position of *Iphiclides* is ambiguous. The three genera share only two derived traits and both are somewhat open to interpretation. The most likely alternative position of *Iphiclides* is as the plesiomorphic sister-group to the rest of the Graphiini (fig. 9). This proposal rests on the observation that the androconial region in *Iphiclides podalirius* appears to be unmodified compared to other species in the tribe. SEM revealed modified scales on the anal margin of *I. podalirius* (fig. 95), but there is no sign of either the bristlelike scales (Character 49), or of deciduous scales (Character 57). The only androconia present are anal brushes, which I suggest are a synapomorphy for the entire Papilioninae (Character 18). Perhaps examination of male and female specimens of *I. podalirinus,* the only other species in the genus, will help solve this problem. Within *Lamproptera,* one species has a highly developed androconial region whereas the other appears to lack androconia. Dramatic variation in androconial morphology between closely related species may be characteristic of butterflies (Jordan, 1907; De Jong, 1982).

Resolution of relationships among graphiine genera requires discovery of additional character complexes. Comparative examination of pupae and larvae may reveal important information. There is an obvious paucity of published data on immatures and life histories of *Eurytides* species. As far as adult skeletal morphology is concerned, few new traits are likely to be discovered that will shed light on generic relationships. Perhaps further research on androconial morphology, comparative study of male-specific scent chemicals, and more detailed characterization of wing pigment chemistry with data for representative species will resolve existing problems.

CLADISTIC RELATIONSHIPS AMONG TROIDINE GENERA: ANALYSIS 3

HISTORY OF THE CLASSIFICATION

Fig. 10. Relationships among genera in the Troidini according to the branching diagram of Ford (1944b).

Understanding phylogenetic relationships within the Troidini has proved to be an especially difficult problem. The group consists of 138 described species and is distributed worldwide, with the areas of highest diversity being Central and South America, and Indo-Australia. A single species, *Pharmacophagus antenor,* occurs on Madagascar, but none are found on the African mainland. Almost every species of the Troidini can be termed monophagous or oligophagous (Wiklund, 1982), with oviposition and feeding restricted to various plant species in a single genus, *Aristolochia* (Aristolochiaceae), though other aristolochiaceous genera, such as *Thottea,* less frequently serve as hosts (Straatman and Nieuwenhuis, 1961; Straatman, 1968). Occasional species have been reported on plants in other families (Scriber, 1984). Plants of the genus *Aristolochia* contain a variety of secondary chemicals (Feeny et al., 1983; Hegnauer, 1964–1973), including essential oils, as well as alkaloids that are known to be toxic to lepidopteran larvae (Miller and Feeny, 1983). It has been suggested that sequestration of such alkaloids, especially aristolochic acids (Rothschild, 1972; Urzua and Priestap, 1985), makes these butterflies unpalatable to their vertebrate predators (Brower, 1984), resulting in their participation in mimetic butterfly complexes (Brower and Brower, 1964; Brown et al., 1981). Although papilionid groups in two subfamilies (the Zerynthiini: Parnassiinae, and Troidini: Papilioninae) feed on the Aristolochiaceae, these groups are distantly related (Hancock, 1983; Analysis 1).

The Troidini have long been recognized as a natural group, largely because the larvae and pupae are remarkably homogeneous morphologically. Carinae are consistently present on abdominal segments 4–7 of the pupae, and the usually purple or dark reddish larvae have rows of fleshy tubercles on the thoracic and abdominal segments. Uniquely derived traits that characterize adults have been much harder to identify.
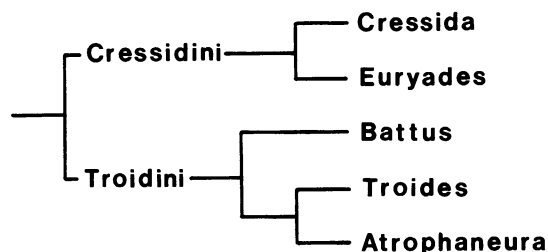
Although the group has been the subject of numerous systematic studies, the history of troidine higher classifications has been characterized by instability. Scopoli (1777) placed all the species in a single genus, *Battus.* Rothschild and Jordan (1906) were among the first authors to look for taxonomic subgroups. In their treatment of the American fauna, they placed these species in Section 1 (*Aristolochia*—Swallowtails) of the huge paraphyletic genus *Papilio.* Within Section 1 they noted a sharp division between the species now in *Parides* and those in *Battus.* Seitz (1906), in his discussion of the Palearctic species, retained the *Aristolochia*-feeders in *Papilio* but suggested two subgenera, *Ornithoptera* and *Pharmacophagus* (= *Atrophaneura* of subsequent authors). Jordan (1907) in addition recognized the genus *Euryades* for two distinct species. Bryk (1929–1930) recognized the genera *Cressida, Euryades,* and *Troides,* the latter including all the birdwings (*Ornithoptera, Trogonoptera, Ripponia,* and *Troides*). The remaining species he retained in *Papilio.*

Ford (1944b), the next major contributor, recognized two tribes of *Aristolochia*-feeding swallowtails within the subfamily Papilioninae. These were the Cressidini, in which he placed the genera *Cressida* and *Euryades,* and the Troidini, consisting of *Battus, Atrophaneura,* and *Troides.* A branching diagram representing his hypothesis is shown in figure 10. Ford's most important original contribution (1944a) showed that species in *Battus* and *Papilio,* as well as a single species in the
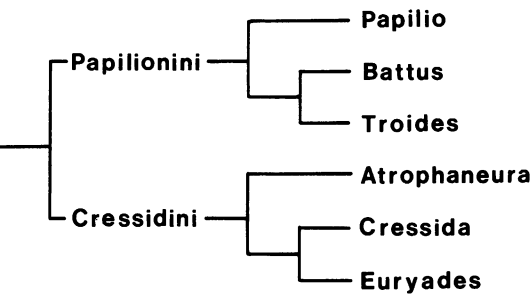
Fig. 11. Relationships among *Aristolochia*-feeding genera in the Papilioninae according to Ehrlich (1958b).

Fig. 13. Relationships among genera in the Troidini according to the branching diagram of Igarashi (1984).

Graphiini, use Pigment B for their red coloring, whereas the rest of the Troidini, as well as the rest of the Lepidoptera tested, use Pigment A. His phylogenetic conclusions suffered because he frequently characterized genera and tribes by the absence of traits found in related groups. In addition, he characterized *Battus* only by the presence of Pigment B (but see discussion of Character 110), and *Atrophaneura* by traits plesiomorphic at the family level.

Ehrlich's (1958b) hypothesis (fig. 11) suffered from similar weaknesses. He largely followed Ford (1944b), but included *Battus* and the birdwings in the Papilionini rather than with the rest of the *Aristolochia*-feeding species in the Cressidini. Both of these tribes
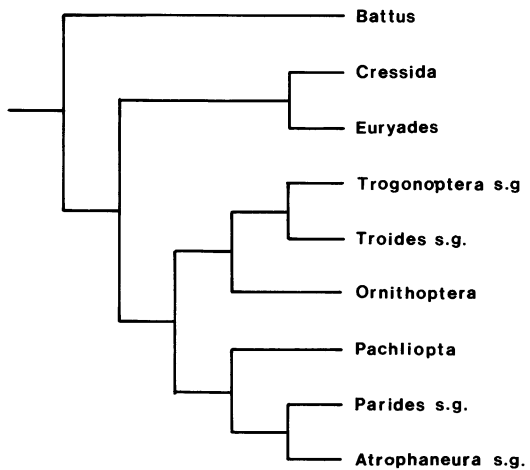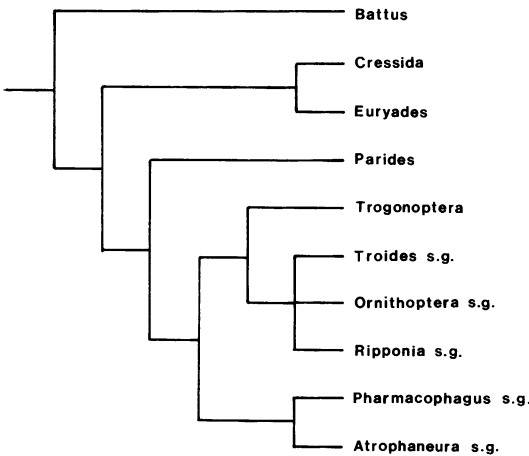

Fig. 12. Relationships among genera and subgenera in the Troidini according to the classification of Munroe (1961), and the branching diagram of Munroe and Ehrlich (1960).
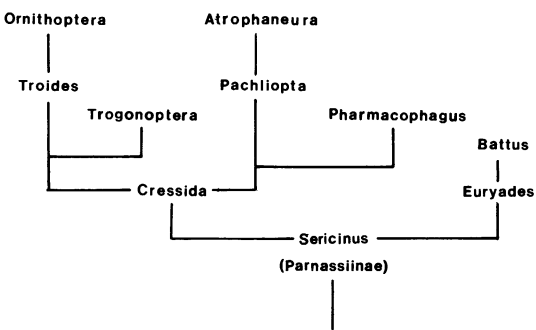
were described either using characters plesiomorphic at the family level, or using traits distributed in both groups (e.g., "Cressidini with spinasternum broad; Papilionini with spinasternum broad or narrow").

Munroe (1961) considered the species in the Papilioninae with red-tuberculate larvae to belong to a single tribe, the Troidini, in which he placed the genera *Battus, Cressida, Euryades, Parides* (which included *Atrophaneura* of previous authors), *Pachliopta, Troides,* and *Ornithoptera*. At least one autapomorphic character was described for each genus with the exception of *Parides,* which Munroe regarded as a "large central group of essentially uniform structure." His genus *Parides* was divided into two subgenera: *Parides,* consisting of only Neotropical species; and *Atrophaneura,* a group comprising four species-groups, all entirely Old World in distribution. One of those species-groups was the *antenor* group, in which he included only *P. antenor* itself. *Pachliopta,* a group of species included by most previous workers in *Atrophaneura,* was given generic status on the basis of distinctive male genitalic features, including having the "valve aborted," and the "socii and lateral remnants of [the] tegumen hypertrophied and heavily sclerotized." Munroe followed Zeuner's (1943) treatment of the birdwing species, considering *Troides* and *Ornithoptera* as genera, but differed in reducing *Trogonoptera* to subgeneric rank within *Troides.* He concluded, following Ford (1944b), that *Cressida* and *Euryades* were each others closest relatives, and were primitive genera within the tribe.

TABLE 5
Troidine Classifications

A. Present classification:

Tribe Troidini
Subtribe Battiti
Genus *Battus* Scopoli
Subtribe Troiditi
Genus *Pharmacophagus* Haase
Genus *Cressida* Swainson
Genus *Euryades* C. and R. Felder
Genus *Pachliopta* Reakirt
Subgenus *Losaria* Moore
Subgenus *Pachliopta* Reakirt
Genus *Troides* Hübner
Subgenus *Trogonoptera* Rippon
Subgenus *Troides* Hübner
Genus *Parides* Hübner
Subgenus *Atrophaneura* Reakirt
Subgenus *Parides* Hübner
Subgenus *Panosmia* Wood-Mason and de
Niceville

B. Classification of Hancock (1980, 1983):

Tribe Troidini
Subtribe Battiti
Genus *Battus* Scopoli
Subtribe Troiditi
Genus *Cressida* Swainson
Genus *Euryades* C. and R. Felder
Genus *Parides* Hübner (= subgenus *Parides*)
Genus *Atrophaneura* Reakirt
Subgenus *Pharmacophagus* Haase
Subgenus *Atrophaneura* Reakirt
nox group (= subgenus *Atrophaneura*)
latreilleii group (= subgenus *Panosmia*)
coon group (= subgenus *Losaria*)
polydorus group (= subgenus *Pachliopta*)
Genus *Trogonoptera* Rippon
Genus *Troides* Hübner
Subgenus *Ripponia* Haugum and Low (= *T. hypolitus* Cramer)
Subgenus *Troides* Hübner
Subgenus *Ornithoptera* Boisduval

C. Classification of Munroe (1961) and Munroe and
Ehrlich (1960):

Tribe Troidini
Subtribe Battiti
Genus *Battus* Scopoli
Subtribe Troiditi
Genus *Cressida* Swainson
Genus *Euryades* C. and R. Felder
Genus *Parides* Hübner
Subgenus *Parides* Hübner
Subgenus *Atrophaneura* Reakirt
antenor group (= genus *Pharmacophagus*)
latreillei group (= subgenus *Panosmia*)
nox group (= subgenus *Atrophaneura*)
coon group (= subgenus *Losaria*)

TABLE 5—(*Continued*)

Genus *Pachliopta* Reakirt
Genus *Troides* Hübner
Subgenus *Troides* Hübner
Subgenus *Trogonoptera* Rippon
Genus *Ornithoptera* Boisduval

Munroe and Ehrlich (1960) proposed a phylogeny and classification for the troidine genera and subgenera (fig. 12, table 5). They considered *Battus* the most distinctive genus in the tribe, and on those grounds erected for it the subtribe Battiti. They suggested two synapomorphies (though not termed as such) for members of the other subtribe, the Troiditi. These were a broad spinasternum and paired sensory pits on each antennal segment (Jordan, 1898).

Igarashi (1979, 1984) proposed a different phylogeny for the Troidini based on morphology of immature stages (fig. 13). In addition to Munroe's genera he recognized *Pharmacophagus,* with a single member, *P. antenor.* Unfortunately, justification of generic status for *P. antenor* was not presented. Igarashi's work is incomplete because important taxa, including *Euryades* and the New World troidines included by Munroe in *Parides,* were not studied. However, he discovered several potentially valuable characters,

Fig. 14. Relationships among genera and subgenera in the Troidini according to the classification of Hancock (1980) and the cladogram of Hancock (1983).

TABLE 6
Data Matrix for Analysis 3; Cladistic Relationships Among Troidine Genera
0 indicates the plesiomorphic state, 1 the apomorphic state

	Character number														
	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113
Papilionini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Battus*															
belus	1	1	1	?	1	1	1	1	1	0	0	0	0	0	0
polydamus[a]	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Genus *Pharmacophagus*															
antenor[a]	1	1	0	0	1	1	0	0	0	1	1	1	1	1	0
Genus *Cressida*															
cressida[a]	1	1	0	1	1	1	0	0	0	1	1	1	0	0	1
Genus *Euryades*															
corethrus[a]	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
Genus *Pachliopta*															
(*Losaria*) neptunus[a]	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1
(*Losaria*) palu[a]	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1
(*Losaria*) coon[a]	1	1	1	1	1	1	0	0	0	1	1	1	0	1	1
(*Pachliopta*) hector	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1
(*Pachliopta*) aristolochiae[a]	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1
Genus *Troides*															
(*Trogonoptera*) brookiana	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1
(*Troides*) hypolitus	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Troides*) aeacus[a]	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Troides*) priamus	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
Genus *Parides*															
(*Atrophaneura*) varuna[a]	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Atrophaneura*) horishanus	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Parides*) photinus	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Parides*) lysander	1	1	1	?	1	1	0	0	0	1	1	1	0	0	1
(*Parides*) agavus[a]	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Panosmia*) latreillei	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
(*Panosmia*) polyeuctes[a]	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1
	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
Papilionini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Battus*															
belus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
polydamus[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pharmacophagus*															
antenor[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Cressida*															
cressida[a]	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Genus *Euryades*															
corethrus[a]	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
Genus *Pachliopta*															
(*Losaria*) neptunus[a]	1	1	?	1	1	1	0	0	0	0	0	0	0	0	0
(*Losaria*) palu[a]	0	1	?	1	1	1	0	1	0	0	1	0	0	0	0
(*Losaria*) coon[a]	1	1	?	1	1	0	0	0	0	0	0	0	0	0	0
(*Pachliopta*) hector	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
(*Pachliopta*) aristolochiae[a]	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Genus *Troides*															
(*Trogonoptera*) brookiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Troides*) hypolitus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Troides*) aeacus[a]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Troides*) priamus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 6—(*Continued*)

	Character number														
	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
Genus *Parides*															
(*Atrophaneura*) *varuna*[a]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Atrophaneura*) *horishanus*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Parides*) *photinus*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Parides*) *lysander*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Parides*) *agavus*[a]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Panosmia*) *latreillei*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Panosmia*) *polyeuctes*[a]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143
Papilionini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Battus*															
belus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
polydamus[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pharmacophagus*															
antenor[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Cressida*															
cressida[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Euryades*															
corethrus[a]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pachliopta*															
(*Losaria*) *neptunus*[a]	0	1	1	1	1	1	1	1	1	0	0	0	0	1	0
(*Losaria*) *palu*[a]	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0
(*Losaria*) *coon*[a]	0	1	1	1	1	1	1	1	1	0	0	0	1	0	0
(*Pachliopta*) *hector*	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0
(*Pachliopta*) *aristolochiae*[a]	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0
Genus *Troides*															
(*Trogonoptera*) *brookiana*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Troides*) *hypolitus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Troides*) *aeacus*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Troides*) *priamus*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Parides*															
(*Atrophaneura*) *varuna*[a]	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
(*Atrophaneura*) *horishanus*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
(*Parides*) *photinus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Parides*) *lysander*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Parides*) *agavus*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Panosmia*) *latreillei*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
(*Panosmia*) *polyeuctes*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158
Papilionini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Battus*															
belus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
polydamus[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pharmacophagus*															
antenor[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Cressida*															
cressida[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Euryades*															
corethrus[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pachliopta*															
(*Losaria*) *neptunus*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 6—(Continued)

	Character number														
	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158
(*Losaria*) *palu*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Losaria*) *coon*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Pachliopta*) *hector*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Pachliopta*) *aristolochiae*[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Troides*															
(*Trogonoptera*) *brookiana*	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1
(*Troides*) *hypolitus*	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0
(*Troides*) *aeacus*[a]	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0
(*Troides*) *priamus*	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
Genus *Parides*															
(*Atrophaneura*) *varuna*[a]	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Atrophaneura*) *horishanus*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Parides*) *photinus*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Parides*) *lysander*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Parides*) *agavus*[a]	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Panosmia*) *latreillei*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
(*Panosmia*) *polyeuctes*[a]	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0

	159	160	161	162	163	164	165	166	167	168	169	170
Papilionini	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Battus*												
belus	0	0	0	0	0	0	0	0	0	0	0	0
polydamus[a]	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pharmacophagus*												
antenor[a]	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Cressida*												
cressida[a]	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Euryades*												
corethrus[a]	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Pachliopta*												
(*Losaria*) *neptunus*[a]	0	0	1	0	0	0	0	0	0	0	0	0
(*Losaria*) *palu*[a]	0	0	0	0	0	0	0	0	0	0	0	0
(*Losaria*) *coon*[a]	0	0	0	0	0	0	0	0	0	0	0	0
(*Pachliopta*) *hector*	0	0	0	0	0	0	0	0	0	0	0	0
(*Pachliopta*) *aristolochiae*[a]	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Troides*												
(*Trogonoptera*) *brookiana*	0	1	1	0	0	0	0	0	0	0	0	0
(*Troides*) *hypolitus*	0	0	0	0	0	0	0	0	0	0	0	0
(*Troides*) *aeacus*[a]	0	0	0	0	0	0	0	0	0	0	0	0
(*Troides*) *priamus*	0	0	0	0	0	0	0	0	0	0	0	0
Genus *Parides*												
(*Atrophaneura*) *varuna*[a]	1	1	1	1	1	1	0	0	0	0	0	0
(*Atrophaneura*) *horishanus*	1	1	1	1	1	1	0	0	0	0	0	0
(*Parides*) *photinus*	1	1	0	0	0	0	1	1	0	0	0	0
(*Parides*) *lysander*	1	1	1	0	0	0	1	1	0	0	0	0
(*Parides*) *agavus*[a]	1	1	1	0	0	0	1	1	0	0	0	0
(*Panosmia*) *latreillei*	1	1	1	0	0	0	0	0	1	1	0	1
(*Panosmia*) *polyeuctes*[a]	1	1	1	0	0	0	0	0	1	1	1	1

[a] Species selected for the second analysis of the Troidini (see Cladistic Methodology, Analysis 3).

making further research on immature stages essential.

Hancock (1980, 1983, 1984) recognized a single tribe of *Aristolochia*-feeding swallowtails within the Papilioninae, and accepted the subtribes Battiti and Troiditi proposed
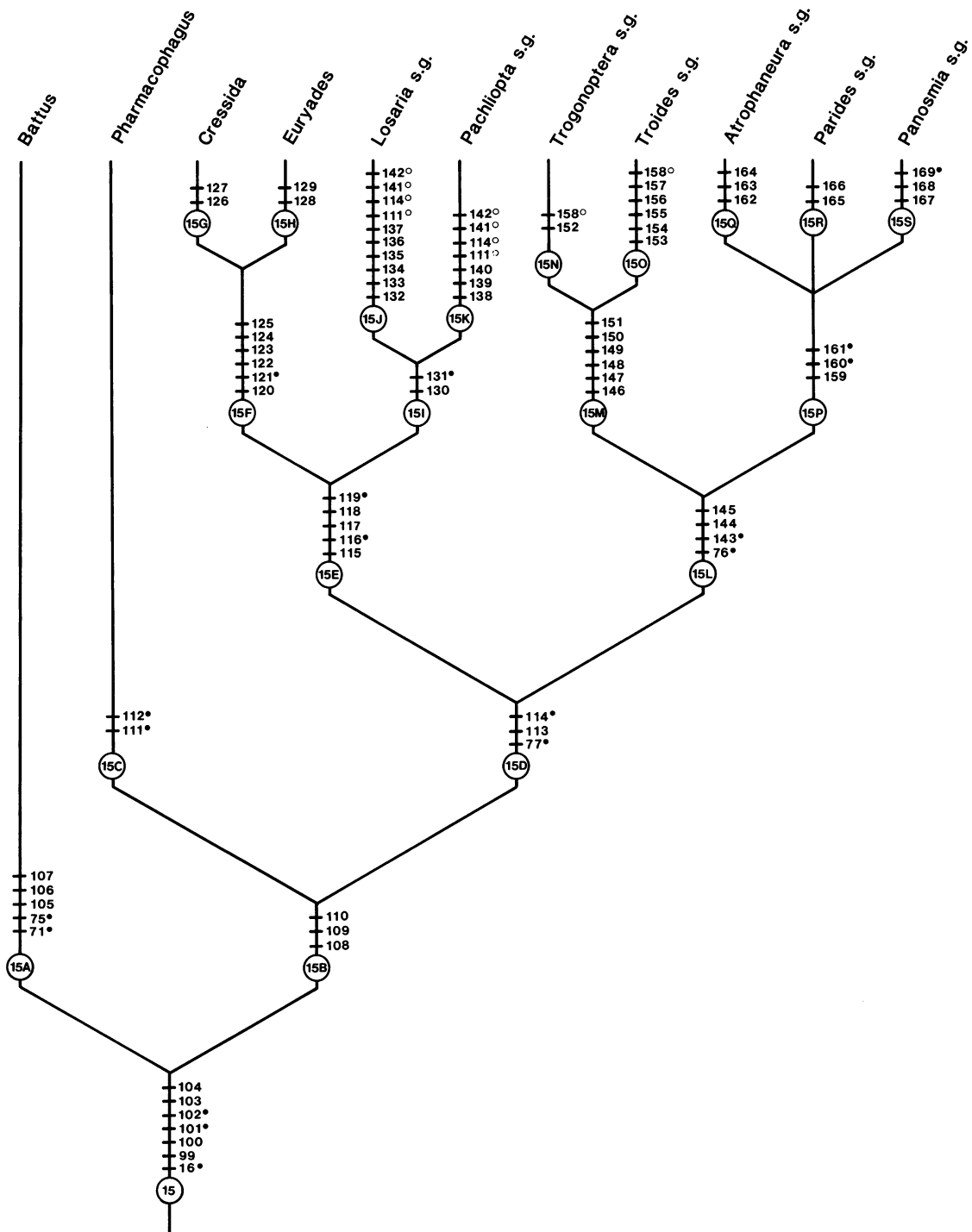
Fig. 15. Hypothesis of cladistic relationships among genera and subgenera in the Troidini (Analysis 3). Closed circles designate homoplasious characters; characters with open circles occur in some members of each group.

by Munroe and Ehrlich (1960). Hancock's (1980) generic concepts differed from those of Munroe on three major points (table 5), the first being acceptance of *Trogonoptera* as a genus and placement of *Ornithoptera* as a subgenus of *Troides*. Secondly, Hancock suggested that reduced valvae in *Pachliopta* are the end result of an evolutionary trend toward reduction that can be seen in some members of Munroe's subgenus *Atrophaneura* (specifically in the *coon* group). He reduced *Pachliopta* to species-group status (*polydorus* group) within the subgenus *Atrophaneura*, of equal rank to the *coon, nox,* and *latreillei* groups. Thirdly, he raised Munroe's Neotropical subgenus *Parides* to generic status, thus recognizing genus *Atrophaneura* with two subgenera, *Pharmacophagus* and *Atrophaneura*.

A comparison of Hancock's cladogram (fig. 14) with the diagram of Munroe and Ehrlich (fig. 12) shows several important similarities; the phylogenetic positions of *Battus, Cressida,* and *Euryades* are the same. The major phylogenetic disagreement concerns the placement of the New World *Parides* species. Hancock considered *Atrophaneura* and the *Troides* complex to be sister-groups, whereas Munroe and Ehrlich (following Munroe, 1961) placed *Atrophaneura* and *Parides* together.

As with all previous research on the Troidini, Hancock's hypothesis has a serious weakness. The monophyly of neither *Parides* nor *Atrophaneura* was firmly established. The characters applied to these groups are either plesiomorphic, or are not unique to the genus (e.g., *Atrophaneura* with "male scent organ woolly, reduced, or absent; valve well-developed, entire, emarginate, or atrophied"). Hancock (1983) listed three apomorphies for *Atrophaneura* on his cladogram. I score all three as plesiomorphic.

CLADISTIC ANALYSIS

Hancock (1983) and I (Analysis 1) suggest that the Troidini and Papilionini are sister-tribes. The Papilionini therefore served as the outgroup for polarizing character states within the Troidini. This data set was analyzed in two ways: (1) The data matrix for the 21 species listed in table 6 was run on PAUP to find all most parsimonious trees (the MULPARS option and global branch swapping, described in Swofford, 1984). (2) A subset of 14 species was chosen and the Branch and Bound option was utilized. It was necessary to select a subset from the original matrix because the Branch and Bound option can be efficiently run only on data sets containing 16 or fewer taxa. The species used to construct the second matrix (indicated in table 6) were chosen to represent groups that could confidently be considered monophyletic based on the first PAUP run. Two equally parsimonious trees were found using Branch and Bound. A consensus tree is shown in figure 15 (consistency index = 0.76). The only difference between the two trees was the relative positions of the three *Parides* subgenera (Clade 15P).

CLASSIFICATION

The classifications of Munroe (1961), Hancock (1980), and myself are compared in table 5. I accept the two subtribes of Munroe and Ehrlich (1960). Although I recognize seven genera (six in Hancock and Munroe), I believe that my classification will ultimately prove to be more stable because I used more character information and avoided defining genera using primitive character states.

CHARACTERS

CLADE 15—Tribe Troidini

The monophyly of the Troidini is quite certain. I list known autapomorphies below.

[16]. Tibiae and tarsi scaleless. All Troidini have scaleless tibiae and tarsi. As was previously discussed, lack of scales on the tibiae and tarsi evolved four times in the Papilionidae: in the Zerynthiini, Teinopalpini, Papilionini, and Troidini.

99. Pleuron of female abdominal segment 8 sclerotized. Though it is hard to generalize concerning the configuration of the female external genitalia, especially in the region of the ostium, the pleural area of segment 8 surrounding the spiracle is always sclerotized to some degree (figs. 45A–65A) in the Troidini, but not in the Papilionini.

100. Female with a row of closely spaced

spines running the length of the tibia. Female foretibiae and tarsi were examined for morphological variation in the sensory structures used during drumming behavior prior to oviposition (Feeny et al., 1983). These structures, and the associated spines presumably used to abrade the host-plant surface during drumming, have been described for several butterfly species (e.g., Fox, 1966; Ilse, 1956; Ma and Schoonhoven, 1973), but have not been used as taxonomic characters. In troidines, a unique arrangement of tibial spines and sensilla was observed. In other papilionids, including the Papilionini, the spines are relatively few and are located on the first and second tarsomeres. The sensilla are concentrated on the first tarsomere and occasionally the second (fig. 1 in Feeny et al., 1983). In the Troidini the spines are more numerous and are arranged in a tight row running the length of the tarsus, with sensilla evenly spaced between them.

[101]. Anal margin of the male hind wing rolled dorsally. I examined the "scent-organ" (Rothschild and Jordan, 1906) of 20 representative troidines using scanning electron microscopy, and found that all possess modified male-specific hind wing scales, including genera (e.g., *Pharmacophagus, Cressida, Euryades*) reported previously to lack androconia (Munroe, 1961; Hancock, 1980, 1983). Males of *Pharmacophagus antenor* have narrow scales (fig. 102) arranged along the edge of the hind wing. (The bristlelike scales located on the extreme margin of the hind wing, and shown in the upper half of the picture, are typical of all butterflies.) I discuss other male-specific hind wing scales in Character 118. The anal margin of the hind wing is rolled dorsally in all troidines except *Pharmacophagus antenor* and *Cressida cressida*. The hind wing roll was apparently lost independently in these two species (the most parsimonious overall explanation).

These scales are presumed to disseminate scent during courtship. Phenylacetaldehyde and other compounds have been isolated from the hind wing of *Parides alcinous* (Honda, 1980a). Rutowski (1980) has argued that the hind wing scent scales in *Colias* (Pieridae) are situated so that they are covered by the forewing at rest in order to avoid evaporation of male pheromones. The dorsally rolled wing margin in troidines may serve a similar function.

[102]. Medial surface of papillae anales with four to seven long hooks per lobe. The medial surfaces of the ovipositor lobes in the Papilionini are often covered with many short hook-shaped sensilla (e.g., fig. 103). In the Troidini, the number of hooks is reduced and they are extremely long (figs. 107–109), with a few exceptions; *Pharmacophagus antenor* has numerous hooks as in the Papilionini, and the *P. (Parides) lysander* and *Battus belus* groups lack hooks.

The function of setae on the papillae anales is unknown. Two groups of contact-chemosensory hairs occur on the ovipositor lobes of *Pieris brassicae* (Pieridae), and are believed to respond to "oviposition deterring pheromone" washed from eggs (Klinjstra, 1982, 1985). These setae do not respond to glucosinolates, compounds characteristic of the cruciferous host plants of *Pieris,* and are probably not involved in host plant recognition. Klinjstra also identified mechanosensory cells in the sensilla and inferred that they may function in the formation of egg batches. The tips of the long, hooklike setae of *Pachliopta coon* look similar to the chemosensory hairs of *Pieris brassicae* (see Klinjstra, 1985), and possibly serve the same function. However, at least four morphologically distinct setal types occur on the ovipositor of each swallowtail species. *Papilio troilus* have hollow setae covered with pores (fig. 105) that resemble the chemosensory sensilla of other insects (Chapman, 1982).

In addition to long hooks, several troidines possess unique club-shaped setae on the lateral lobes (figs. 108, 110; Rothschild and Jordan, 1906). *Battus* have spatulate setae on the same part of the lobe which may be homologous with the club-shaped ones of *Parides*.

Detailed morphological characterization of ovipositor lobe setae and more complete documentation of their taxonomic distribution may prove extremely valuable for understanding phylogenetic relationships within the Troidini. Sensory hairs on the papillae anales occur in other lepidopteran families including the Noctuidae (Waladde, 1983; Chadha and Roome, 1980), Sphingidae (Eaton, 1986), Gelechiidae (Valencia and Rice, 1982), and

Bombycidae (Yamaoka et al., 1971). It is likely that they will be taxonomically informative in many groups.

103. Larvae with fleshy tubercles on thoracic and abdominal segments; pupae with protuberances on abdominal segments 4–7. I did not investigate these characters thoroughly, but they have been used to describe the Troidini in most previous works (figures in Straatman and Nieuwenhuis, 1961; Straatman, 1968; Igarashi, 1979). "Red-tuberculate" *Aristolochia*-feeding larvae, a term used to describe members of both the Troidini and Parnassiinae (Ehrlich and Raven, 1964; Munroe, 1961; Munroe and Ehrlich, 1960), belong to two widely separate groups (Hancock, 1983; Analysis 1). I suggest that tubercles in the two groups are not homologous; the Troidini have fleshy tubercles, as opposed to the setose tubercles of the Parnassiinae. The abdominal pupal carinae of troidines are not characteristic of parnassiine pupae (Igarashi, 1979), nor are they found in other swallowtail groups.

104. First anal vein with a prominent groove. The Troidini have a prominent groove on the first anal vein of the male hind wing (Munroe, 1961). I also found the groove clearly defined in females. Papilionini lack the groove (e.g., *Papilio troilus,* fig. 165).

CLADE 15A—Subtribe Battiti

Battus is the only included genus, and there is little doubt that it is a monophyletic group. Cladistic relationships among the *Battus* species are poorly understood, but there are many characters that should prove useful for future research. The following corroborate the monophyly of *Battus:*

[71]. Forewing upper discocellular (udc) longer than middle discocellular (mdc). *Battus* is the only troidine or papilionine with the forewing udc longer than the mdc (fig. 166). A long udc evolved independently in *Graphium.*

[75]. Ductus bursae membranous. In *Battus* species the ductus bursae appears membranous, but the polarity of this trait is difficult to interpret. Having the ductus bursae either sclerotized or membranous is a homoplasious trait within all papilionid tribes except the Zerynthiini and Parnassiini, where the ductus is universally sclerotized (Character 11). *Meandrusa* has the base of the duc-

tus bursae sclerotized, but it is membranous in its sister-genus, *Papilio.* Within the Troidini it is equally variable. The base of the ductus bursae is heavily sclerotized in several species and the ostium is relatively unmodified. Munroe (1961) suggested that the subgenus *Pachliopta* could be distinguished from other troidine groups by the heavily sclerotized ductus bursae. He failed to notice that several species within his *Parides* (for example *P. antenor, P. neptunus,* and *P. coon;* figs. 47A, 50A, 52A) have an apparently homologous condition. Usually the ductus seminalis enters just distal to the region of sclerotization. In *Euryades corethrus* (fig. 49A) the sclerotization is weak but clearly present in the region around the ostium. In *Cressida cressida* (fig. 48A) the sclerotized area protrudes from the abdomen and lies at rest within a pocket formed by invagination of the sternal region posterior to the ostial opening. I consider it to be homologous with the base of the ductus bursae in the species above. This interpretation is somewhat speculative considering the highly modified nature of the bursa and ductus bursae in *C. cressida. Troides brookiana* is slightly sclerotized (fig. 55A). Thus, I regard a sclerotized ductus bursae as plesiomorphic for the tribe, and a membranous ductus as having arisen independently in *Battus* and in the members of Clade 15L. I do not consider it to be homologous with the membranous ductus bursae of *Lamproptera meges.*

105. Androconia in hind wing fluted. Several features of the andoconial system on the male hind wing are unique. The naked streak has been mentioned by several authors (e.g., Munroe, 1961, discussion of Character 118). Though clearly associated with the androconia located under the folded anal margin (fig. 111), its function is unknown. The scales themselves (figs. 112–118) are unlike those found in other swallowtails. Their saclike shape and fluted surface (fig. 116) may provide an increased surface area for dissemination of scent chemicals. Taxonomically interesting variation in scale shape occurs within *Battus* (figs. 112–118).

106. Vein 1A+2A in the male hind wing swollen. The swollen anal vein (vein 1A+2A; figs. 166, 167) appears to be a uniquely derived character in *Battus.* Cleared wing preparations show it to be thin-walled and tubular

in shape. It has been suggested for other butterfly species that wing veins transport materials to the glandular bases of androconia for the subsequent production of male-associated scents (Boppré, 1984). Whether the swollen anal vein in *Battus,* along which the majority of their androconia are found, acts as a reservoir for scent precursor or for scent itself is unknown. The androconial system of *Battus* certainly deserves further physiological, behavioral, and morphological study.

107. Membrane anterior to ostium with setose protuberances. The area around the opening of the ductus bursae forms a large concavity in *Battus.* This region can be everted after specimens have been cleared, and a pair of fuzzy, possibly glandular, structures can be seen (figs. 45A, 46A). These were briefly noted by Rothschild and Jordan (1906). Females of some species in the Pieridae possess structures with a similar appearance (figs. 19A–21A, and figures in Pierce and Beirne, 1941; van Son, 1949), but they are unlikely to be homologous with the structures described here. The function of these organs in *Battus* is unknown, though one could speculate that they secrete chemicals or provide an important stimulus during mating.

CLADE 15B—Subtribe Troiditi

This subtribe, originally proposed by Munroe and Ehrlich (1960), includes all troidine genera except *Battus.*

108. Antennae with paired sense pits. All butterflies have sensilla on the ventral surface of the antennae (Jordan, 1898). Jordan noted that Troiditi have these sensilla in paired pits, one pair to a segment. Subsequent authors suggested that *Battus* is primitive within the tribe because it lacks pits.

109. Collar, head, thoracic pleuron, and abdomen with red scales. Jordan (1907) described this character, which appears to be consistent (Hancock, 1983). Almost all species, including *Pharmacophagus antenor* and representatives of the other lineages, have some red scales on the pronotal region, on the head and frons, and usually on various parts of the thorax, coxae, and abdomen. This color pattern does not occur in *Battus* (though pale yellow patches sometimes occur) or in members of the Papilionini.

110. Red color composed of Pigment A.

Ford (1944a) discovered Pigment A, and used it as a character state (1944b). He found that *Papilio, Iphiclides podalirius* (Graphiini), and *Battus* use Pigment B, unique in the Lepidoptera, to produce red color. Other species with red colors utilize Pigment A. If one uses the Papilionini to polarize this trait for the Troidini, Pigment A arose independently within the troidines and is consistent with paired antennal sense pits. The alternative explanation would be that Pigment B arose independently in *Battus* and *Papilio.*

A more sophisticated chemical analysis than Ford's might provide a solution to this problem. Perhaps Pigment B is not homologous in the groups in which it is found, or perhaps Pigment A in the Troiditi is not homologous with Pigment A in other Lepidoptera. Because the Papilionini has been chosen as the outgroup to polarize characters, presence of Pigment B is hypothesized to be the plesiomorphic state for the Troidini.

CLADE 15C—Genus *Pharmacophagus*

Pharmacophagus contains a single species, *P. antenor.* Two nonmorphological features are unique to *P. antenor,* both of which have been noted by previous workers. First, it is the only troidine reported to feed on a plant in the Combretaceae (*Quisqualis grandidieri*), though it also feeds on *Aristolochia acuminata* (Igarashi, 1979). In addition, this is the only troidine species found on Madagascar. None are endemic to Africa. The other papilionine tribes, the Graphiini and Papilionini, are well-represented in Africa, and *Aristolochia* is found throughout much of the continent (Moore, 1978). Autapomorphic characters for *P. antenor* may become known when the larva and pupa are described in detail. Two male genitalic features are unusual in *P. antenor,* but traits superficially similar in appearance are found elsewhere in the tribe. They are the following:

[111]. Pseunduncus small. A small pseunduncus evolved independently in *P. antenor* (fig. 47E), *Pachliopta* (Clade 15I), and *Troides* (*Trogonoptera*) *brookiana.* Hancock (1983) mistakenly reported that *P. antenor* lacks a pseunduncus.

[112]. Uncus elongate. The papilionine and troidine uncus is not unusually large and is usually membranous distally. However, the

uncus of *P. antenor* (fig. 47B), *Pachliopta* (*Losaria*) *coon* (fig. 52B), and *P.* (*Losaria*) *rhodifer* is elongate and not membranous distally. In addition, the uncus of *P. antenor* lacks coarse setae on the distal portion of the uncus.

CLADE 15D

The monophyly of this clade is best substantiated by Character 113, the two-segmented labial palpi. The group is equivalent to the subtribe Troiditi of Munroe and Ehrlich (1960) except that *Pharmacophagus* is excluded.

[77]. Anterior apophysis absent. Apophyses on the anteroventral margin of the female 8th tergite, possibly associated with muscular control of the ostial region, occur throughout the Lepidoptera. They are found in the Papilionini (figs. 37A–44A) but not in Clade 15D. They are present in *Battus* (figs. 45A, 46A), and *Pharmacophagus antenor* (reduced in size; fig. 47A). I suggest that they have been lost separately in *Lamproptera.*

113. Labial palpi 2-segmented. The labial palpi of all troidines except *Battus* and *Pharmacophagus antenor* are 2-segmented (fig. 71). In addition, only *Battus* and *P. antenor* have the "basal fleck" (Reuter, 1896) on the first palpal segment (figs. 120–123), a common feature in Lepidoptera. It is likely that the 2-segmented condition results from reduction or loss of the first palpal segment. Surprisingly, this character has not been previously described.

[114]. Pseuduncus hinged on 8th tergite. The presence of a pseuduncus is hypothesized to be a synapomorphy for the Papilioninae (Character 17). Further, fusion of the male 8th tergite and tegumen by sclerotization of the intersegmental membrane is a synapomorphy for the Troidini/Papilionini (see Character 31). However, within the Troiditi, a clearly defined break occurs between the pseuduncus and the rest of the 8th tergite so that the pseuduncus is hinged on the tergum and can freely bend ventrally (e.g., *Cressida cressida*, fig. 48E; *P.* (*Panosmia*) *latreillei*, fig. 64E). The functional significance of the "transverse suture" (Hancock, 1980) is unknown.

Hancock's (1980) interpretation of the "hinged pseuduncus" differs markedly from mine. He incorrectly stated that "in *P. antenor* the pseuduncus is absent," but it is small, without a hinge (Character 111). Hancock claimed that *Losaria* (= *coon* group) and *Pachliopta* (= *polydorus* group) have an "incomplete suture, being fused medially." I found a complete suture in all species of *Losaria* except *P.* (*Losaria*) *palu* (figs. 50E–52E), and no suture in the subgenus *Pachliopta* (figs. 53E, 54E). Thus, the species without a transverse suture are *Battus,* the subgenus *Pachliopta, P. antenor,* and *T. brookiana* (fig. 55E).

Hancock argued that *Atrophaneura* can be distinguished from New World *Parides* on the basis of the following: "In *Atrophaneura,* as in *Parides,* a suture separates the pseuduncus from the 8th tergite, but in *Parides* this suture does not extend down the mid-line of the pseuduncus, as it does in all species of *Atrophaneura* where the suture is medially present" (1980: 30). I found this medial suture absent in all of Hancock's *Atrophaneura* species groups, but present in *Troides* (figs. 56E, 57E). Further, it is present in some New World *Parides* as well (e.g., *P. photinus,* fig. 61E). The medial suture is a vaguely defined weakening along the midline of the pseuduncus and cannot be used to distinguish *Atrophaneura* from *Parides.*

Character Not Used in the Analysis: I mention one character that was not included in the phylogenetic analysis because it is currently too poorly understood. In many *Papilio* species (e.g., *P. troilus*), some members of *Battus,* and *Pharmacophagus antenor* there are blue-green scales on the dorsal surface of the hind wing. They are not metallic or iridescent, such as those found in members of *Troides* or *Parides.* Scales of this type appear to be absent in all members of Clade 15D, and their loss would therefore represent a synapomorphy for this group. Further research is needed to more accurately characterize the morphology of troidine wing scales.

CLADE 15E

Cressida, Euryades, and *Pachliopta* (sensu lato) have never been placed together, but evidence supporting this hypothesis is sub-

stantial. Ford (1944b) recognized a morphological similarity in the valvae (Character 115), but did not suggest that these groups are closely related.

115. Valvae small, reduced dorsally. Hancock (1980) concluded that reduction of the valve is a synapomorphy for the subgenera *Losaria* and *Pachliopta,* but *Cressida* and *Euryades* also have reduced valvae (figs. 48B–54B). Ford (1944b) suggested that this character state is homologous among *Pachliopta, Cressida,* and *Euryades,* though his view was disputed by Munroe and Ehrlich (1960). Reduction has resulted in valvae of various shapes, but in all cases the dorsal portion appears to be displaced ventrally, the point where the valve attaches being lower on the vinculum. *P. coon* males exhibit this trait to a lesser degree (fig. 52B), but it can be clearly seen even in pinned specimens. This trait is suggested to be homologous in these groups.

[116]. Clasper elongate and thornlike. *Cressida* (fig. 48B), *Euryades* (fig. 49B), and the subgenus *Pachliopta* (figs. 53B, 54B) have a very narrow clasper. This character is possibly correlated with reduction of the valve. No clasper is present in *Losaria* (Character 132).

117. Vein 1A+2A short. In the Papilionini the anal vein (1A+2A) runs down the hind wing margin to within a short distance of CuA_2 (see for example figs. 150, 164, 165). Males of several troidine groups have the anal vein shortened in relation to vein CuA_2. In addition, the region of the cubital cell between the point at which 1A+2A terminates and the end of CuA_2 is very long and narrow. This condition occurs in the subgenera *Losaria* and *Pachliopta* (figs. 171–175), and in *Cressida cressida* (fig. 169). Vein 1A+2A in *Euryades corethrus* (fig. 170) is longer than that of other species in Clade 15E, but the long, narrow region of the cubital cell is present.

118. Anal vein with long, bristlelike scales on dorsal surface of male hind wing. Hancock (1980, 1983) incorrectly recorded lack of a male hind wing scent-organ in *Cressida* and *Euryades. Euryades* has a well-developed dorsal fold in the anal margin of the hind wing. *Cressida* males lack a dorsal fold (Character 101), but possess a distinct scent organ.

C. cressida is the only troidine other than *Battus* to exhibit a naked streak in the male hind wing. Figure 131 shows the scent organ of *C. cressida* with typical wing scales (top), the naked streak (center), and androconia (bottom).

Along with the subgenera *Losaria* and *Pachliopta, Cressida* and *Euryades* share a row of long, bristlelike scales on vein 1A+2A. These scales do not appear to be deciduous (Character 143). The arrangement described here occurs in all species belonging to this clade, but is most clearly observed in *Pachliopta neptunus* (figs. 124–128) and *Pachliopta palu* in which the bristles, as well as the other scales in the androconial region, are white—contrasting with the rest of the wing. Only a single type of androconia (figs. 126–130) occurs on the male hind wing margin of *P. neptunus* and other members of Clade 15E, with the exception of the bristlelike scales (fig. 125) that are restricted in location to the anal vein. This is in contrast to the species belonging to Clade 15L in which two types of scales cover the entire scent organ (Character 143).

[119]. Valve with a dorsal process located basally. All species in Clade 15F (figs. 48B, 49B), and two species in *Losaria* (*neptunus* and *palu*; figs. 50B, 51B), have a basal process located on the dorsal margin of the valve. Though this trait is considered homologous in these species, it is not present throughout Clade 15E, being absent in *P. (Losaria) coon* (fig. 52B) and *P. rhodifer,* as well as the subgenus *Pachliopta* (figs. 53B, 54B). Because species in the latter group have extremely reduced valvae, perhaps the lobe was lost. *Baronia* has a lobe on the lateral surface of the valve (Character 5) which is not considered homologous with the process described here.

CLADE 15F

All authors have considered *Cressida* and *Euryades* to be each others' closest relative.

120. Signum absent. Paraphrasing Munroe (1961), Hancock (1983) claimed that *Cressida* and *Euryades* have a "short, heavily sclerotized bursa." This is inaccurate. The bursa of *Euryades corethrus* (fig. 49A) is

somewhat smaller than in most other troi-dine species but is not heavily sclerotized. In *C. cressida* (fig. 48A) the bursa is extremely small, with the ductus seminalis arising from a point at the distal end of the bursa. The female genitalia of these genera are hard to homologize morphologically, but the absence of a signum is unique within the Troidini.

[121]. Sphragis alate. The sphragis, an ex-ternally visible mating plug produced by male accessory gland secretion, has been found in almost all butterfly families (Ehrlich and Ehr-lich, 1978). In the Papilionidae, Taylor (1967) reported a sphragis in *Papilio,* and one has long been noted in scattered groups within the Parnassiinae (Character 14). The sphragis of both *Cressida* and *Euryades* is extremely large ("alate" in Munroe, 1961; fig. 6 in Com-mon and Waterhouse, 1981) and has been considered one of the most important traits uniting these two groups (Hancock, 1983). However, a sphragis also occurs in the sub-genera *Trogonoptera* and *Troides* (Haugum and Low, 1978–1979), in various members of the *ascanius* group (subgenus *Parides*; Munroe, 1961), and in occasional species of the subgenera *Pachliopta* and *Losaria* (e.g., *P. (Losaria) palu,* personal obs.). The sphra-gis in these troidine taxa, though clearly vis-ible externally in pinned museum specimens, is less spectacular than in *Cressida* or *Eu-ryades,* looking superficially like a mass of secretion with no consistent form. Aside from members of Clade 15F, only *P. palu* has the sphragis developed as a large leaflike struc-ture protruding posteriorly from the ostium. The possibility exists that a plug, not visible without dissection, fills the ductus bursae of many other troidine species. Ehrlich and Ehr-lich (1978: 679) suggest that production of mating plugs is a much more widespread phe-nomenon in butterflies than has been pre-viously suspected, partially because "most plugs are small and inconspicuous, largely in-ternal, and often detectable only by micros-copy." Further physiological research on the sphragis would be extremely interesting and potentially informative from a phylogenetic standpoint. At present I consider the distri-bution of this trait within the Troidini in-completely known.

122. Juxta narrowed laterally. The troi-dine juxta is usually T-shaped with the arms of the T somewhat thinner than the stem. This is roughly the shape of the juxta in many members of the Papilionini (figs. 37D–44D). In *Cressida* (fig. 48D) the lateral arms of the juxta are long and drawn out. In *Euryades* they form extremely long apodemes that are joined by a membrane to apodemes arising from the tegumen (fig. 49B, D). The juxta in these two groups may serve to guide acces-sory gland secretion to the ostium of the fe-male during formation of the sphragis.

123. Dorsal lobe of valve membranous. In *Cressida* and *Euryades* the valve is composed of two distinct parts; a ventral portion on which the clasper is located, and a membra-nous dorsal part. In *E. corythrus* the mem-branous section is set apart from the rest of the valve (fig. 49B), whereas in *C. cressida* it overlaps the rest of the valve (fig. 48B). In the other troidines with a dorsal process on the base of the valve, *Pachliopta neptunus* and *P. palu* (Character 119), this structure is much smaller, is not set off from the rest of the valve as distinctly, and is not as mem-branous as it is in *Cressida* and *Euryades.*

[124]. Wings transparent. Both of these genera have transparent wings. This trait was considered homologous with the transparent wings of parnassiines by Ford (1944b) and, in addition to the presence of a sphragis in these same groups, led him to suggest the Cressidini as "primitive" relative to the Troi-dini. Because parnassiines and troidines are now believed to be distantly related (Han-cock, 1983; Analysis 1), it is unlikely that transparent wings are homologous in these two groups. In general, this character remains quite vaguely defined. In *Cressida cressida* males, the forewings are transparent due to reduction of the size of the scales. The ma-jority of wing scales in females are absent and only small pegs remain. The wings of *Eu-ryades* species are much less transparent than those of *C. cressida.* Scales on the female wing are slightly smaller than those of other troi-dines, but in males scale size is not reduced and as a result their wings are not transparent. To further confuse the issue, the forewings of species in the subgenus *Losaria* are trans-parent. Those of *P. palu* males are almost as clear as the wings of *C. cressida* males, and

have small scales of similar shape. Further study of this character is warranted.

125. Spinasternum broad. Munroe and Ehrlich (1960) suggested that a broad spinasternum characterizes the subtribe Troiditi, presumably on the basis of Ehrlich (1958b). According to their hypothesis, one would then predict a narrow spinasternum in members of the genera *Battus, Meandrusa,* and *Papilio,* and a broad spinasternum in all other troidines. My own study of this character revealed a broad spinasternum in the Graphiini, a fairly narrow spinasternum in most members of *Papilio,* and a very narrow one in *Meandrusa.* Within the Troiditi there is much variation in spinasternal width. That of *Battus* is narrow, but so too is the spinasternum of *Pharmacophagus antenor,* the subgenus *Losaria,* and *Parides (Panosmia) latreillei. Troides* have a relatively broad spinasternum, and its shape in several troidines, including *Parides (Atrophaneura) varuna, Parides (Parides) lysander,* and *Pachliopta (Pachliopta) aristolochiae* is neither narrow nor broad. In addition, variation within these subgenera is unexamined. A comprehensive study of this structure is required. Regardless, the character will likely prove to be homoplasious.

Ehrlich (1958b) correctly noted that *Cressida* and *Euryades* have the lateral arms of the spinasternum attached posteriorly, giving it a unique shape (Ehrlich's fig. 35, p. 367). I did not, however, find a similarly shaped structure in *Parides* (Ehrlich, 1958b), and I consider spinasternum shape a synapomorphy for the members of Clade 15F.

CLADE 15G—Genus *Cressida*

Almost every feature of the female genitalia is extremely modified in *Cressida* (Character 75), and all appear to be uniquely derived. In addition, the wing pattern is unique (Hancock, 1983). Other autapomorphies including the following:

126. Females with the majority of wing scales absent. *Cressida cressida* males have transparent forewings due to reduction of scale size (Character 124). In females the wings are also transparent, but this results from complete loss of most of the scales covering the

wing surface. Only small pegs remain where the scales were present. Loss of wing scales was observed nowhere else in the Papilionini or Troidini.

127. Precostal cell large. Munroe (1961) and Hancock (1983) noted the large precostal cell in *C. cressida* (fig. 169). Hancock called the precostal cell "relatively large" in *Euryades,* a purported synapomorphy with *Cressida.* However, the precostal cell of *Euryades corethrus* (fig. 170) is not large, but is fairly typical compared to other Troidini and Papilionini. A large cell is an autapomorphy for *Cressida.*

CLADE 15H—Genus *Euryades*

The area around the ostium of the female (Character 75) and the extremely long apodemes of the male genitalia (Character 122) are unique to the two species in the genus. Other autapomorphies include the following:

128. Ovipositor lobes melanized. The female terminal segments, including the ovipositor lobes, are more heavily melanized in the two species of *Euryades* (fig. 49A) than in other troidines.

129. Precostal vein club-shaped. Hancock (1983) noted a forked precostal vein in all troidines except *Cressida* and *Euryades.* Munroe (1961) concluded that the precosta is "strongly forked" in *Parides,* "weakly forked" in *Euryades,* and "unforked" in *Cressida.* My own investigation did not substantiate either of these claims. The term "forked" is an exaggeration of the condition. The precostal vein of *Euryades* (fig. 170) is unique in shape because it lacks the distal portion of the vein, which normally tapers to a point. The shape of the precostal vein is otherwise quite consistent throughout the Troidini, and nowhere can it accurately be termed "forked" (figs. 166–184).

CLADE 15I—Genus *Pachliopta*

Several authors noted a superficial similarity between adults in the subgenera *Losaria* and *Pachliopta* (e.g., Hancock, 1980; Corbet and Pendlebury, 1978). None, however, hypothesized that the two groups are sister-taxa as is suggested here. The mono-

phyly of Clade 15I is supported by the following:

130. Anterodorsal portion of tegumen broad. The subgenus *Pachliopta* has a tegumen with a humped appearance (figs. 53B, 54B), most clearly seen in the male of *P. (Pachliopta) hector*. A humped tegumen also occurs in the subgenus *Losaria*. *Pachliopta (Losaria) coon* (fig. 52B) and *P. (Losaria) rhodifer* have a tegumen with a broad anterodorsal portion that appears to be less heavily sclerotized than the rest of the tegumen. The tegumen of *P. (Losaria) palu* is also quite broad and has an expanded area set off from the rest of the tegumen (fig. 51B). Such a configuration is less developed in *P. (Losaria) neptunus* but can be clearly observed (fig. 50B). Other species in the subgenus *Pachliopta*, such as *P. polyphontes* (not figured), have a broad tegumen with a less heavily sclerotized region. This trait therefore represents a synapomorphy for these two subgenera.

[131]. Male hind tibia swollen, covered with a mat of short spines. This trait is the character least congruent with the phylogenetic hypothesis proposed for the Troidini and deserves further investigation. I found it throughout *Pachliopta,* but a similar state occurs in the subgenus *Atrophaneura* (= *nox* group), several species in *Troides,* and a few New World *Parides*. In the subgenus *Troides* the spines on the male hind tibia appear to be more numerous than on the other legs, but the tibia is not obviously swollen. Many troidines that superficially lack the mat of spines have a mat of very small golden-colored hairs that are possibly homologous with the short spines. The swollen male tibia and associated spines may prove to be a plesiomorphic character within the Troidini. The trait will likely require examination with scanning electron microscopy before it can be understood.

CLADE 15J—Subgenus *Losaria*

I dissected males and females of all four species in *Losaria*: *coon, rhodifer, neptunus,* and *palu. Pachliopta coon* and *P. rhodifer* are indistinguishable morphologically, and are possibly color forms of the same species. Hancock (1984) dissected and figured a male of *P. palu* (currently in the collection of the British Museum, Natural History). Male and female specimens were kindly offered to me by Jason Weintraub (Department of Entomology, Cornell University), and I describe and figure the female genitalia for the first time. *P. palu* exhibits all the traits characteristic of the subgenus *Losaria,* where Hancock (1984) placed it. It shares derived character states with *P. coon/rhodifer* as well as with *P. neptunus*. Three synapomorphies are shared by *P. palu* and *P. coon/rhodifer*: a similar configuration of the ostium in the female (figs. 51A, 52A), resembling somewhat the ostium of *Pharmacophagus antenor* (fig. 47A); a ventral protuberance of the distal portion of the valve; and a distally emarginate valve (figs. 51B, 52B). *Pachliopta palu* shares four synapomorphies with *neptunus*: the presence of a very large juxta with a recurved basal portion (figs. 50B, D, 51 B, D); an uncus of essentially the same shape (figs. 50B, 51B); the presence of white scales in the male hind wing scent patch, though this is also characteristic of some members of *Troides* and *Parides*; and in males and females entirely yellow abdominal segments 4 through 8, a trait unique to these two species. A dorsal protuberance, located basally on the valve (figs. 50B, 51B), occurs in both species, but is considered homologous with the dorsal lobe found in *Cressida* (Character 119). Interestingly, I found a large, externally visible sphragis in the two female specimens of *P. palu* available for study (Character 121). It is essential to learn more about the biology of *P. palu* and other *Pachliopta*. I identified six characters that support the monophyly of the subgenus *Losaria*:

132. Clasper absent. All members of the subgenus *Losaria* lack a clasper, unlike other Troidini and Papilionini. Hancock (1984) incorrectly claimed that the clasper is "long and pointed" in *P. coon* (fig. 52B). The valve of *P. coon* has a ridge running its length, possibly a vestige of the clasper (Talbot, 1949), but nothing resembling an actual clasper.

133. Signum small and invaginated into the corpus bursae. Though the exact shape and orientation of the signum vary within the Troidini, it is usually a narrow band somewhat similar to that found in the Papilionini (e.g., figs. 37A–44A). In *P. neptunus, P. palu, P. coon,* and *P. rhodifer* I found a small, al-

most round signum invaginated into the bursa (figs. 50A–52A).

134. Ostium projecting posteriorly. In all *Losaria,* the sclerotized rim of the ostium projects posteriorly well beyond the intersegmental membrane so that it is visible in dried museum specimens.

135. Male with forewings narrow. In addition to having the hind wing tails petiolate (Munroe, 1961), male *Losaria* have narrow forewings (figs. 171–175) compared to other troidines and papilionines. Munroe (1961) and Hancock (1980, 1983, 1984) noted this trait.

136. Male hind wing margin sharply indented at cell Cu. Males in *Losaria* have a distinct indentation at the distal margin of cell Cu (figs. 172, 174) that is unique in the Troidini and Papilionini.

137. Abdomen bent ventrally. *Losaria* specimens have the abdomen bent sharply downward at about the 5th segment, especially in males.

CLADE 15K—Subgenus *Pachliopta*

Hancock (1980) suggested that *P. hector* is the plesiomorphic species within the subgenus *Pachliopta* (see discussion of Character 139), but more detailed study will be required to confirm his hypothesis. The female genitalia in this subgenus appear to offer few phylogenetically informative characters.

138. Male tergite 8 and tegumen widely separated. The extremely modified male genitalia (Gosse, 1882; Munroe, 1961) occur only in the subgenus *Pachliopta.* The valve, clasper, and pseuduncus are small, and the tegumen is ventral to the tergite. The tergite and tegumen are thus widely separated by an unsclerotized intersegmental membrane (figs. 53B, 54B).

139. Uncus hypertrophied. Another unique feature of the male genitalia, found only in the subgenus *Pachliopta,* is the presence of a heavily sclerotized and hypertrophied uncus (Monroe, 1961; though he calls this structure "socii"). Of the species dissected, *P. hector* has an uncus most similar in appearance to the uncus of other troidines as well as to members of the outgroup. In *P. hector* (fig. 53B) the membranous distal portion of the uncus—typical of other troidines—is present, whereas in species such as

P. aristolochiae (fig. 54B), the membranous portion appears to have been lost.

140. Two portions of uncus separated medially. In other papilionids the two halves of the bifid uncus are fused, often for their entire length, and the tegumen is a single piece. In the subgenus *Pachliopta* the two parts of the uncus are separated medially, being connected only by a membrane. Further, the tegumen is separate, thus forming two distinct dorsal parts (fig. 66L).

The following derived character states are shared by some members of both subgenera, and raise the possibility that the subgenus *Pachliopta* is paraphyletic with respect to one or more species in *Losaria.* Only when all *Pachliopta* species are studied in detail will the phylogeny of this group become clearer.

[111]. Pseuduncus small. Within the Troidini a small pseuduncus occurs in *Pharmacophagus antenor, Troides (Trogonoptera) brookiana,* and several members of the genus *Pachliopta,* but interpretation of this trait within *Pachliopta* is difficult (figs. 50E–54E). Most species in the genus are characterized by the presence of a small pseuduncus. Conversely, both *P. coon* and *P. rhodifer* have a long pseuduncus. If a small pseuduncus is postulated to have arisen once within this genus, then the subgenus *Pachliopta* would be paraphyletic with respect to both *P. neptunus* and *P. palu* in the subgenus *Losaria.*

[114]. Transverse suture of pseuduncus absent. The members of Clade 15D have been described as having the pseuduncus hinged on tergite 8 due to the presence of a transverse suture. In the subgenus *Pachliopta* (figs. 53E, 54E) and *P. (Losaria) palu* (fig. 51E) the pseuduncus is fused to tergite 8. The character state in the genus *Pachliopta* could thus represent either the plesiomorphic condition, or it could be secondarily developed. The most parsimonious cladogram suggests the latter. For the trait to have arisen only once within *Pachliopta,* the subgenus *Pachliopta* would be paraphyletic with respect to *P. palu* in *Losaria.*

[141]. Aedeagus thin and heavily sclerotized. The aedeagus shows much variation in both width and shape within the Troidini, but of the species examined, it is long, thin, and heavily sclerotized only in *P. (Losaria) palu* (fig. 51C), *P. (Losaria) rhodifer, P. (Lo-*

saria) *coon* (fig. 52C), and *P. (Pachliopta) hec-tor* (fig. 53C). To explain the distribution of this trait, it was lost in *P. neptunus* (fig. 50C) and other members of the subgenus *Pachliopta,* such as *P. aristolochiae* (fig. 54C).

[142]. Saccus elongate. In the subgenus *Pachliopta* (figs. 53B, 54B) and *P. (Losaria) neptunus* and *P. (Losaria) palu* (figs. 50B, 51B), the saccus is extremely long, projecting anteriorly. The trait has been lost in *P. coon* (fig. 52B) and *P. rhodifer* according to the hypothesis proposed here.

CLADE 15L

I suggest that *Troides* and *Parides* are sis-ter-genera. Characters shared by these two groups have not been recognized by previous authors, who have perhaps been mislead by superficial differences in adult morphology, including dramatic differences in size and pigmentation patterns, all of which are aut-apomorphic.

[76]. Ductus bursae membranous. As pre-viously described, a sclerotized ductus bursae is plesiomorphic for the Troidini. In *Troides* and *Parides* the ductus is membranous, but is slightly sclerotized in *Troides (Trogonop-tera) brookiana* (fig. 55A). However, the duc-tus seminalis in *T. brookiana* enters the duc-tus bursae close to the ostial opening, unlike other species with a sclerotized ductus bursae where the ductus seminalis enters distal to the area of sclerotization. I tentatively suggest that ostial sclerotization in *T. brookiana* is not homologous with that observed in other papilionids.

[143]. Male hind wing margin with decid-uous scales. In addition to the androconial modifications described above, some groups of troidines have an unusual type of andro-conia, described here as deciduous. The cot-tony male scent-organ in Troidini (Roth-schild, 1895) can be characterized in more detail. Using *Parides (Parides) photinus* as an example, two types of androconia occur in the anal region of the hind wing. The first is long and hairlike, while the second is shorter and broader. Unlike the bristlelike scales in Clade 15E (Character 118), these hairlike scales are found over the entire surface of the androconial region. Figure 133 shows basic wing scales, the hairlike scales, and the curly, lower-level scales on the hind wing of *P. pho-*

tinus. The lower-level scales (fig. 134) are ir-regularly sculpted between the longitudinal braces (fig. 135), unlike typical wing scales. Such sculpturing is a feature common to many troidine androconia such as those of *Battus* (fig. 116), *Losaria* (figs. 127, 128), and others. It may disseminate scent during the courtship flight (see below). Two features of the hairlike scales were observed only in members of Clade 15L: (1) the scale bases are smaller than those of other wing scales, possibly indicating a glandular function (M. Boppré, personal commun.), and (2) these scales are very easily detached from the wing and will stick to a probe if touched. *Parides (Parides) bunichus* is a neotropical species closely related to *P. photinus.* In a culture of this butterfly (in the laboratory of P. Feeny, Cornell University), males performed a looping flight during courtship. During this flight they pass be-neath the female, in front of her, behind her, and beneath her again in a continuous loop while she flies slowly forward. As the male passes anterior to the female he drags his hind wings over her antennae and head. Large numbers of deciduous scales, which are white in this species, become fixed to the female and she then lands prior to the next phase in the courtship sequence. Androconial scents may inhibit female flight and allow copula-tion (Rutowski, 1980).

Deciduous scales are found only in the sub-genera *Troides, Trogonoptera, Panosmia, Atrophaneura,* and *Parides.* Examples of the hairlike and lower-level scales are shown for representatives of these groups in figures 133–145, 148, and 149. The sockets of the decid-uous scales appear very similar morpholog-ically in these species (see *Parides (Parides) photinus,* fig. 134; *P. (Panosmia) latreillei,* fig. 141; and *P. (Atrophaneura) horishanus,* fig. 145). According to the character distribution suggested here, the species formerly recog-nized as *Ornithoptera* have lost the deciduous scales. Males of these species possess a patch of unique scales on the forewing (figs. 146, 147) and a well-developed set of bristlelike scales on the underside of the hind wing vein 1A+2A (Character 18). The latter are found in other papilionines and are considered ple-siomorphic relative to this clade.

144. Male hind wing with anal cell en-larged. A character congruent with the pres-ence of deciduous scales in the male hind

wing (Character 143) of *Troides* and *Parides,* and possibly correlated with it, is the presence of a greatly enlarged anal cell (shown with the anal cell unfolded in figs. 176, 177, and 179–182). The anal margin is typically folded, but rolled dorsally along vein 1A+2A (figs. 178, 184), forming a large pouch which encloses the androconia. A dorsally folded male hind wing margin (Character 101) is plesiomorphic in the Troidini, while the enlarged first anal cell is restricted to *Troides* and *Parides.* The anal cell is extremely large and the cubital cell expanded in members of the subgenus *Atrophaneura* (fig. 180). *Troides priamus* lacks hind wing deciduous scales, but has a broad anal cell (fig. 177), corroborating the hypothesis that deciduous scales were lost.

145. Membrane between ostium and sternite 7 fluted. In Clade 15L the membrane anterior to the ostium and posterior to sternite 7 is expanded and usually has sclerotized, fluted ridges (figs. 58A, 61A). When the ostium and surrounding membranes are everted during dissection, this region can be clearly observed.

Character Not Used in the Analysis: Hancock (1983) proposed that an asymmetrical hind wing discal cell defines groups within the Troidini. He described the discal cells of *Battus* and *Cressida* as "symmetrical" and those of *Parides* and *Troides* as "asymmetrical," but noted reversal to the symmetrical condition within the subgenera *Troides* and *Parides.* The meaning of "asymmetrical" was not made clear. It may be that Hancock's asymmetry refers to a narrow cell, such as occurs in *Parides* (*Atrophaneura*) *varuna* (fig. 180), in which the bases of M_2 and M_3 are close together on the discal cell. However, Hancock placed species such as *Pharmacophagus antenor,* which does not have a narrow cell, in a clade with Old World subgenera *Panosmia* and *Atrophaneura.* Furthermore, Rothschild (1895) observed "great variation" in the length and width of the hind wing cell within a single species (*Parides* (*Panosmia*) *polyeuctes*) as well as sexual variation. Hancock's interpretation is questionable. As with "precosta forked" (Character 129), more species will have to be examined and the trait redefined before it can be made useful for understanding relationships within the Troidini.

CLADE 15M—Genus *Troides*

Few authors have questioned the monophyly of the birdwing species. They have probably been more thoroughly studied than any other papilionids. Haugum and Low (1978–1979) detail the species and subspecies. As was noted in the introduction to this analysis, rarely have two authors agreed on the generic or subgeneric status of the four birdwing groups: *Troides, Ripponia, Ornithoptera,* and *Trogonoptera.*

One result of the special attention given to the birdwings is that all definable subgroups have at one time or another been raised to generic rank. Haugum and Low (1975) argued that *T. hypolitus* is sufficiently distinct to warrant its own genus, *Ripponia.* This is unjustified. Haugum and Low listed characters unique to *hypolitus,* such as its unusual wing pattern and the distinctive configurations of the valve and clasper, but these traits are autapomorphic and provide no information on the phylogenetic position of *T. hypolitus.* Haugum and Low did not identify characters that support placement of *T. hypolitus* as the sister-species to the rest of *Troides.* They suggested (1975: 111) that the characters of *T. hypolitus* "are in some ways intermediate between *Troides* and *Trogonoptera,*" but did not document their claim. Creating the genus *Ripponia* raises the possibility that *Troides* (sensu Haugum and Low) is paraphyletic with respect to *T. hypolitus,* requiring the naming of even more genera within it. Such a situation would promote instability. Furthermore, the morphological differences between *T. hypolitus* and the rest of *Troides* are slight. The female genitalia of all these species are similar in almost every respect (figs. 56A–58A).

For the sake of nomenclatural stability, and because of the morphological homogeneity of the birdwing species, I unite all within a single genus, *Troides.* Phylogenetic relationships among the species remain to be determined. I recognize two subgenera, *Trogonoptera* and *Troides.*

146. R_1 in forewing arising opposite CuA_2. This trait, first described by Zeuner (1943) and noted by most subsequent authors, is found in all *Troides* (fig. 176; figures in Haugum and Low, 1978–1979).

147. Middle discocellular and upper dis-

cocellular in line. Munroe (1961) suggested that in the subgenera *Troides* (excluding *Ornithoptera*) and *Trogonoptera* the mdc and udc were "in line" (fig. 176). I support his finding, but also found it in "*Ornithoptera*" (figures in Haugum and Low, 1978–1979). This trait supports the monophyly of the birdwings.

148. **Wing scales iridescent.** Cockayne (1924; also Ford, 1944b) argued that iridescent scales in *Troides* contain a unique pigment which gives a greenish-yellow fluorescence in ultraviolet light. He demonstrated that this pigment is confined to the birdwings.

149. **Valve with a marginal process.** Zeuner (1943) figured the left valvae of 32 birdwing species, most of which were also figured by Haugum and Low (1978–1979). In the majority, a small process is present on the margin of the valve, usually located distally (figs. 55B–58B). The process of *T.* (*Trogonoptera*) *brookiana* is relatively large and is located dorsally on the valve.

150. **Signum with concentric folds.** The birdwing species lack a distinct signum (Munroe, 1961; Hancock, 1980, 1983), but raised ridges and folds (figs. 55A–58A) with surface spicules occur on the bursa. In *T. aeacus* there is a well-defined sclerotization in the center of the folds (not clearly seen in the figure). These structures in the birdwings are most likely homologous with the signum of other papilionids.

151. **Appendix bursae present.** In the species examined, an additional pouch contiguous with the corpus bursae (appendix bursae of Klots, 1970) occurs in *Trogonoptera* (fig. 55A), and *Troides* (figs. 57A, 58A). The pouch in *Troides helena* and *T. hypolitus* (fig. 56A) is less distinct. A weakly defined structure is present in *Battus* (figs. 45A, 46A).

CLADE 15N—Subgenus *Trogonoptera*

Niculescu (1980) argued that *Trogonoptera,* containing *brookiana* and *trojana,* is sufficiently distinct to be considered a genus. He based his decision on the following evidence: (1) the pseuduncus is a short, lightly sclerotized lobe (fig. 55B, E), whereas in the rest of *Troides* it is long and heavily sclerotized (figs. 56B, E–58B, E); (2) the valve is short and the harpe is a large plate (fig. 55B); (3) the aedeagus and juxta differ from those in the rest

of *Troides* (figs. 55B, D–58B, D); and (4) a sphragis is present in *Trogonoptera* (Munroe, 1961), but is absent in *Troides* according to Niculescu. Haugum and Low (1978–1979), however, document the presence of a sphragis in *Troides* as well. I follow Munroe (1961) and retain *Trogonoptera* and *Troides* in a single genus.

In addition to the male genitalic characters discussed by Niculescu, *Trogonoptera* exhibits uniquely derived female traits:

152. **Numerous folds present in membrane dorsal to ostial opening.** The invagination dorsal to the ostial opening, usually sclerotized in other troidines (Character 159), is membranous in *Trogonoptera* and has numerous folds in its surface. In addition, the ductus bursae is extremely wide and the ostial region is lightly sclerotized compared to those of other species in the Troidini.

CLADE 15O—Subgenus *Troides*

I unite *Troides, Ripponia,* and *Ornithoptera* of Haugum and Low (1978–1979) within subgenus *Troides.* The following characters corroborate the monophyly of this clade:

153. **Ostium with a medial process.** The configuration of the ostium in all species is essentially the same. A conspicuous projection occurs ventral to the opening of the ductus bursae (figs. 56A–58A) in subgenus *Troides,* but nowhere else in the Troidini. In addition, all have a thickened and heavily sclerotized lateral collar anterior to the opening of the ductus bursae.

154. **Lobes of uncus bent ventrally.** The two uncal lobes in the subgenus *Troides* are sharply bent ventrally (figs. 56B–58B), whereas in the rest of the Troidini their position is more horizontal.

155. **Clasper with basal hook.** All species in the subgenus *Troides* have a spine, termed the basal hook by Haugum and Low (1978–1979), on the proximal portion of the clasper. Some species have two hooks, one formed from a dorsal projection of the valve and one at the base of the clasper (*T. aeacus,* fig. 57B). In a few species, such as *T. priamus* (fig. 58B), the basal hook of the clasper is small, but in most it is prominent (figs. 56B, 57B). Additional species figured in Haugum and Low (vol. 1), show a well-developed basal hook. *Trogonoptera* lacks the hook, though the ori-

entation of the clasper is unique, and the fold at the dorsal portion (fig. 55B) may be homologous with the basal hook of *Troides*.

156. Clasper with distal spines. The claspers of most species in the subgenus *Troides* are broadened basally with a series of stout spines on the distal portion (Zeuner, 1943; Haugum and Low, 1978–1979). The clasper of *T. hypolitus* (fig. 56B) is unique, leading Haugum and Low (1975) to raise it to generic status, but the distal spines are clearly present.

157. Abdomen with androconia. Male *Troides* have a patch of abdominal androconia dorsally. Zeuner (1943) proposed that they transfer scent to the stiff, brushlike scales (anal brushes, Character 18) on the ventral surface of the male hind wing. Although he considered anal brushes to be restricted to these species, they are also well developed in *Battus* and other troidines, such as *Panosmia*. Abdominal androconia are tentatively treated as a synapomorphy for the subgenus *Troides*. SEM analysis of abdominal scales in *Trogonoptera* and other troidines may change the status of this character.

[158]. Juxta with spines. *Troides* (*Trogonoptera*) *brookiana* and *T.* (*Troides*) *priamus* have a pair of large spines located dorsolaterally on the juxta (figs. 55D, 58D). They are not present in all *Troides* species (figs. 56D, 57D).

CLADE 15P—Genus *Parides*

Parides contains three subgenera: *Parides*, *Panosmia* [= *latreillei* group of Munroe (1961) and Hancock (1980)], and *Atrophaneura* (= *nox* group). The latter two are Old World groups and the first is Neotropical and corresponds to Munroe's (1961) genus *Parides*. The monophyly of each subgenus appears to be relatively well-founded, but I could not resolve relationships among them. The following corroborate the monophyly of the genus *Parides*:

159. Large sclerotized invagination dorsal to opening of ductus. Within the Papilionini and Troidini an invagination occurs in the membrane dorsal to the opening of the ductus bursae. Presumably it accepts the uncus or pseuduncus during copulation. Its function is speculative because I have been unable to study the mechanics of copulation in papil-

ionids, but the structure is consistently present. Within the Troidini it is usually a sclerotized pocket opening dorsally (e.g., *Battus polydamus*, fig. 45A). In *Parides* this structure is unusually large. It is fused to the intersegmental membrane above the opening of the bursa in the subgenus *Panosmia* (figs. 64A, 65A), while in the subgenera *Atrophaneura* and *Parides* it projects posteriorly from the intersegmental membrane (figs. 59A–63A). Because this structure protrudes to some degree in birdwings (figs. 56A–58A), fusion in *Panosmia* is considered an autapomorphy (Character 167). The structure is very large in *P.* (*Parides*) *proneus*, *P.* (*Parides*) *hahneli*, and in other New World taxa.

[160]. Ductus bursae wide. The ductus bursae is wide and usually short in *Parides* (figs. 59A–65A). The only other taxon that has a wide ductus bursae is *T.* (*Trogonoptera*) *brookiana*. Its structure is superficially different from that of *Parides*. A wide, short ductus appears to be roughly correlated with the presence of a wide aedeagus.

[161]. Vesica large. The vesica is small in most troidine species. In the Papilionini it is moderately large (figs. 37C–44C) and in *Parides* it is quite large. This character is not totally consistent. Some members within the subgenus *Parides* have a relatively small vesica (see, e.g., *P. photinus*, fig. 61C). However, this was not typically true within the subgenus. Some species, such as *P.* (*Parides*) *hahneli* (not figured) have large vesicas with quite complex configurations. It is impossible to know whether the small vesica in these *Parides* species is convergently derived without a detailed cladistic analysis of the entire genus. Until such work is done, I consider the presence of a large, expanded vesica a synapomorphy for Clade 15P.

CLADE 15Q—Subgenus *Atrophaneura*

162. Valve with two distal spines. This trait (figs. 59B, 60B) was discussed by both Munroe (1961) and Hancock (1980, 1983). The shape of the valve is also characteristic.

163. Aedeagus dorsoventrally depressed. The aedeagus is flattened dorsoventrally and irregular in shape, with small bumps and knobs on its surface (figs. 59C, 60C).

164. Male with hind wing cell Cu enlarged. See Characters 143 and 144.

CLADE 15R—Subgenus *Parides*

Though this is the largest subgenus within the Troidini—45 species in three species groups—I found only two synapomorphies. Understanding phylogenetic relationships within the subgenus *Parides* remains the single largest systematic problem in the Troidini.

165. Signum oriented dorsoventrally. Both Munroe (1961) and Hancock (1980, 1983) characterized the signum as V-shaped but that is inaccurate. It is often U-shaped but can be almost straight (e.g., *P. agavus*, fig. 63A). Usually it has a somewhat scalloped appearance (figs. 61A–63A). The most unique feature of the signum in the subgenus *Parides* is its dorsoventral orientation.

166. Lower-level androconia curled. "Hairlike" and "lower-level" androconia are characteristic of Clade 15L (Character 143). Lower-level scales in the subgenus *Parides* are broad and distinctly curled (figs. 134, 148, 149). The scales of some species outside this group, such as *P. (Panosmia) latreillei,* are slightly curled (fig. 141), but not markedly.

CLADE 15S—Subgenus *Panosmia*

167. Invagination dorsal to ostium fused to membrane. See Character 159.

168. Ostium fluted. The shape of the region around the ostium is unique in *Panosmia*; it is fluted and forms a corona around the ostial opening (figs. 64A, 65A).

[169]. Pseuduncus with horns. Basal projections on the pseuduncus, in addition to the medial projection, occur in *P. polyeuctes* (fig. 65B, E), *P. dasarada,* and *P. alcinous,* but are absent in *P. latreillei* (fig. 64B, E). These horns may define a monophyletic group within *Panosmia.* Similar convergently derived protruberances occur in *Pharmacophagus antenor* (a pair of very small dorsal bumps; fig. 47B, E) and in *Meandrusa sciron* (fig. 43B, E).

Jordan (1928) figured claspers of the species in *Panosmia* and described them as being broad and toothed marginally (e.g., figs. 64B, 65B). However, species in other *Parides* subgenera also have a broad clasper, toothed marginally (e.g., *P. (Parides) lysander,* fig. 62B).

I found a character that suggests a sister-group relationship between the subgenera *Panosmia* and *Parides.* It may be useful to future research on these groups.

[170]. Vesica of aedeagus with a sclerite. In *Panosmia* and some species of subgenus *Parides,* I found a sclerite, perhaps originally part of the aedeagus, laterally on the vesica. In *P. (Panosmia) latreillei* (fig. 64C) the sclerite is close to the distal portion of the aedeagus, but in *P. (Panosmia) polyeuctes* (fig. 65C) it is distinctly separate from the aedeagus. This sclerite also occurs in *P. (Parides) agavus* (fig. 63C), *P. gundlachianus,* and *P. proneus* (both in the *ascanius* group; Hancock, 1983). In *P. (Parides) hahneli* (*aeneas* group) the sclerite is located at the distal end of a long, fingerlike evagination of the vesica. *P. photinus* (*ascanius* group; fig. 61C) and *P. lysander* (*lysander* group; fig. 62C) lack the sclerite.

DISCUSSION

The most significant result of this analysis is finding that *Atrophaneura* of previous authors is a polyphyletic group comprising three separate elements: *Parides* (subgenera *Atrophaneura* and *Panosmia*), *Pachliopta* (subgenus *Losaria*), and *Pharmacophagus antenor*. The monophyly of these groups is well documented, but their affinities are surprising. Hancock (1980; also noted by Corbert and Pendlebury, 1978) suggested a close relationship between the subgenera *Losaria* and *Pachliopta,* but retained both within his genus *Atrophaneura.* I suggest that *Losaria* and *Pachliopta* are sister-taxa and that their closest relative is *Cressida.* I also suggest that two Old World groups previously placed in the genus *Atrophaneura,* subgenus *Panosmia* (=*latreillei*) and subgenus *Atrophaneura* (=*nox*), belong to a clade which includes Neotropical *Parides.* The third element from *Atrophaneura* of previous authors, *Pharmacophagus antenor,* appears on my cladogram as the sister-group to the rest of the Troiditi. Though most workers have acknowledged *P. antenor* as distinctive, none have recognized how distantly related this species is to the other members of the genus in which it was placed.

I consider several regions of the troidine cladogram to be tentative. *Pharmacophagus*

antenor is either the sister-group to the rest of the Troiditi, or to the rest of the Troidini (fig. 16A). Three characters (108–110) suggest placement of *P. antenor* within the Troiditi and two (101 and 102) indicate that it is the sister-group to all other troidines including *Battus*. The solution to this problem may come from a study of immature stages. Larval antennae of *Battus* species have unique configurations of setae and sensilla (Dethier, 1941). A comprehensive study of larval antennae, larval mouthpart morphology, larval tubercle and setal arrangements, pupal morphology, and other such character complexes may provide answers. Unfortunately, I have been unable to obtain larval specimens of *P. antenor*. Complete documentation of its life history combined with detailed comparative work on immature stages representing the rest of the Troidini is essential. Igarashi (1979, 1984) has laid a foundation for such research, though more detailed analyses, including SEM studies, are also required.

The taxonomic distribution of swollen male hind tibiae (Character 131) indicates that *Pachliopta* might be more closely related to *Parides* than to *Troides*. Male hind tibiae are not swollen in *Cressida* or *Euryades*, but a rearrangement involving *Pachliopta* would nevertheless have to address the relationship between *Pachliopta* and *Cressida/Euryades*. Perhaps the entire clade (15E) is the sister-group of *Parides* (fig. 16B). The monophyly of Clade 15E is corroborated by five derived characters, but two (116 and 119) are absent in some species. Larvae of *Cressida cressida* and *Euryades corethrus* have unique maxillary palpi that are broad and flattened distally with the tip covered by a mat of short sensilla. Again, examination of the mouthparts of additional troidine larvae will perhaps offer additional information concerning the distri-
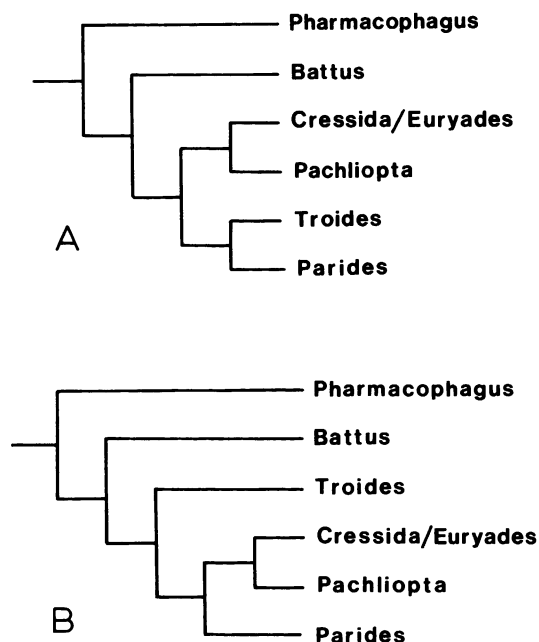
Fig. 16. Alternative hypotheses for the Troidini (see Discussion, Analysis 3). A. A possible hypothesis for the phylogenetic placement of *Pharmacophagus*. B. A possible hypothesis for the phylogenetic placements of *Pachliopta* and *Cressida/Euryades*.

bution of this trait and may corroborate or refute the monophyly of Clade 15E.

Monophyly of the genus *Pachliopta* is weakly supported, and species relationships are not clear. Further study may reveal that the subgenus *Pachliopta* is paraphyletic with respect to one or more species in the subgenus *Losaria*.

Although the monophyly of Clade 15P is well substantiated, we have no understanding of interrelationships in the three subgenera, or of cladistic relationships within each.

BIOGEOGRAPHY AND AGE OF THE PAPILIONINE GENERA

I have overlaid geographical distributions on the terminal taxa of troidine and graphiine cladograms (figs. 185, 186). Both area cladograms apparently lack biogeographic patterns such as might be predicted by a vicariant plate tectonic model. Furthermore, these area cladograms show little congruence. A classical Gondwanan distribution would include

taxa endemic to Africa, Madagascar, India, Australia, New Zealand, and South America. Swallowtails, on the other hand, are often widespread, some occurring in more than one biogeographical region. For example, *Battus* and the subgenus *Panosmia* are distributed in areas once belonging to Gondwanaland and Laurasia. Widespread taxa provide no information on the relationships of areas (Platnick, 1981).

Still, the area cladograms raise several interesting issues. Many important swallowtail genera—*Teinopalpus, Meandrusa,* subgenus *Pazala*—are endemic to the region from the eastern Himalayan foothills east to Southeast Asia. These groups seem to have something in common; each contains only a few species, but is the sister-group to a speciose clade whose members show relatively little morphological variation. *Pazala* (four species) is the sister-group to the rest of *Graphium* (84 species); *Meandrusa* (two species) to the rest of *Papilio* (220 species); and *Teinopalpus* (two species) to the Papilionini/Troidini. The significance of this finding is unknown, but may be correlated with the collision of the Indian subcontinent with Asia, between 55 and 53 million years ago (Brown and Gibson, 1983).

Some swallowtail taxa apparently diverged as a result of the fractionation of Gondwanaland. For example, the common ancestor of *Cressida* and *Euryades* (Clade 15F) was probably once distributed throughout Gondwanaland (fig. 186). However, the sister-group to these taxa, *Pachliopta* (Clade 15I), occurs from Pakistan to the Solomons and Eastern Australia, a pattern not typical of Gondwanan distributions. A second example

of a possible Gondwanan distribution is *Protographium,* endemic to eastern Australia, and *Eurytides,* with a largely South American distribution. If the divergence of groups such as *Cressida/Euryades* and *Protographium/Eurytides* did accompany the breakup of Gondwanaland, this would lend support to the hypothesis that they are between 50 and 80 million years old, the approximate geological date at which Australia and South America split apart (Brown and Gibson, 1983).

The fossil record provides little information to refute or support such a proposed age for swallowtail genera. Two fossil species (dated as being 48 million years old), *Praepapilio colorado* and *P. gracilis,* were described by Durden and Rose (1978) and placed in their own papilionid subfamily, Praepapilioninae. The fossils purportedly have cervical sclerites united ventromedially (Character 4). Hancock (1983) placed them phylogenetically between the Baroniinae and the rest of the Papilionidae. As is the case with most fossil insects, wing venation provides the majority of characters for phylogenetic analysis. *Praepapilio* shares one derived character state with each extant subfamily, and its phylogenetic position is therefore ambiguous. *Praepapilio* has a basal spur (Character 19), a synapomorphy for the Papilioninae. It also has forewing vein R_4 absent (Character 6), a character state restricted to *Baronia* (Baroniinae) and *Parnassius* (Parnassiinae). The discovery of *Praepapilio* confirms that genera within the Papilionidae are at least 48 million years old, but provides little additional information.
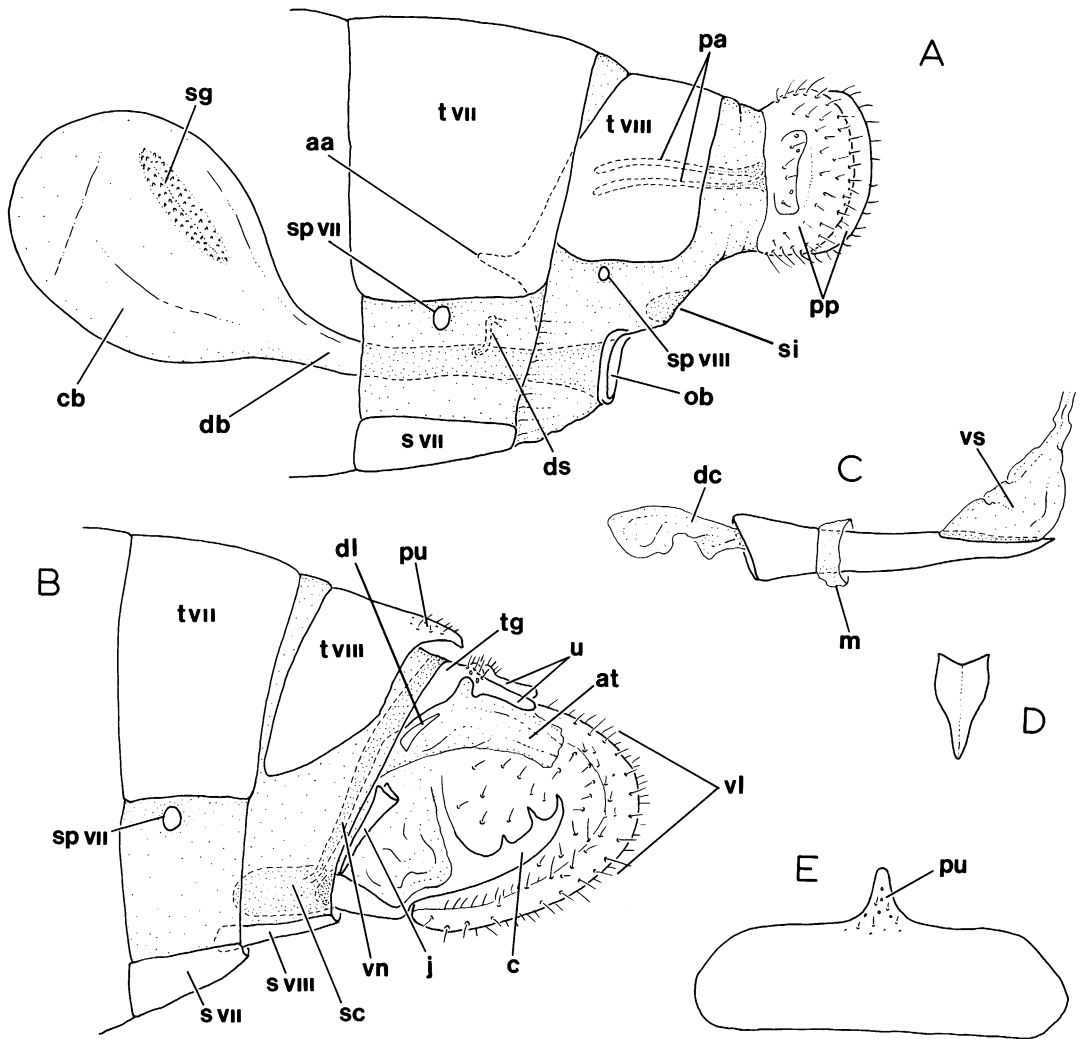
Fig. 17.　Diagrammatic representation of papilionid genitalia. Nomenclature is from Klots (1970), except the dorsolateral sclerite (dl) and sclerotized invagination (si) for which no previous names exist. A. female in lateral view; B. male in lateral view with left valve and aedeagus removed; C. aedeagus in lateral view with distal portion at right; D. juxta in anal view; E. dorsal view of 8th tergite. **aa** = anterior apophysis; **at** = anal tube; **c** = clasper; **cb** = corpus bursae; **db** = ductus bursae; **dc** = ductus communalis; **dl** = dorsolateral sclerite; **ds** = ductus seminalis; **j** = juxta; **m** = manica; **ob** = ostium of the bursa; **pa** = posterior apophysis; **pp** = papillae anales; **pu** = pseuduncus; **s** = sternite; **sc** = saccus; **sg** = signum; **si** = sclerotized invagination; **sp** = spiracle; **t** = tergite; **tg** = tegumen; **u** = uncus; **vl** = valve; **vn** = vinculum; **vs** = vesica.
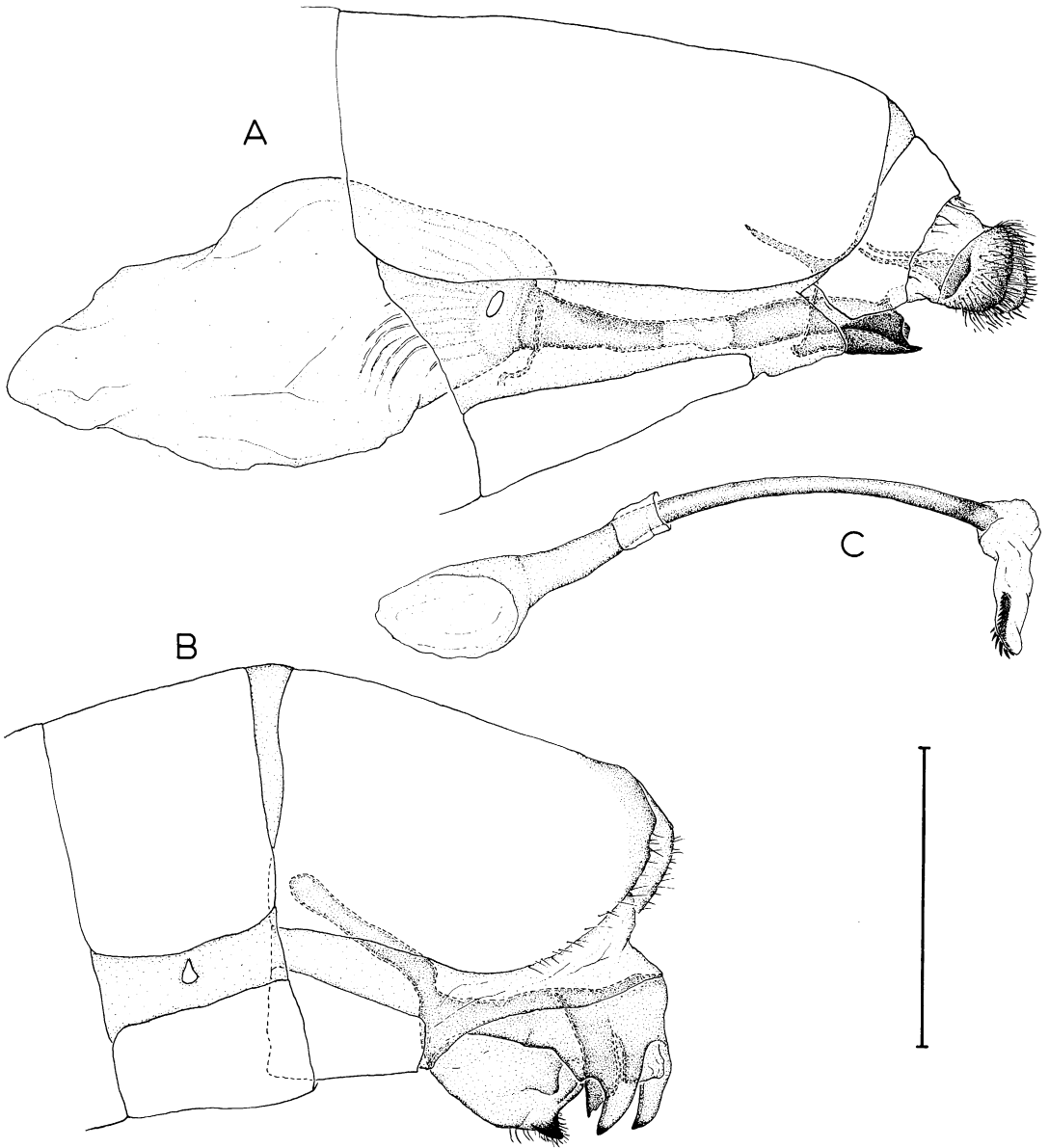
Fig. 18.   Male and female genitalia of *Dismorphia amphione* (Cramer; Pieridae). A. female in lateral view; B. male in lateral view with left valve and aedeagus removed; C. aedeagus in lateral view with distal portion at right. Scale line = 2 mm.
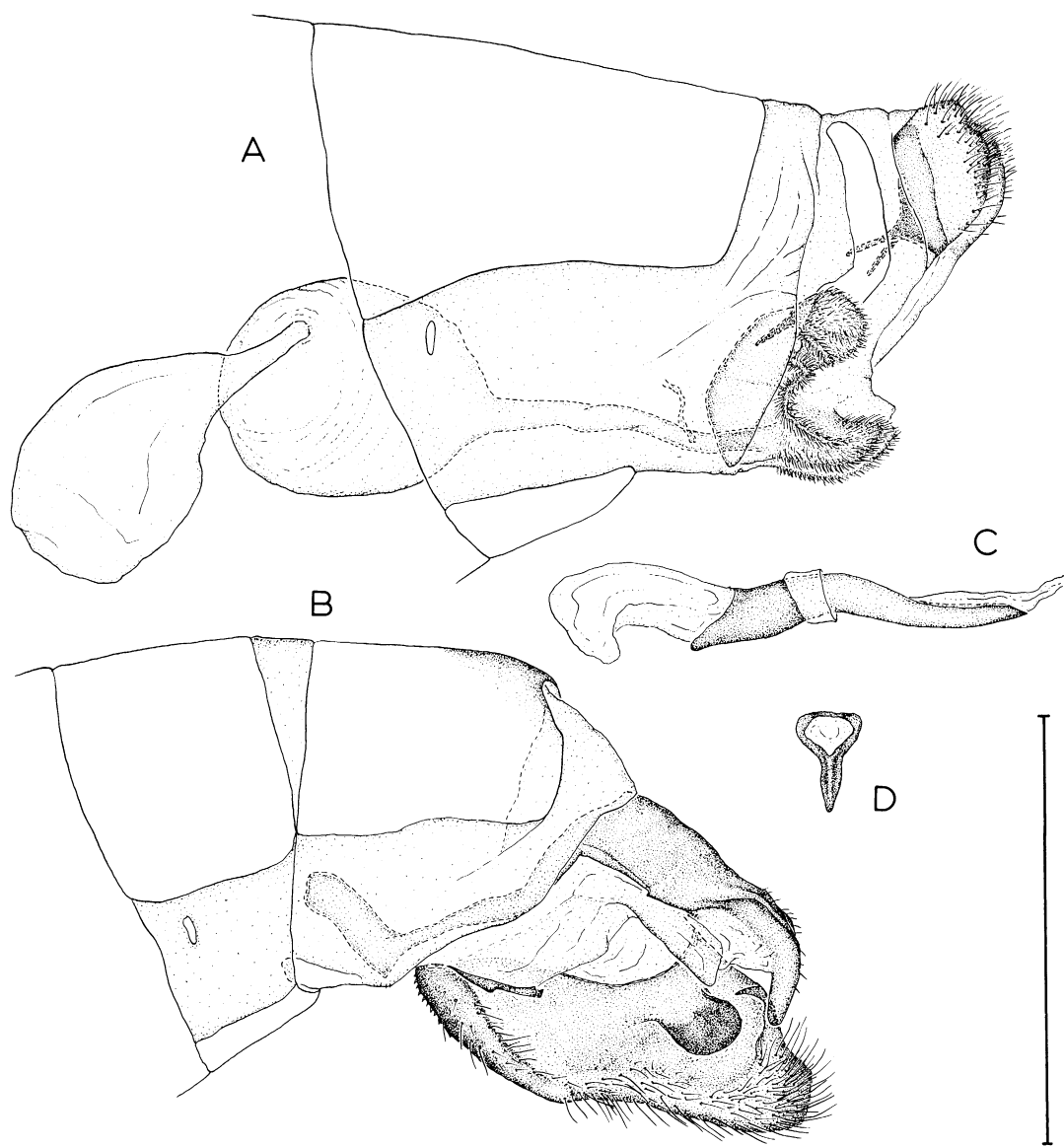
Fig. 19. Male and female genitalia of *Euchloe hyantis* (Edwards; Pieridae). A. female in lateral view; B. male in lateral view with left valve and aedeagus removed; C. aedeagus in lateral view with distal portion at right; D. juxta in anal view. Scale line = 2 mm.
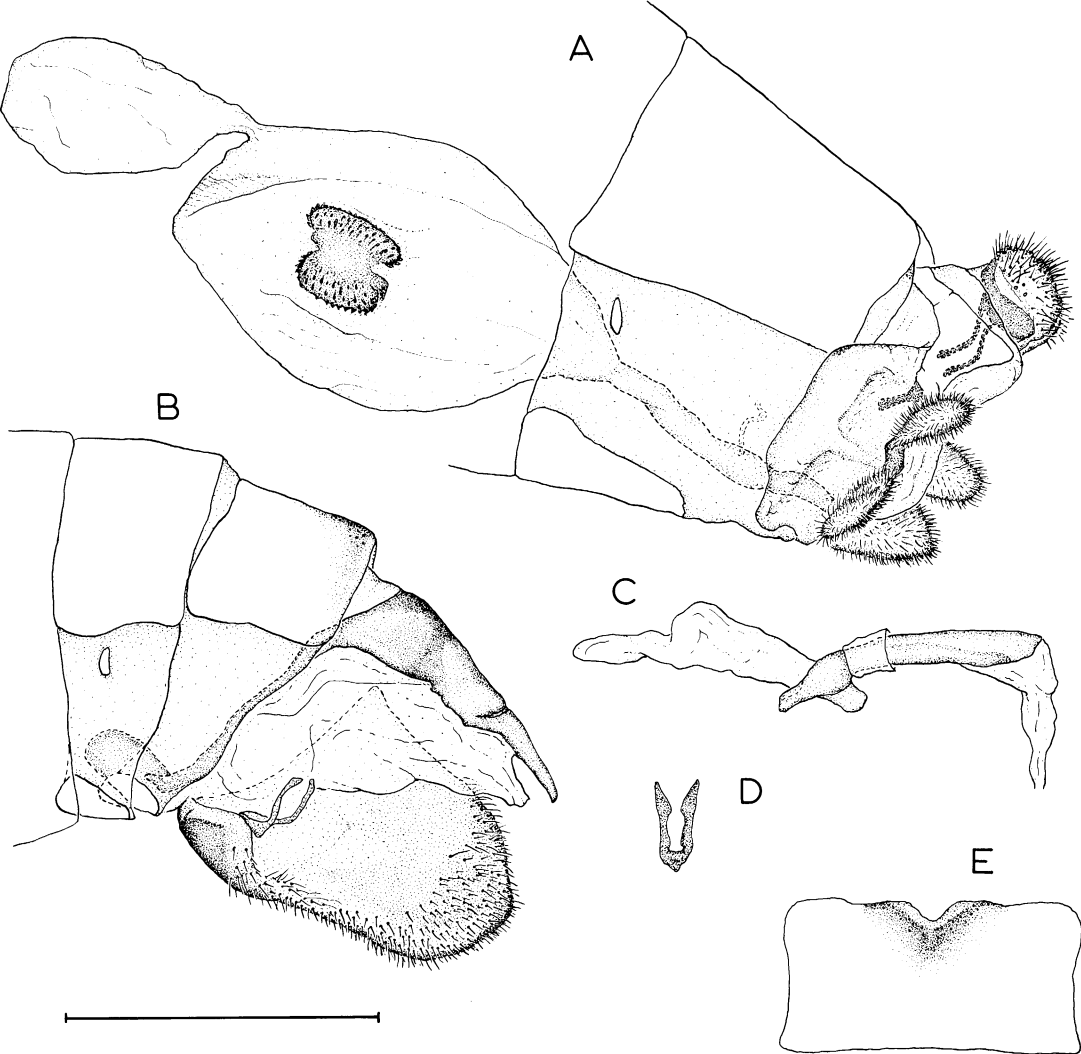
Fig. 20.   Male and female genitalia of *Pieris rapae* (L.; Pieridae). A. female in lateral view; B. male in lateral view with left valve and aedeagus removed; C. aedeagus in lateral view with distal portion at right; D. juxta in anal view; E. dorsal view of 8th tergite. Scale line = 2 mm. Names of specific structures are shown in figure 17.
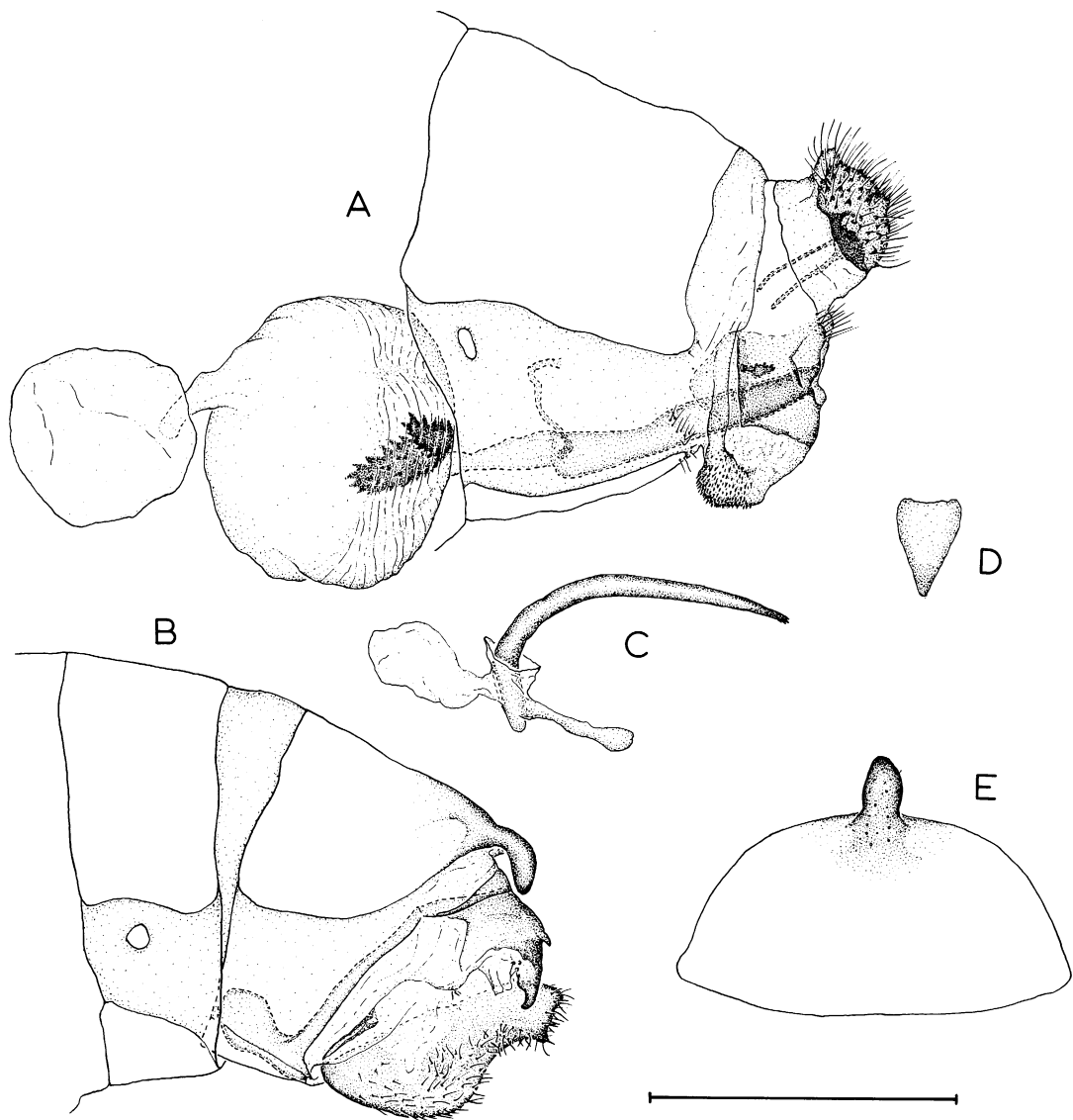
Fig. 21. Male and female genitalia of *Colias philodice* (Godart; Pieridae). For scale length and key to structures refer to figure 20.
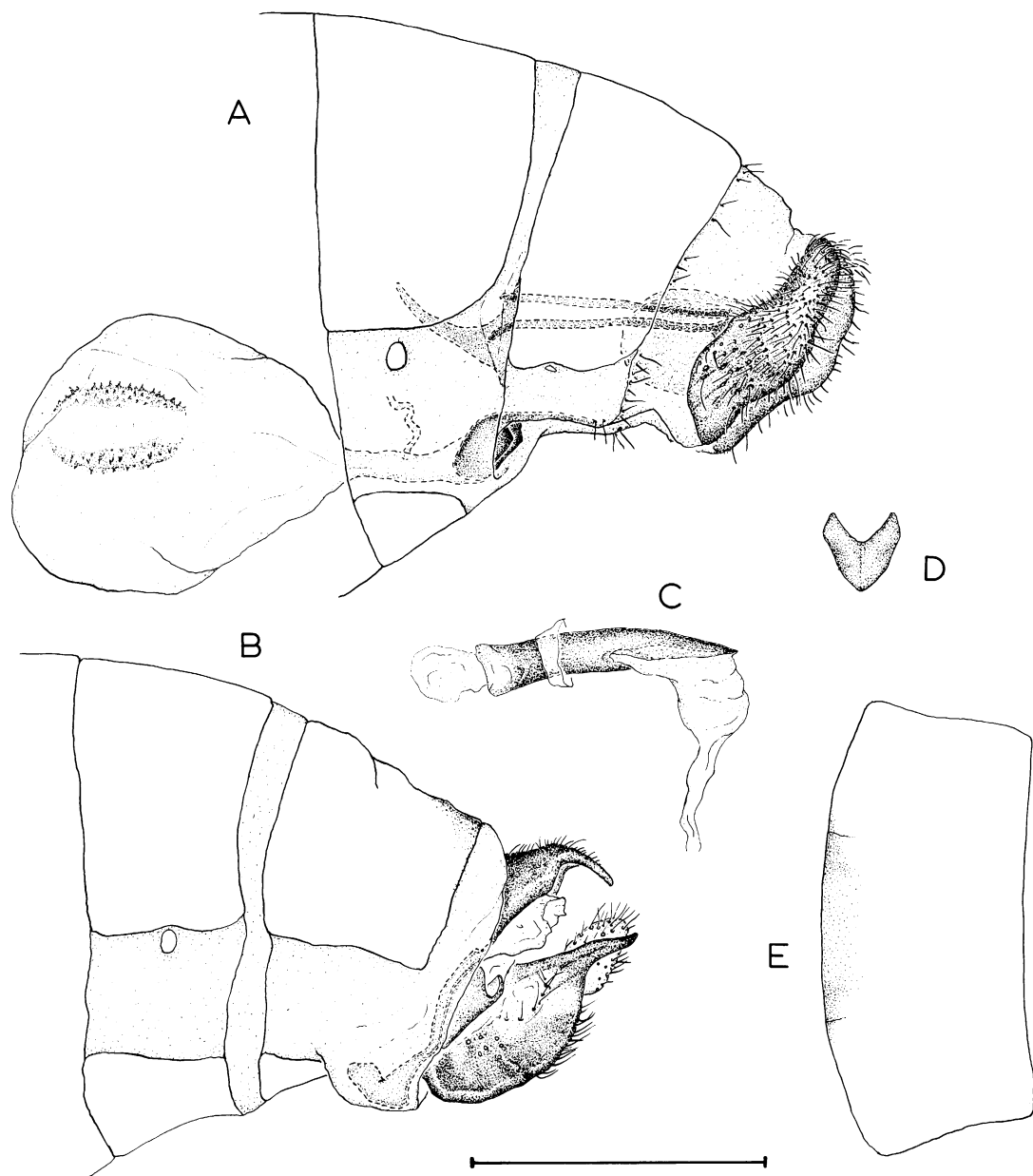
Fig. 22. Male and female genitalia of *Baronia brevicornis* Salvin. For scale length and key to structures refer to figure 20.
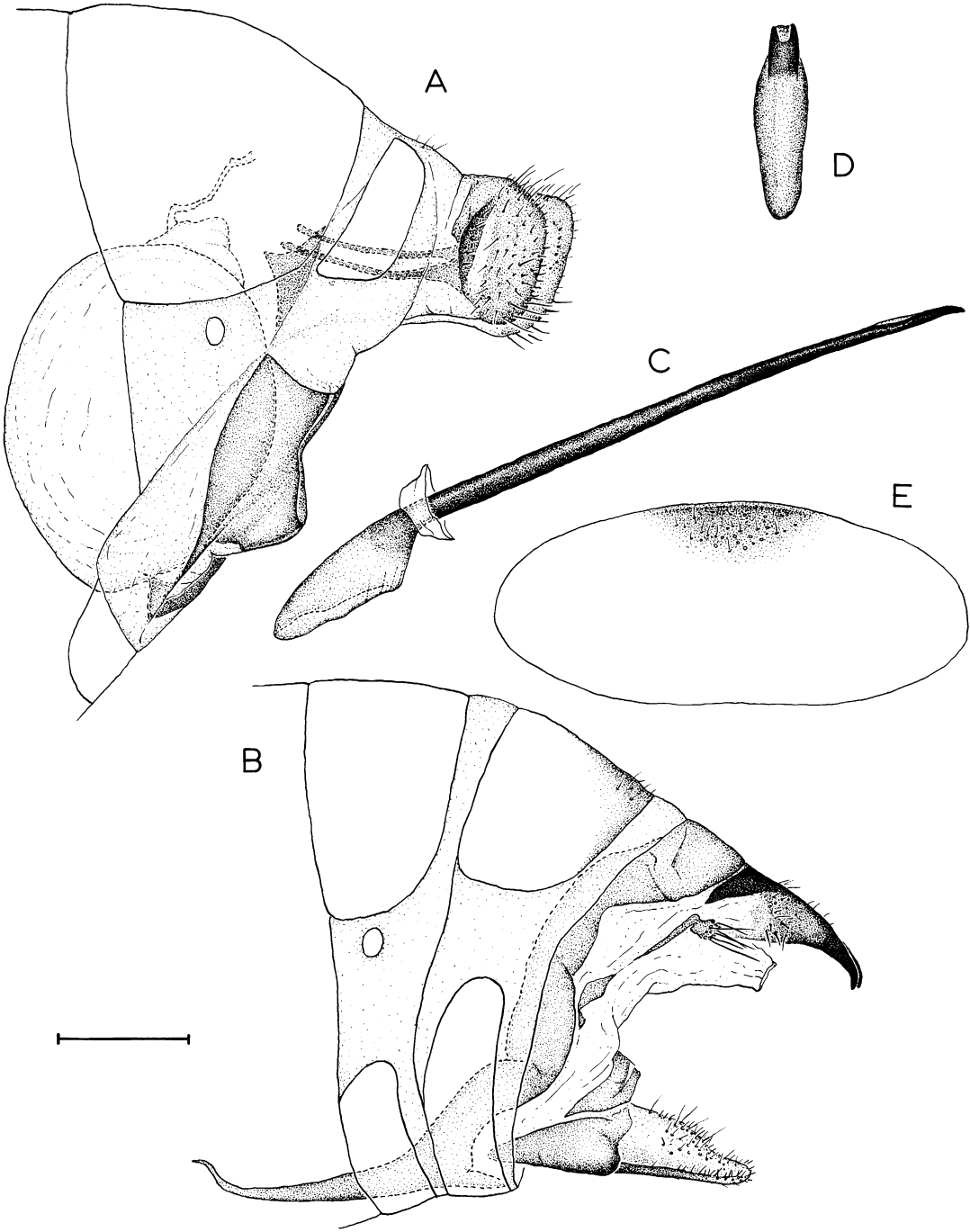
Fig. 23.   Male and female genitalia of *Archon apollinus* (Herbst). For scale length and key to structures refer to figure 20.
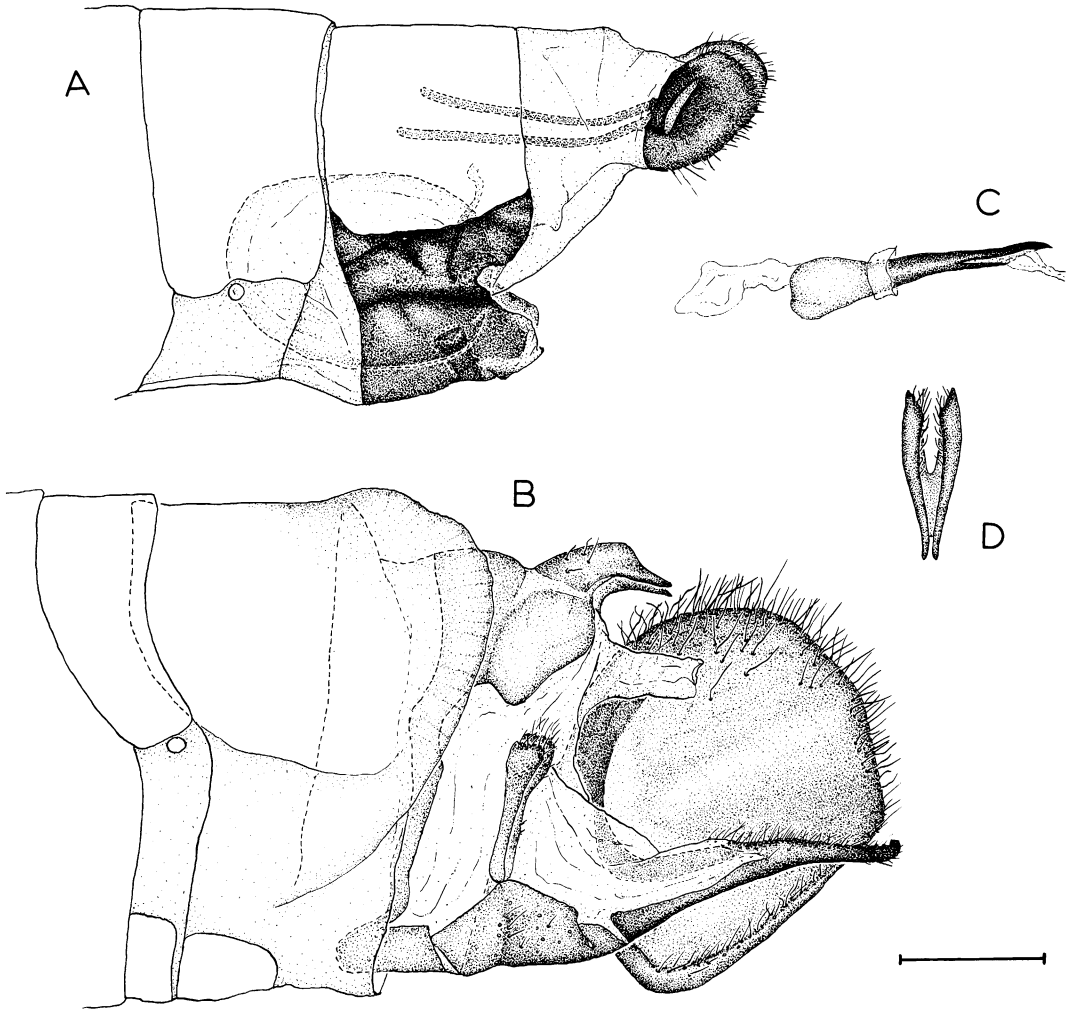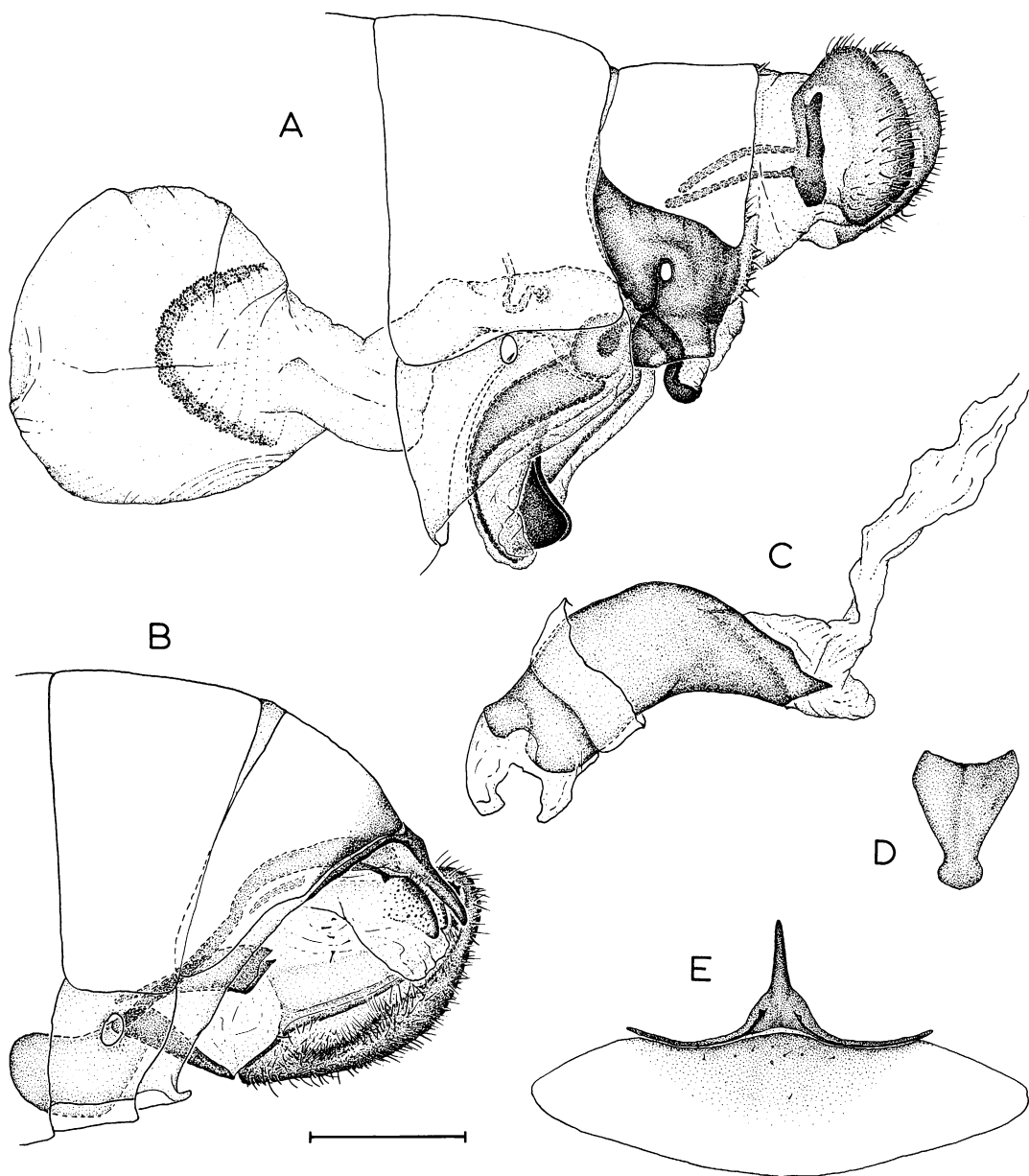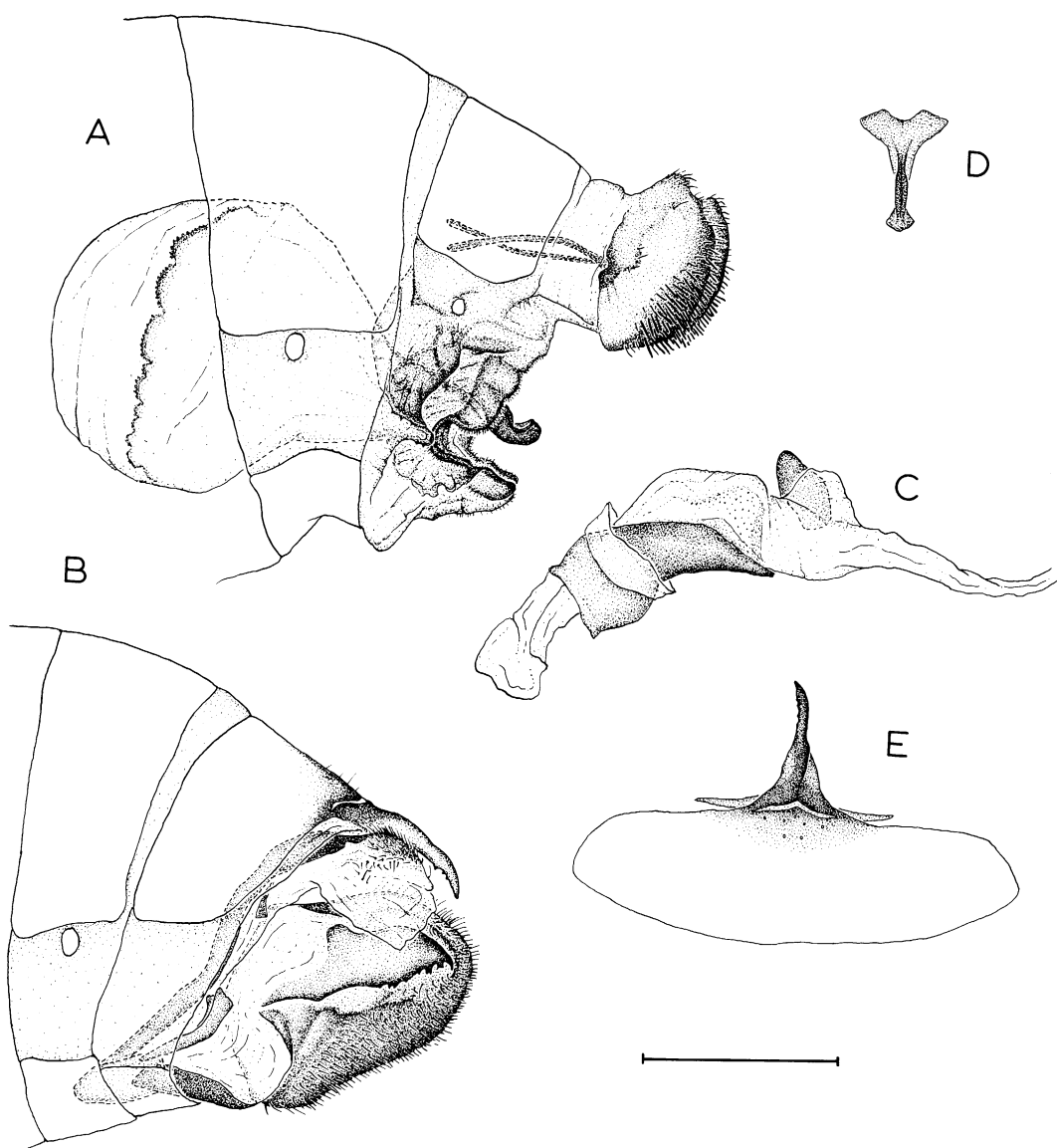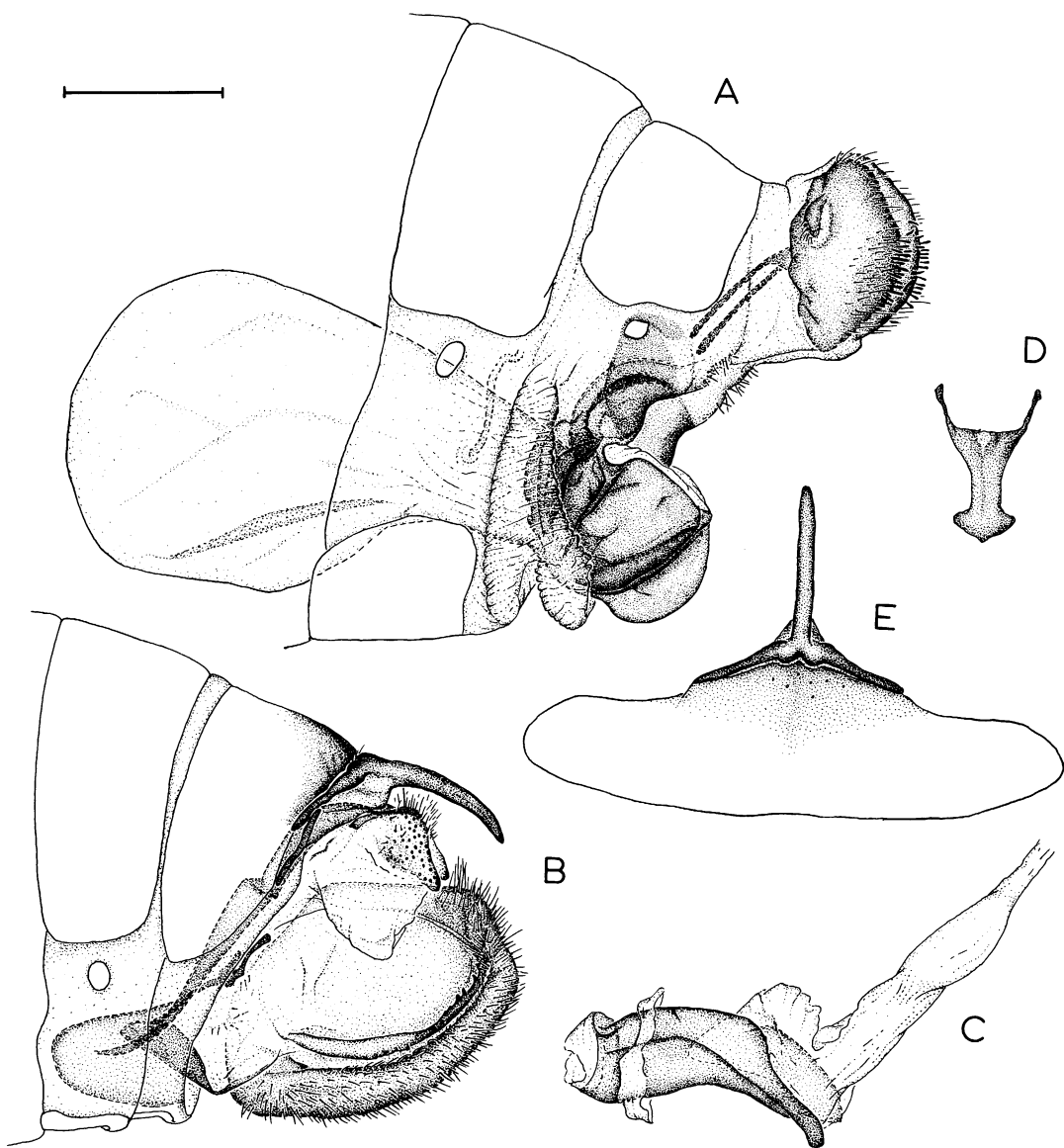
Fig. 24.   Male and female genitalia of *Parnassius szechenyii* Frivaldszky. For scale length and key to structures refer to figure 20.
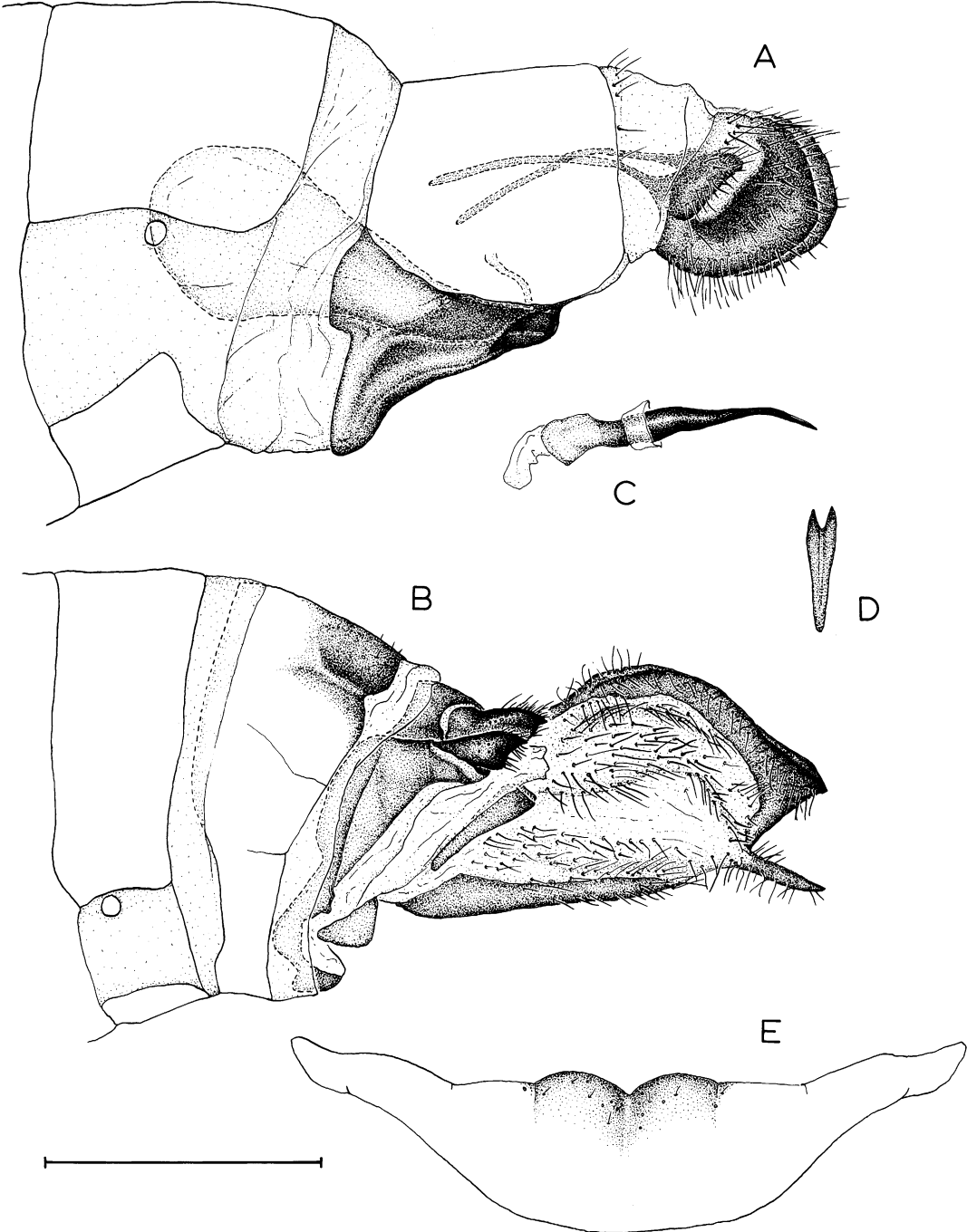
Fig. 25.   Male and female genitalia of *Parnalius polyxena* (Denis and Schiffermuller). For scale length and key to structures refer to figure 20.
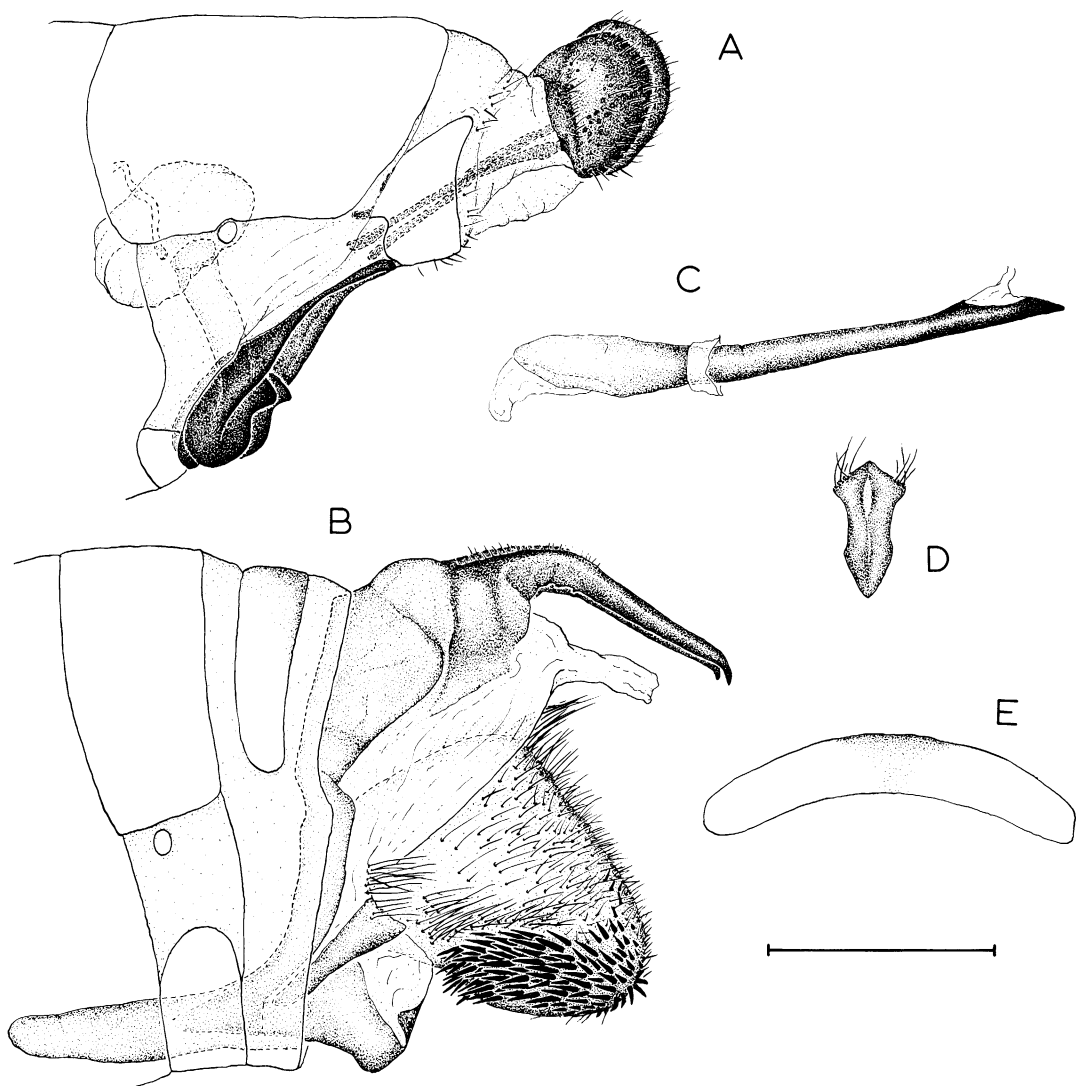
Fig. 26.   Male and female genitalia of *Luehdorfia japonica* Leech. For scale length and key to structures refer to figure 20.
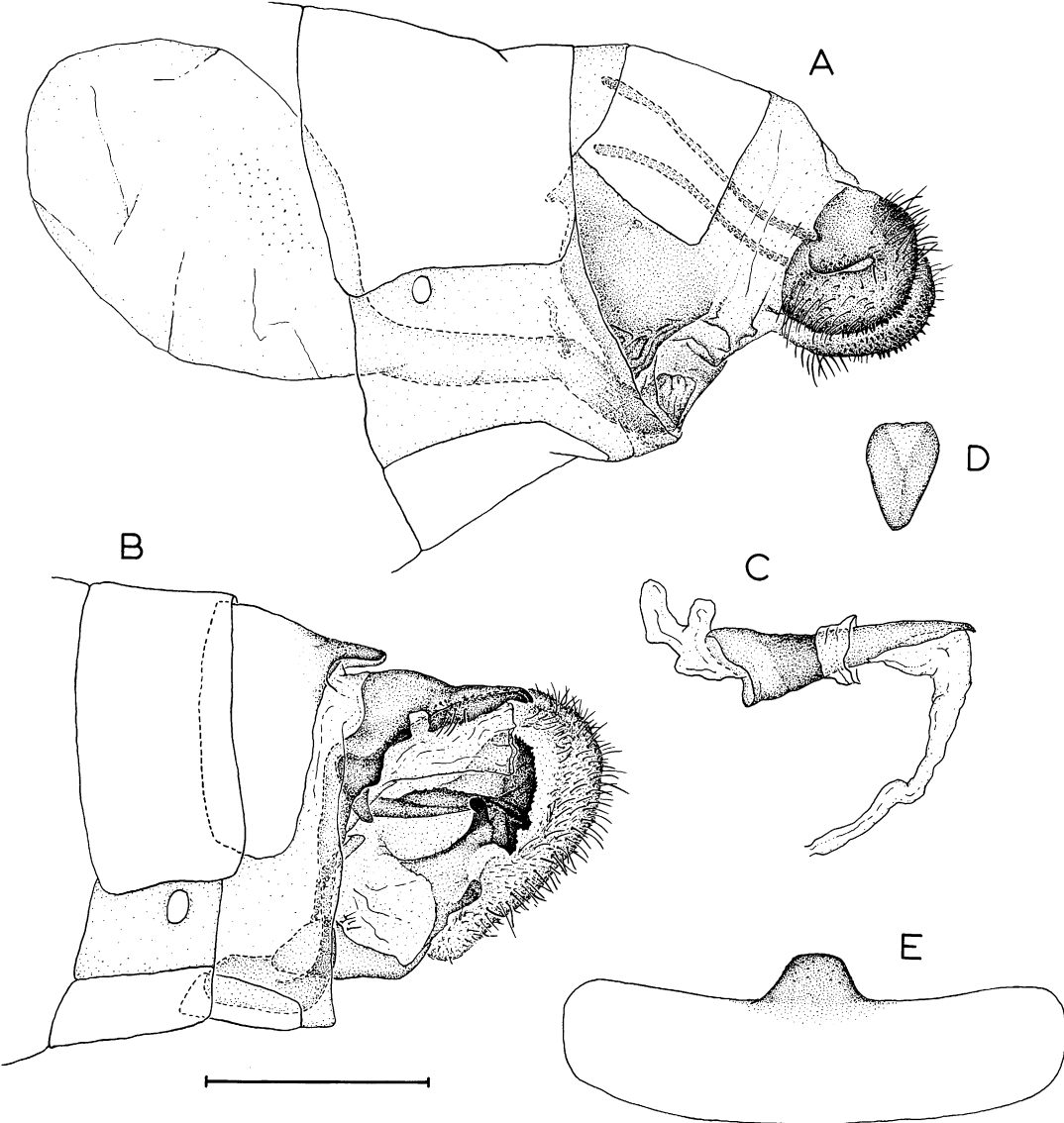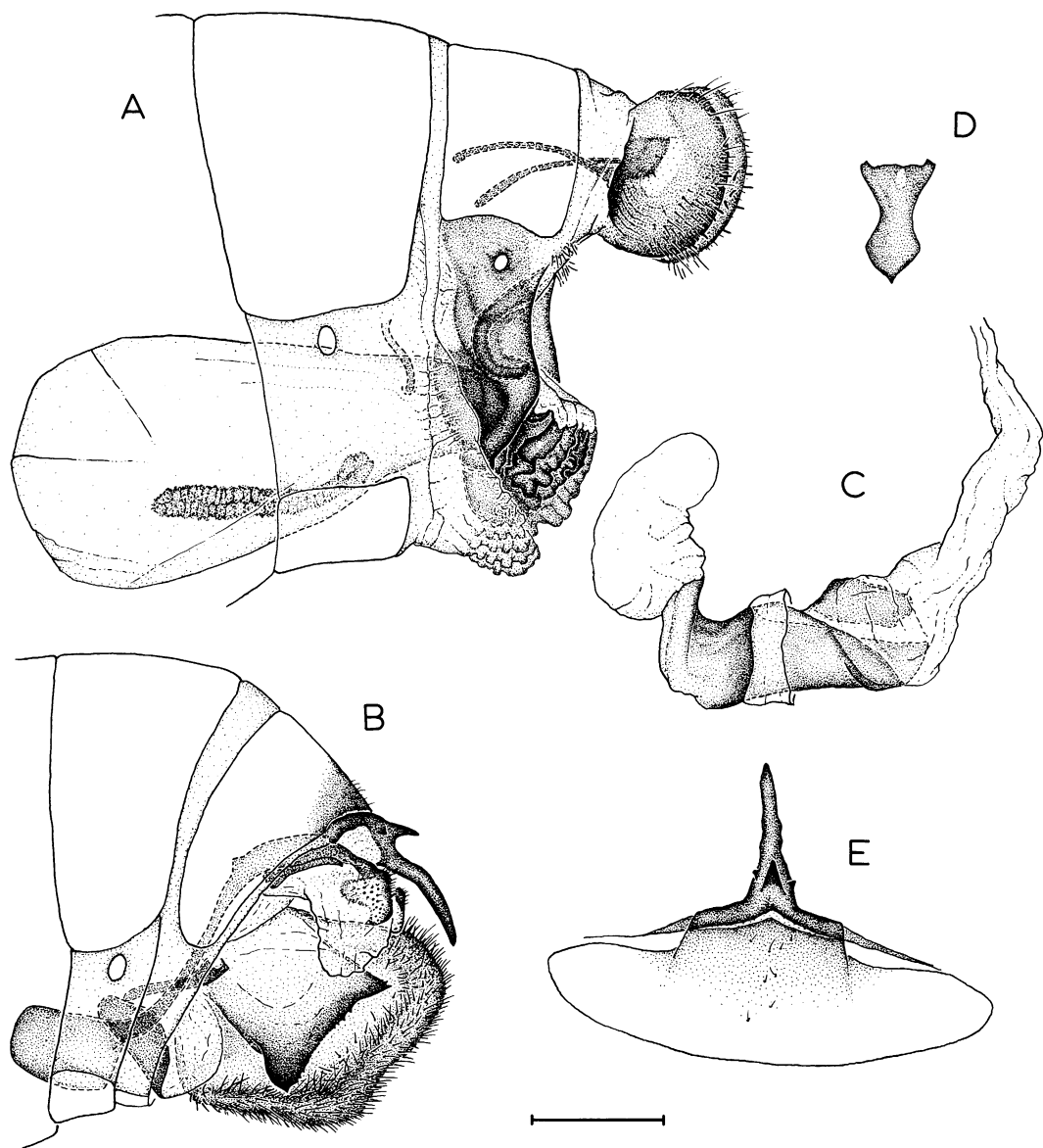
Fig. 27.   Male and female genitalia of *Eurytides epidaus* (Doubleday). For scale length and key to structures refer to figure 20.
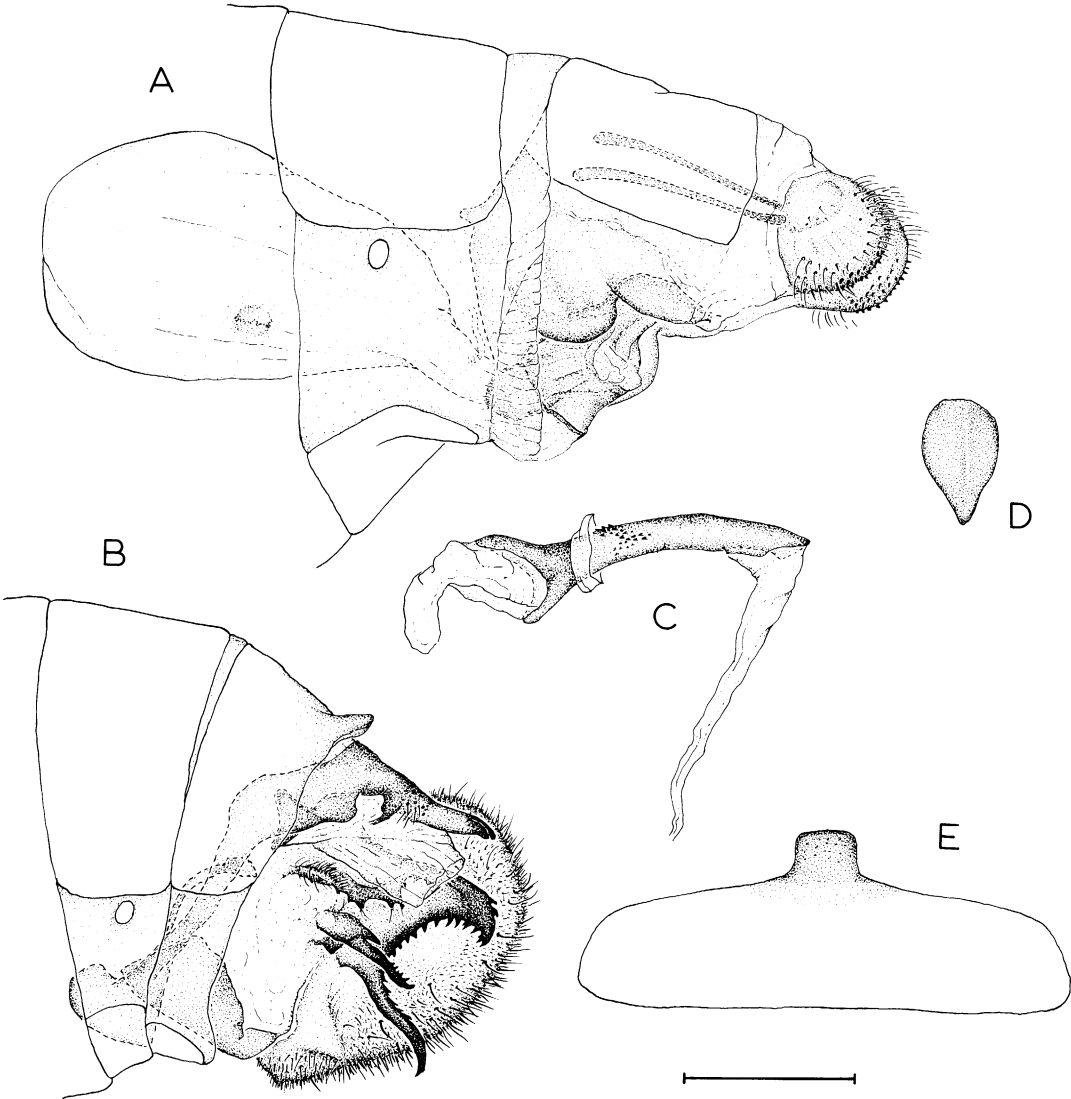
Fig. 28.   Male and female genitalia of *Eurytides telesilaus* (C. and R. Felder). For scale length and key to structures refer to figure 20.
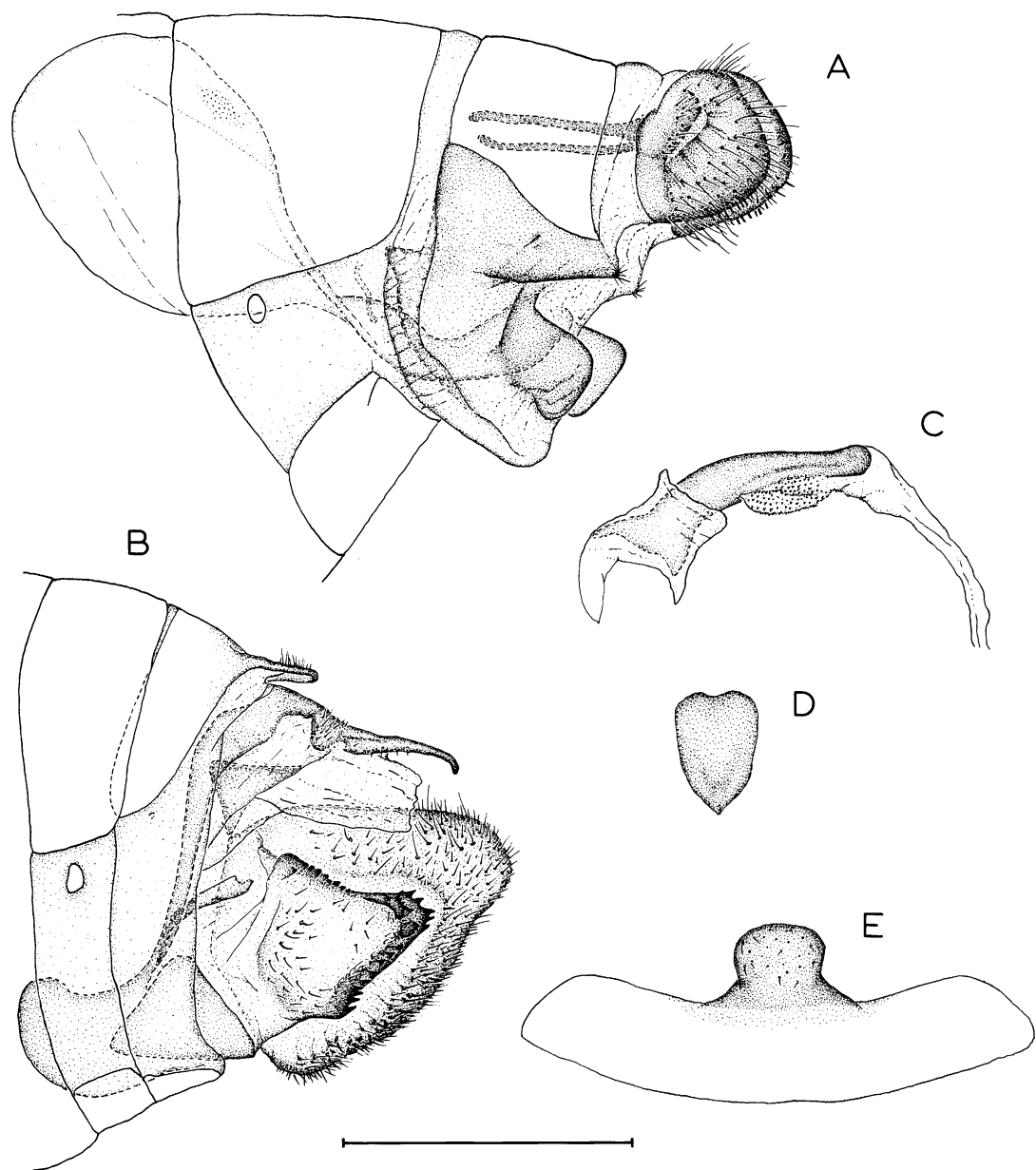
Fig. 29. Male and female genitalia of *Protographium leosthenes* (Doubleday). For scale length and key to structures refer to figure 20.
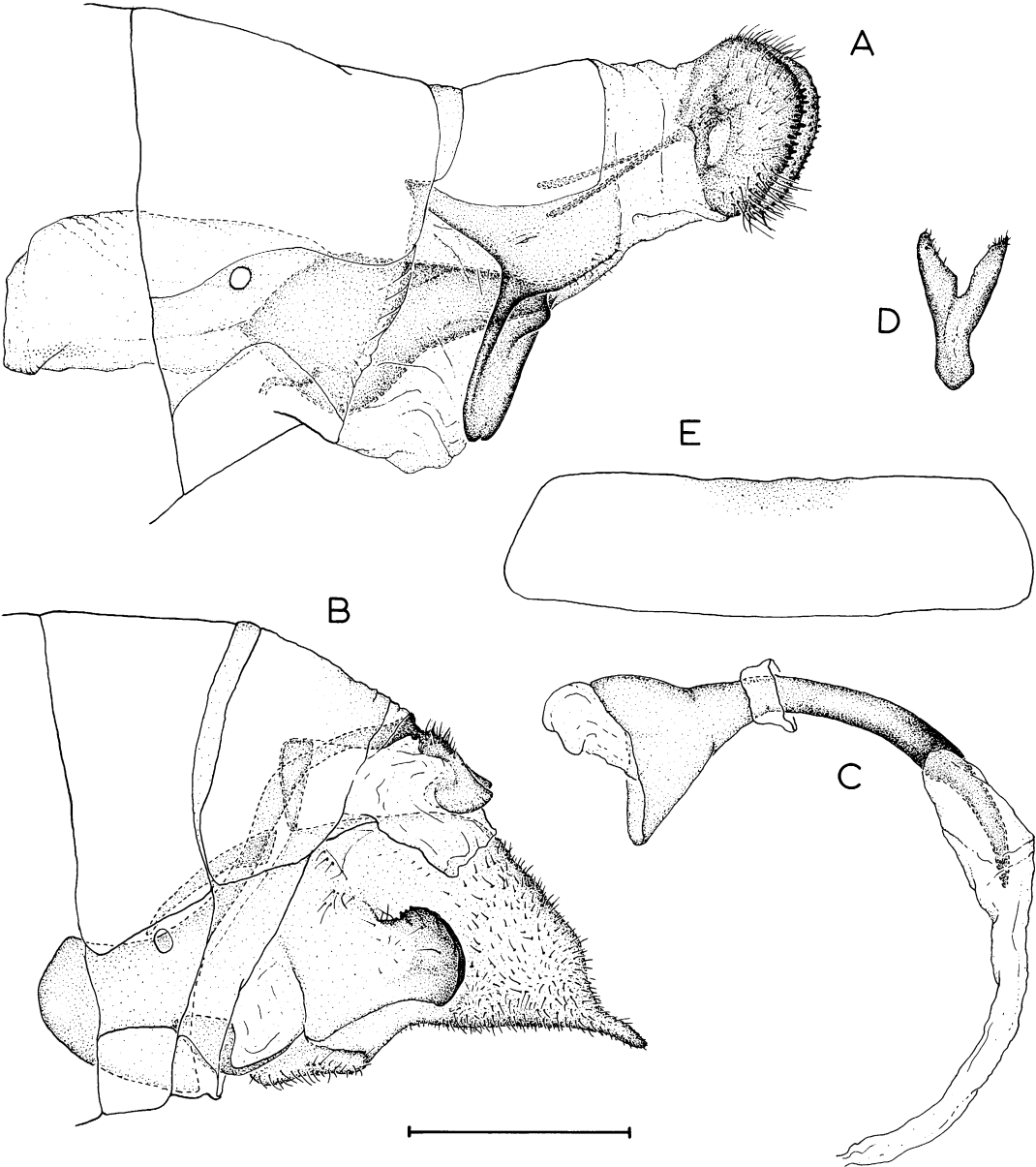
Fig. 30.   Male and female genitalia of *Iphiclides podalirius* (L.). For scale length and key to structures refer to figure 20.
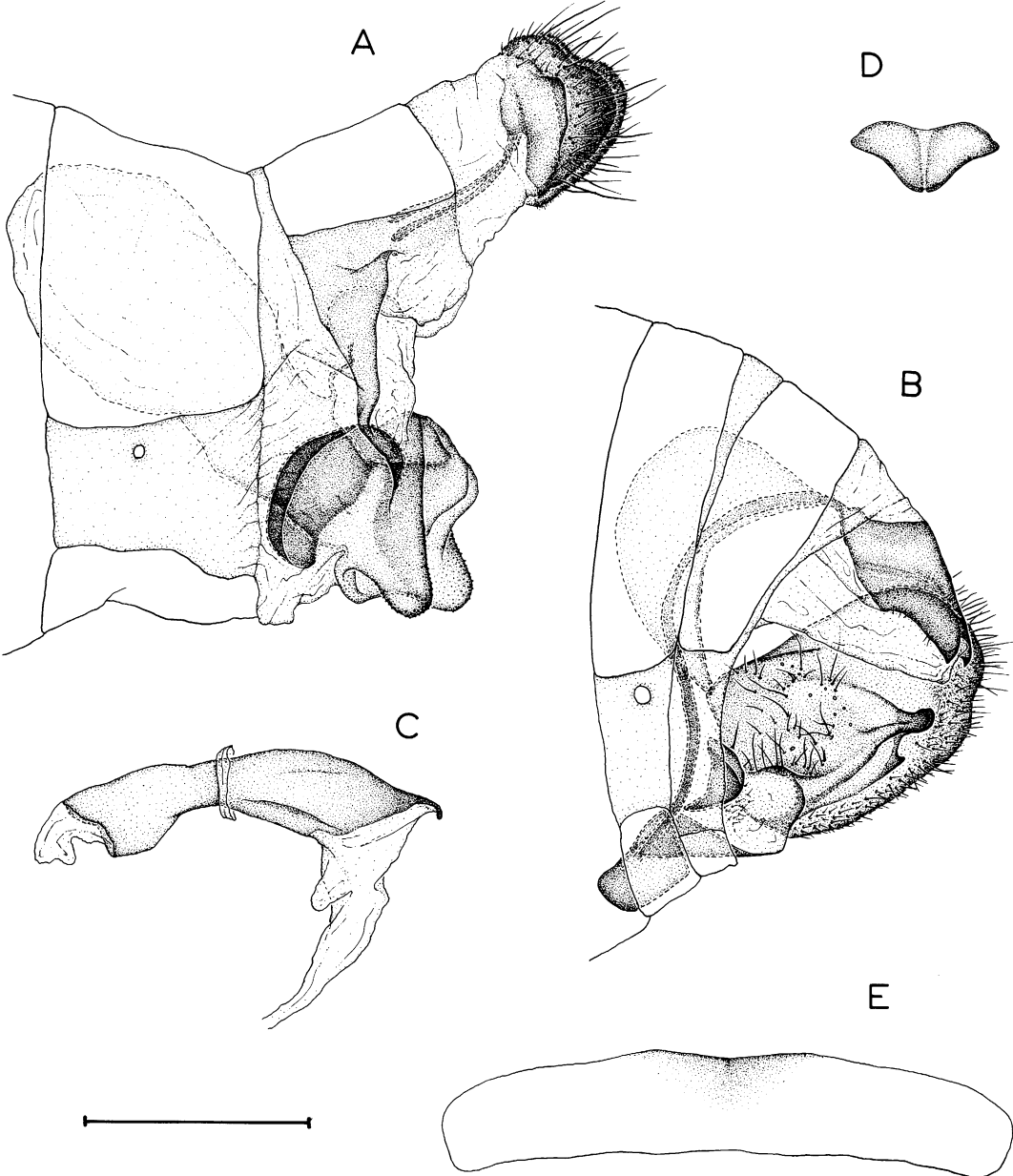
Fig. 31. Male and female genitalia of *Lamproptera meges* (Zinken-Sommer). For scale length and key to structures refer to figure 20.
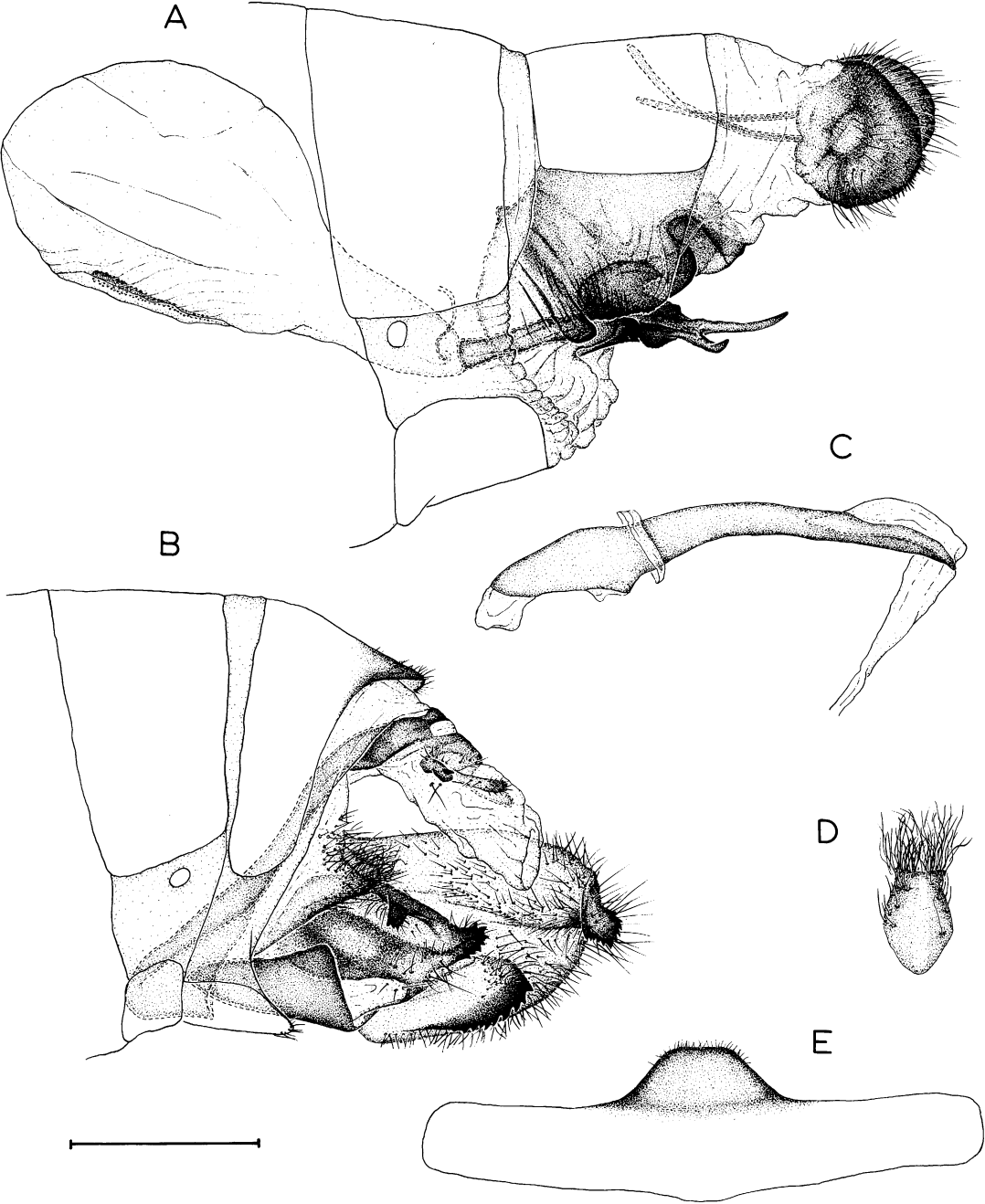
Fig. 32.   Male and female genitalia of *Graphium* (*Pazala*) *eurous* (Leech). For scale length and key to structures refer to figure 20.
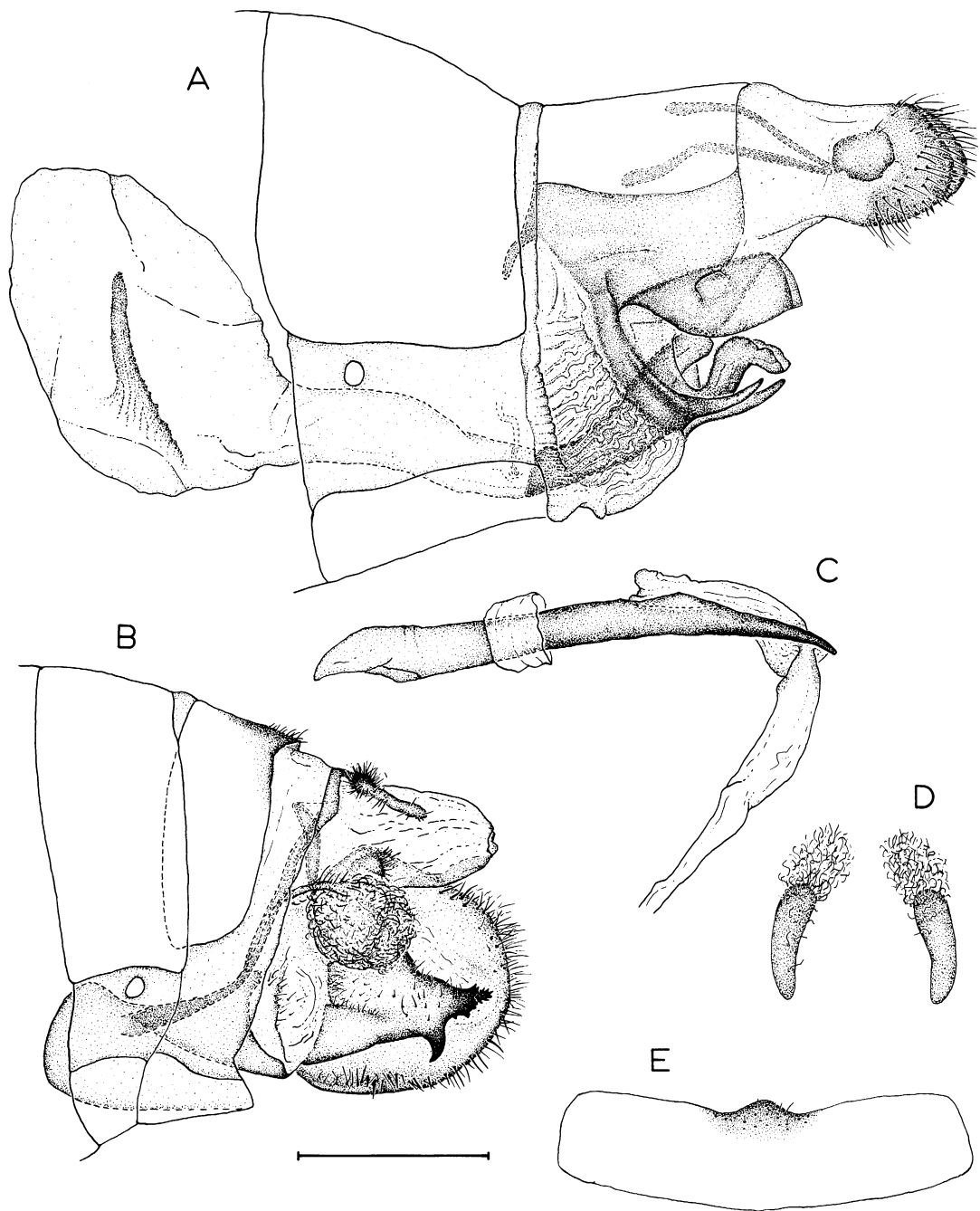
Fig. 33.　Male and female genitalia of *Graphium* (*Graphium*) *euryplus* (L.). For scale length and key to structures refer to figure 20.
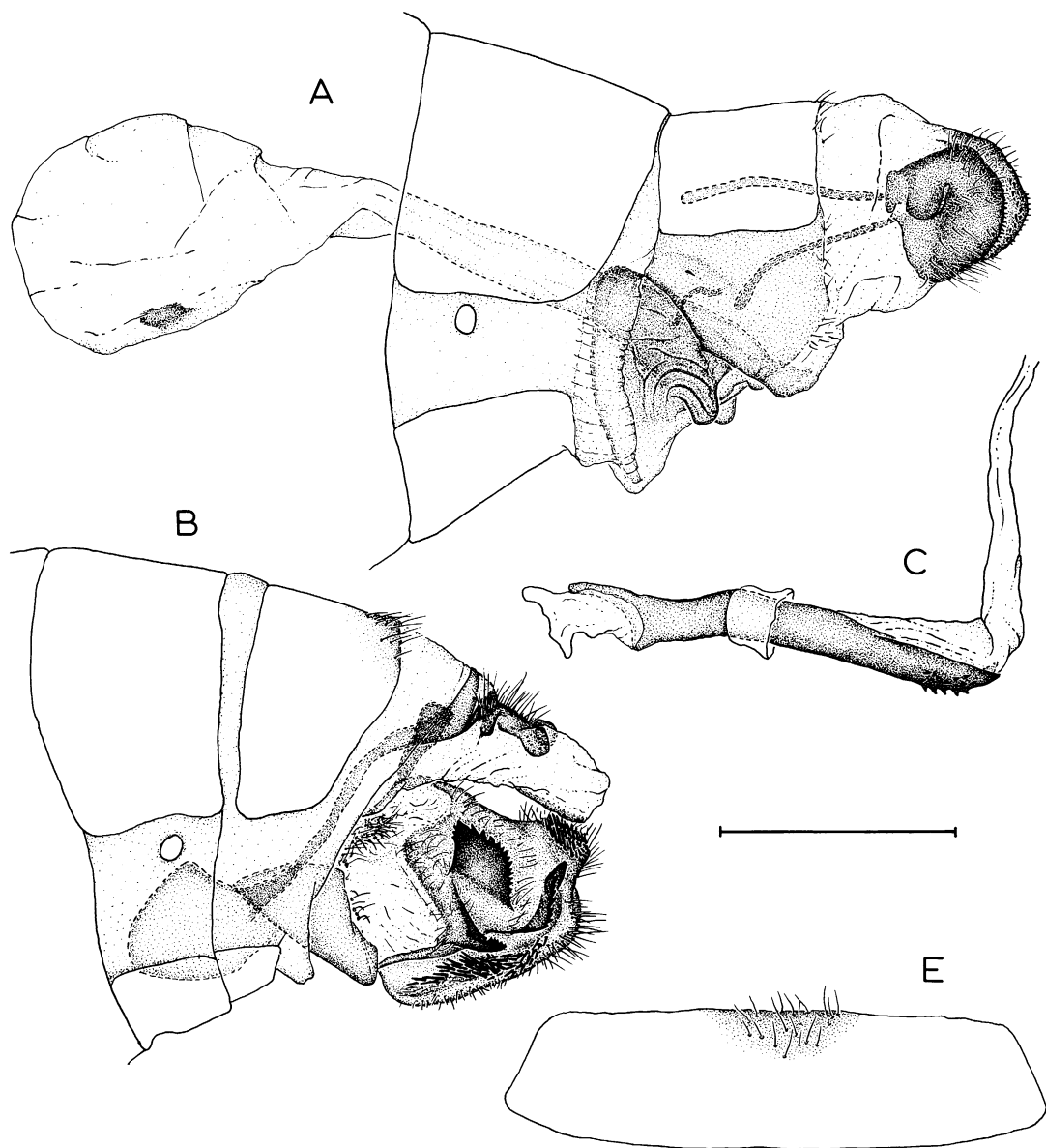
Fig. 34.   Male and female genitalia of *Graphium* (*Pathysa*) *nomius* (Esper). For scale length and key to structures refer to figure 20.
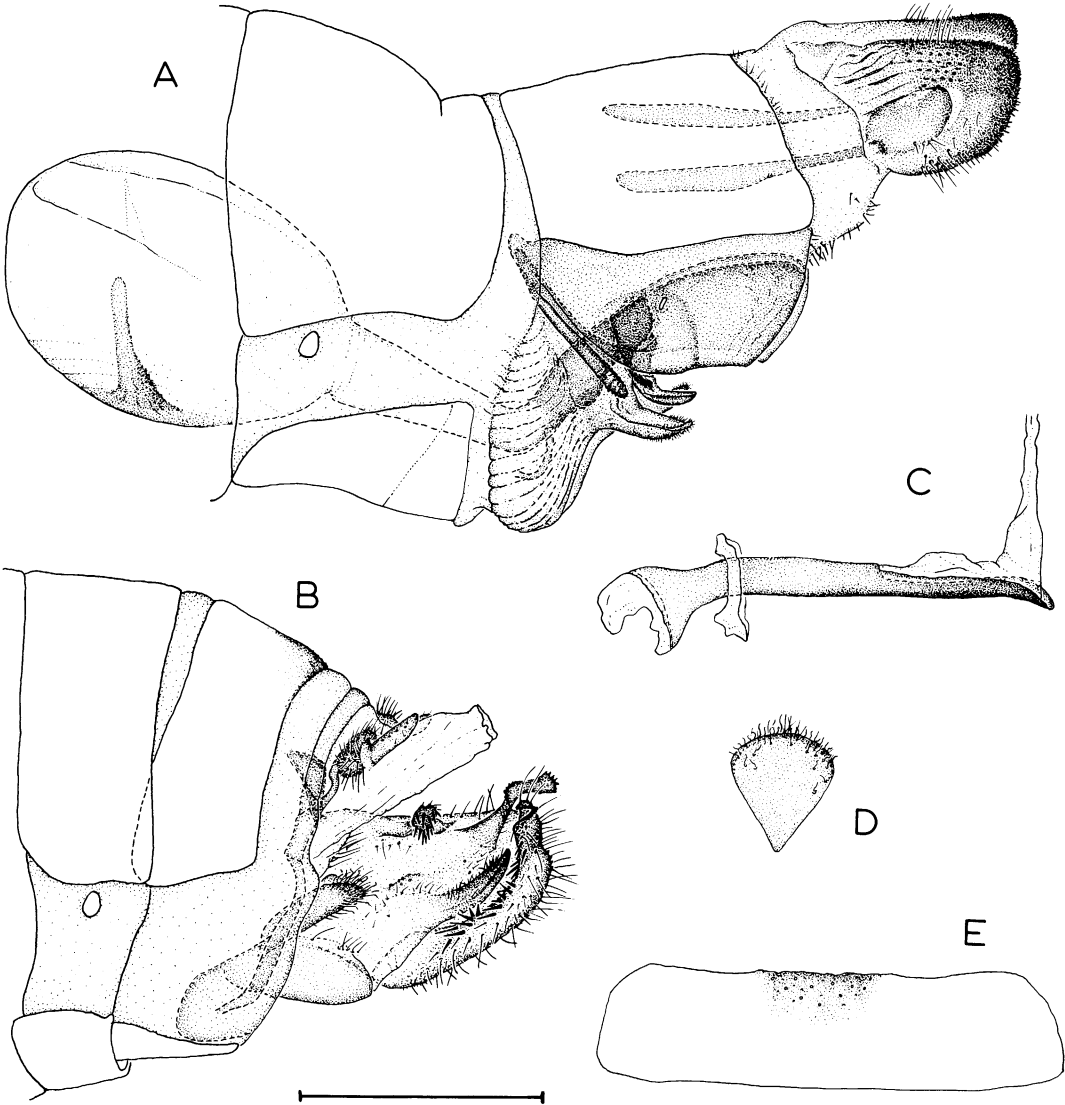
Fig. 35.   Male and female genitalia of *Graphium* (*Arisbe*) *philonoe* (Ward). For scale length and key to structures refer to figure 20.
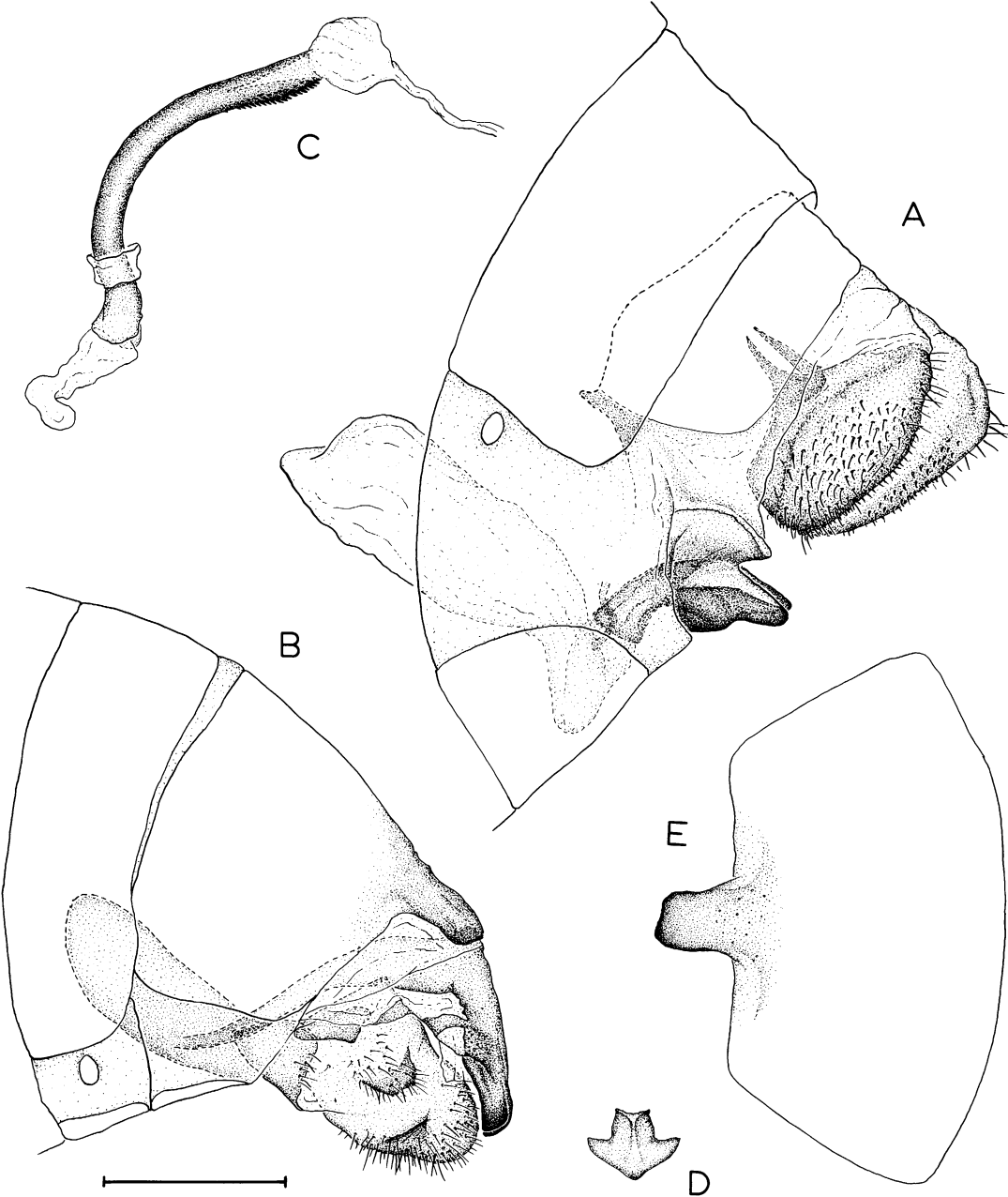
Fig. 36.   Male and female genitalia of *Teinopalpus imperialis* Hope. For scale length and key to structures refer to figure 20.
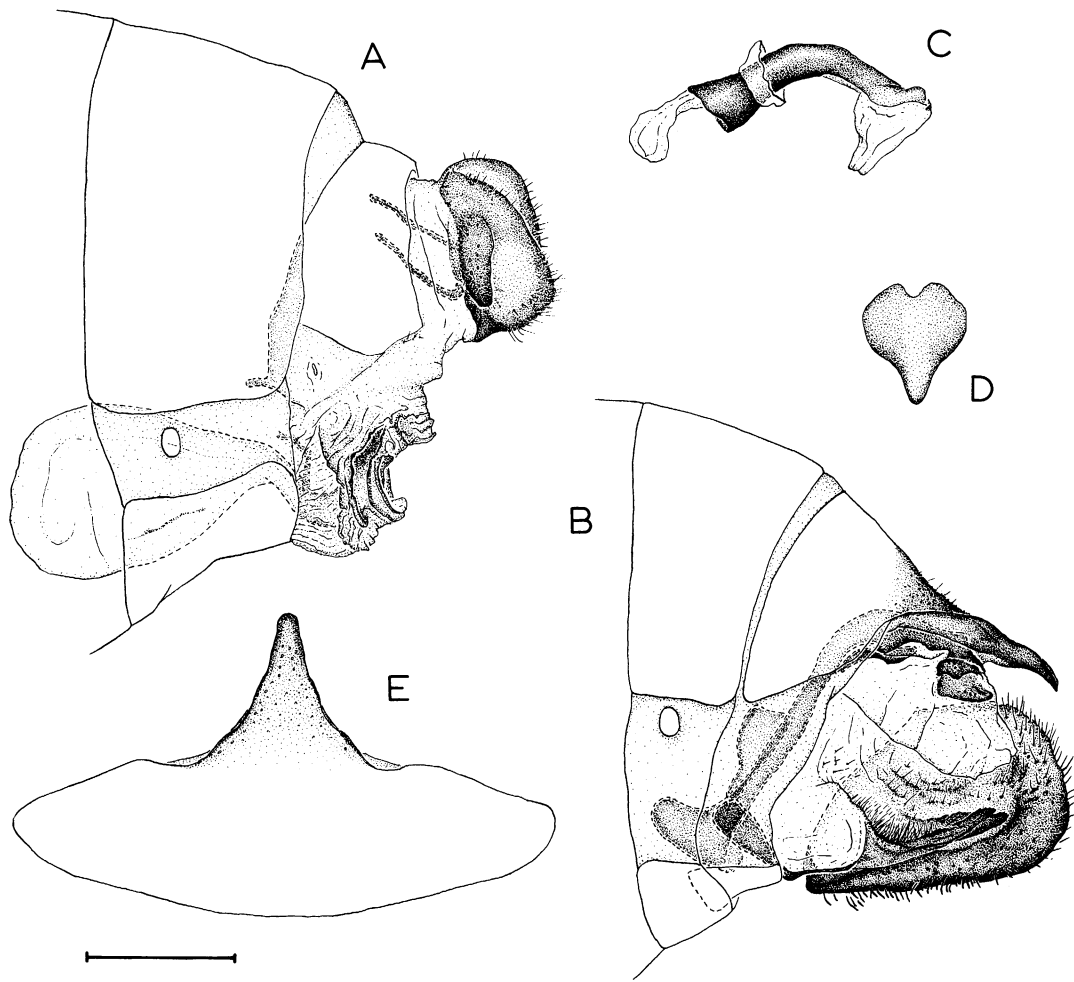
Fig. 37.   Male and female genitalia of *Papilio toboroi* (Ribbe). For scale length and key to structures refer to figure 20.
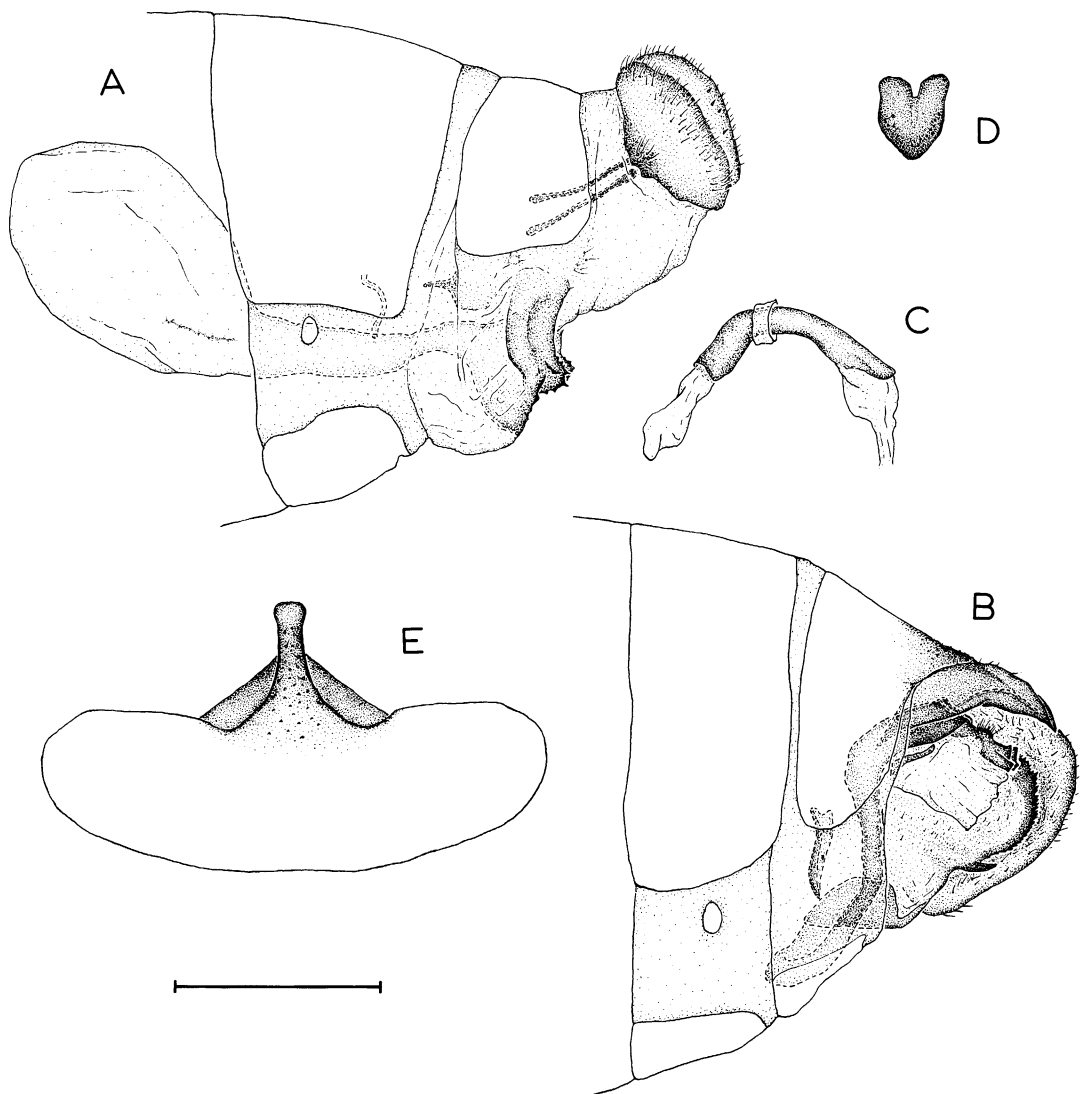
Fig. 38.   Male and female genitalia of *Papilio anactus* (Macleay). For scale length and key to structures refer to figure 20.
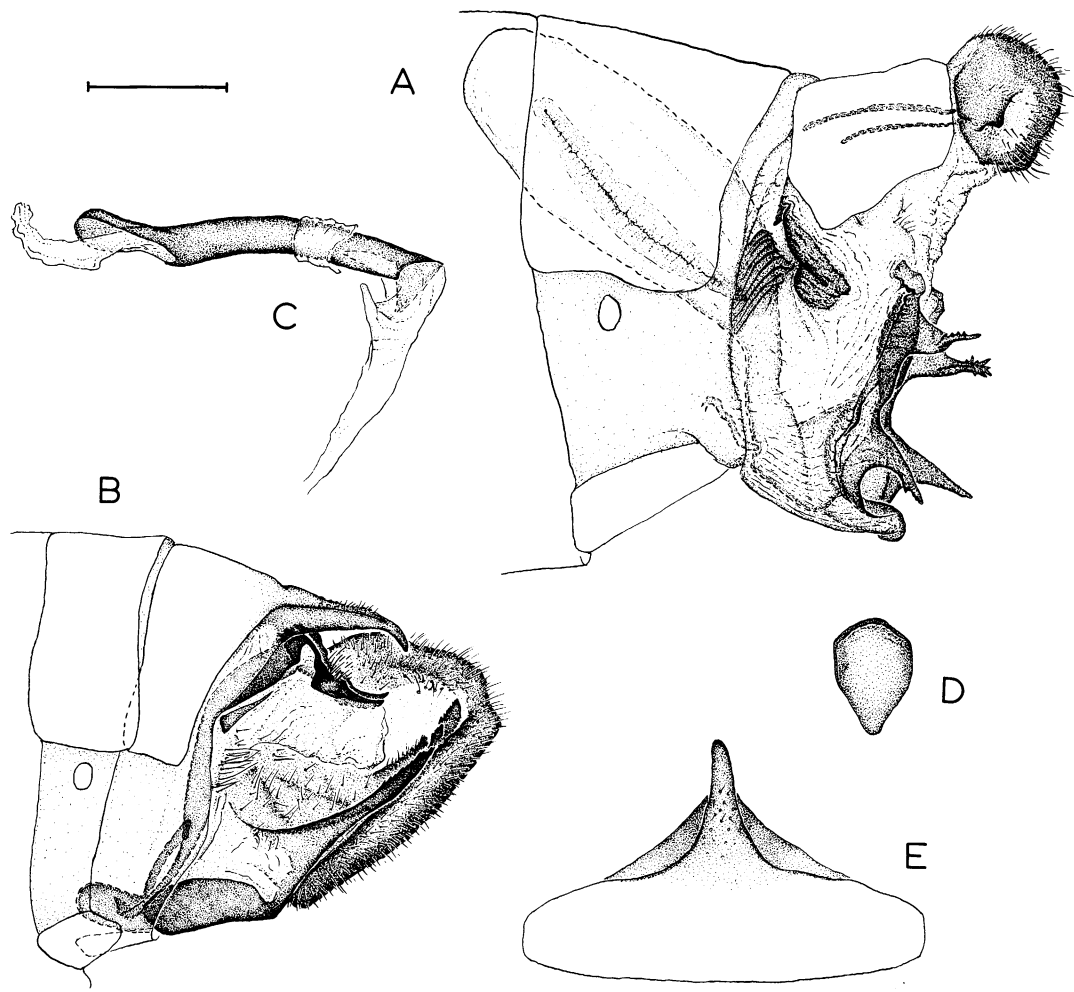
Fig. 39.   Male and female genitalia of *Papilio protenor* (Cramer). For scale length and key to structures refer to figure 20.
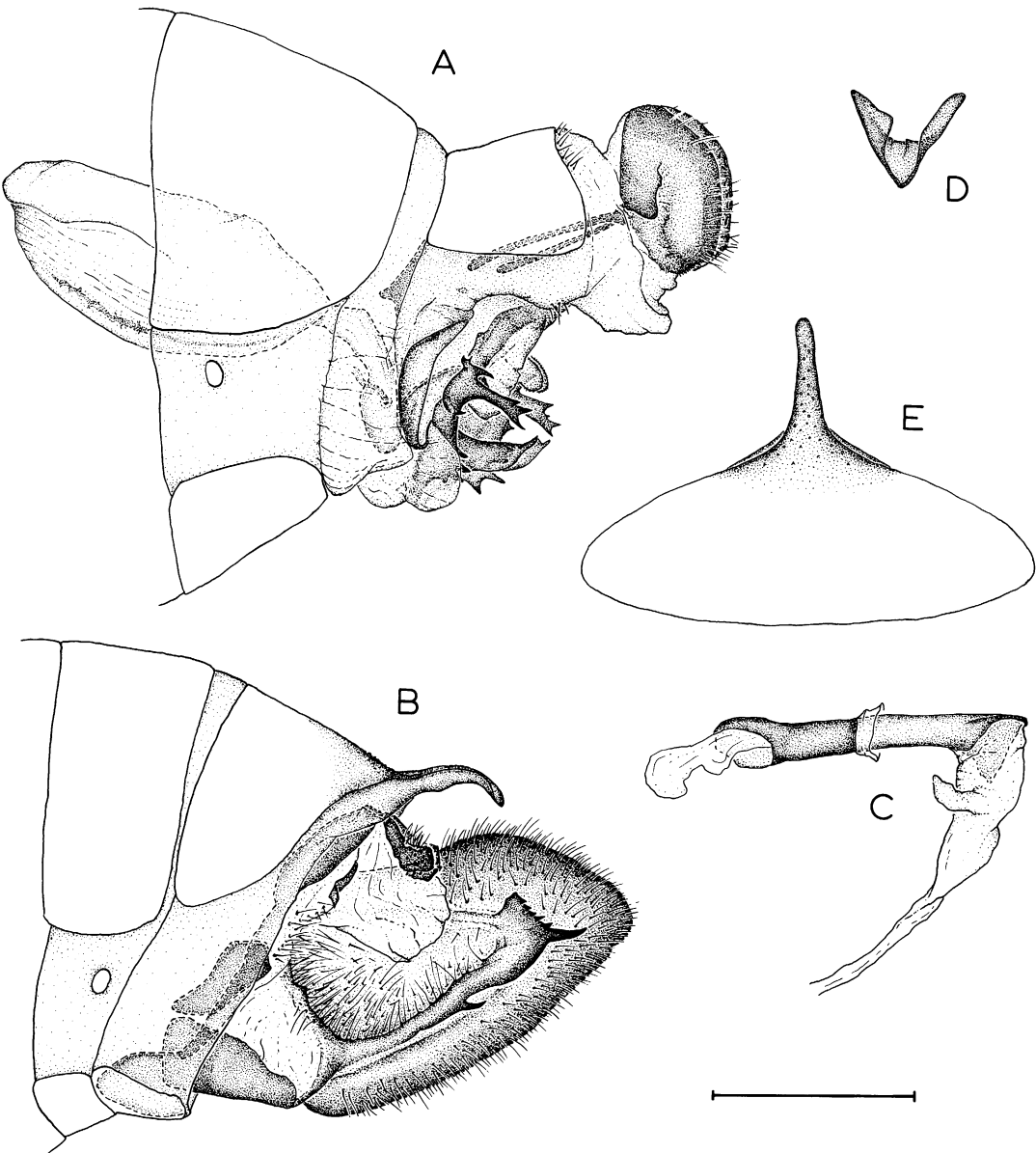
Fig. 40.   Male and female genitalia of *Papilio troilus* (L.). For scale length and key to structures refer to figure 20.
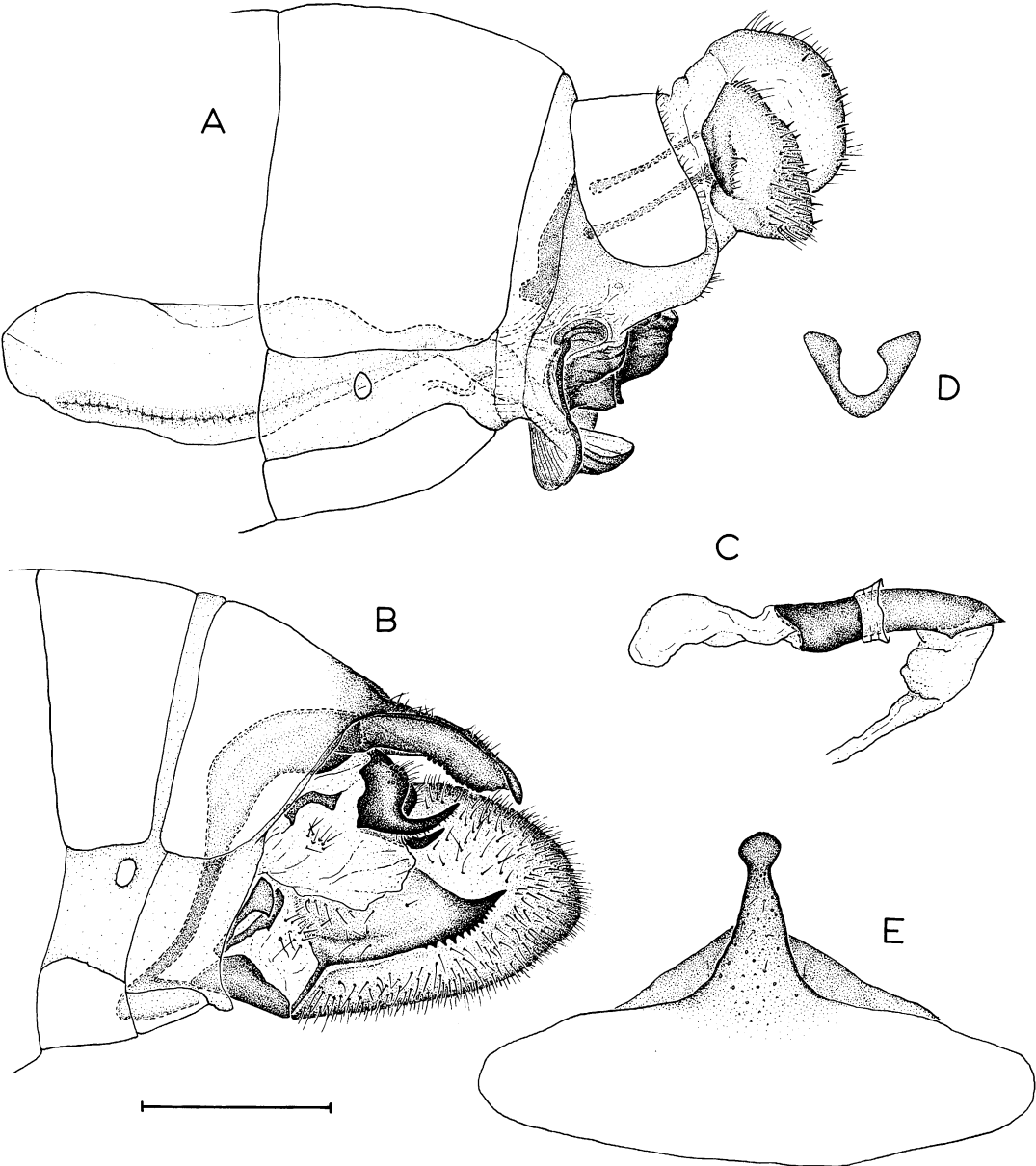
Fig. 41. Male and female genitalia of *Papilio thoas* (L.). For scale length and key to structures refer to figure 20.
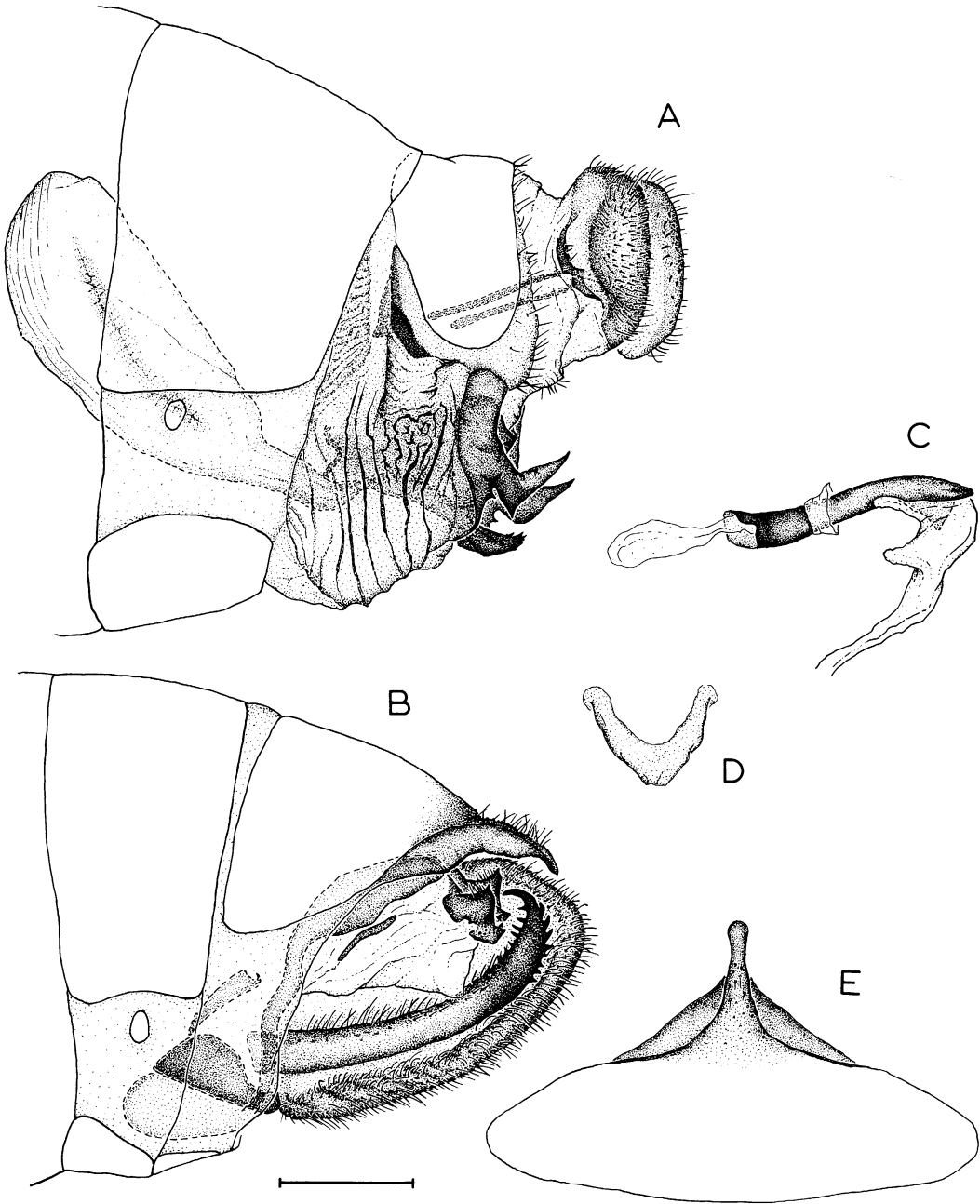
Fig. 42.   Male and female genitalia of *Papilio victorinus* (Doubleday). For scale length and key to structures refer to figure 20.
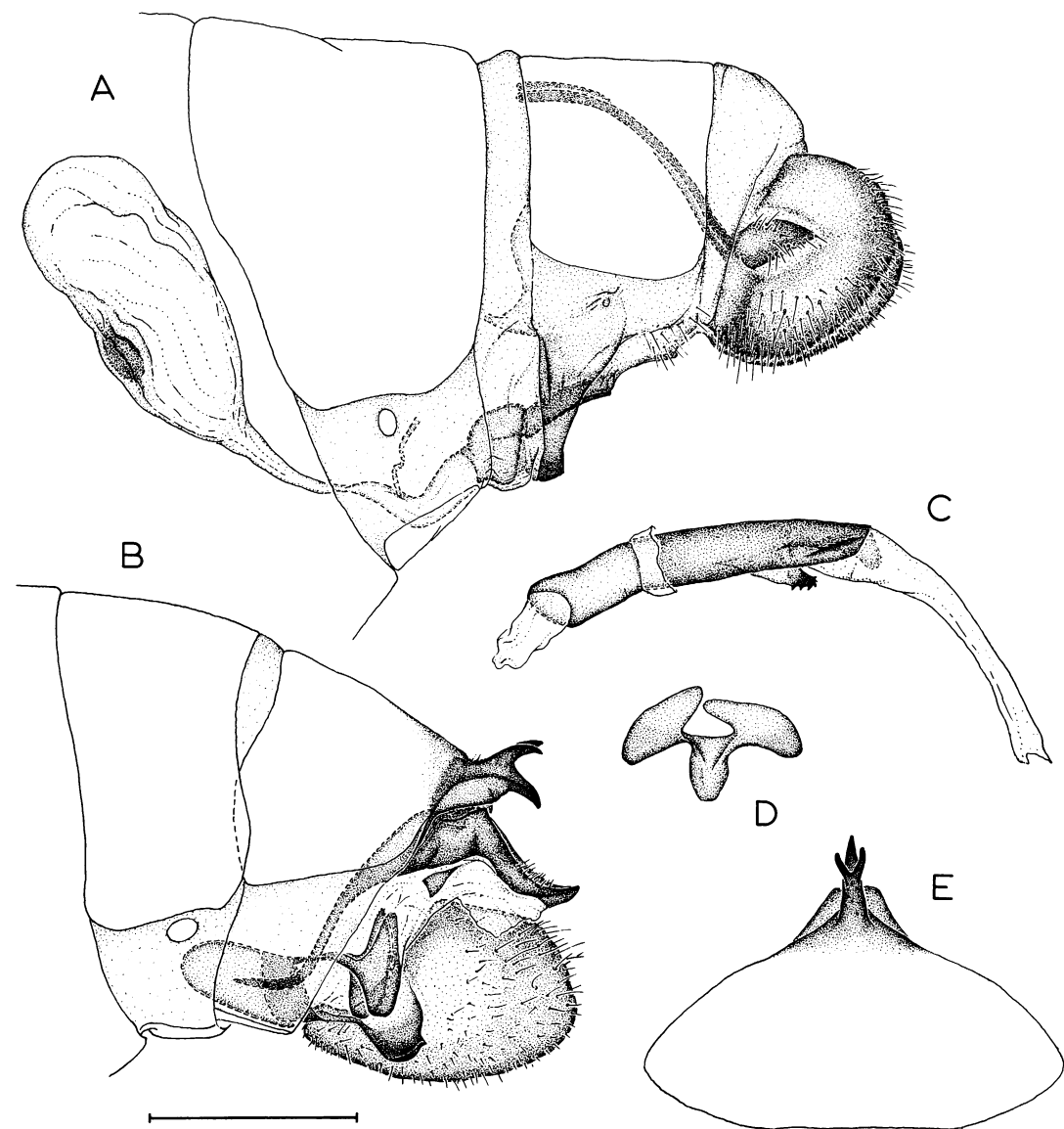
Fig. 43.   Male and female genitalia of *Meandrusa sciron* (Leech). For scale length and key to structures refer to figure 20.
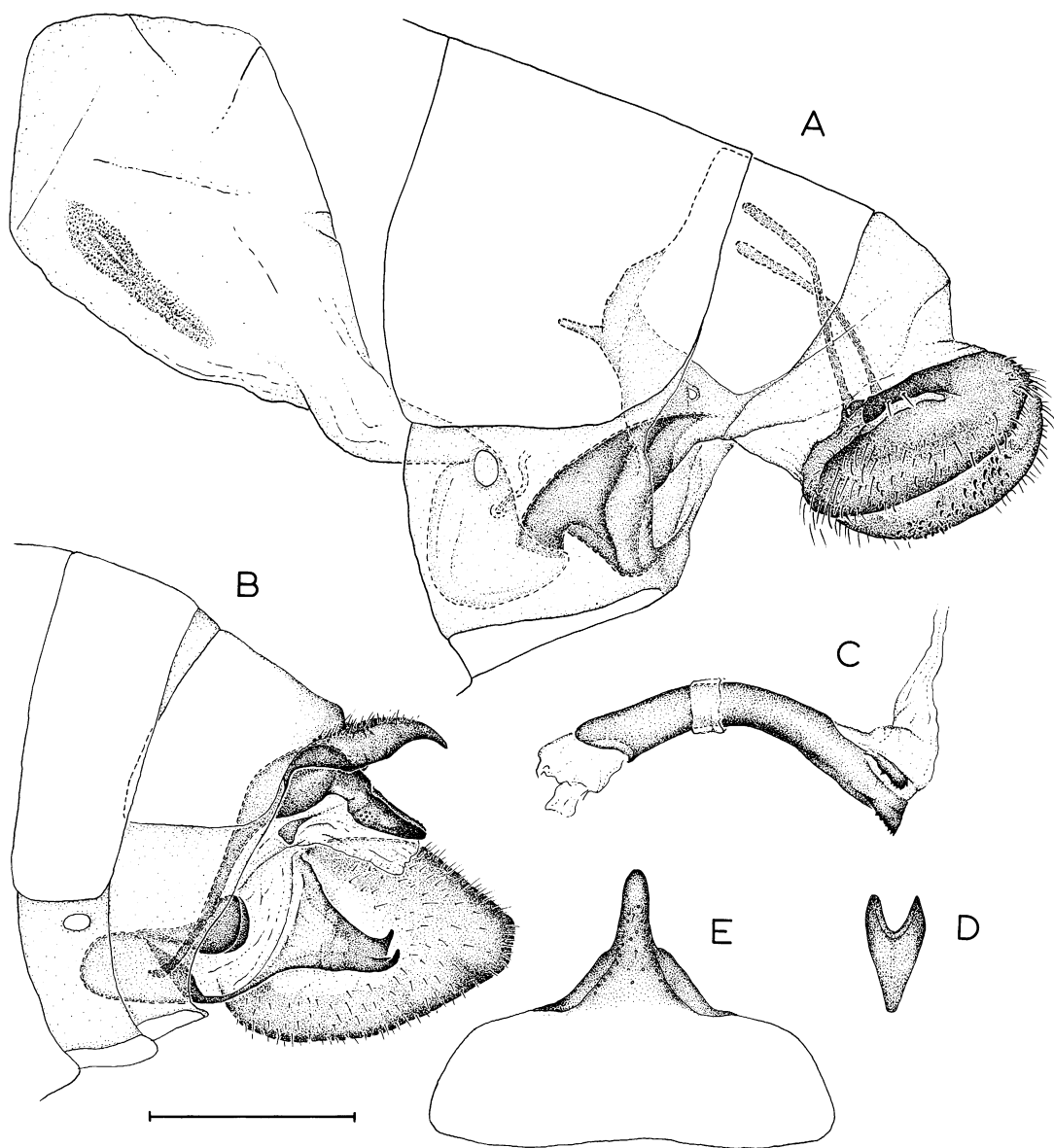
Fig. 44.   Male and female genitalia of *Meandrusa payeni* (Boisduval). For scale length and key to structures refer to figure 20.
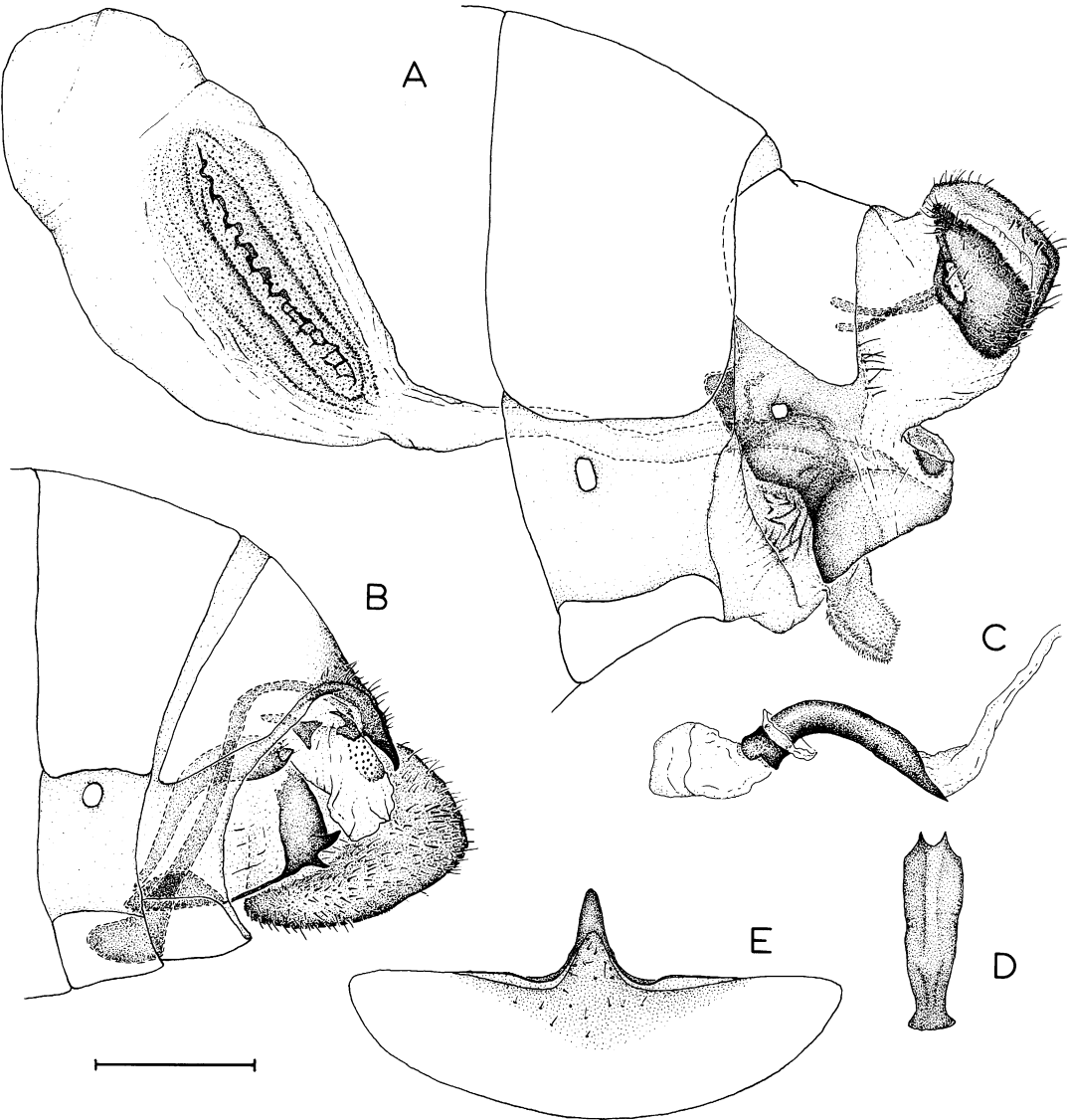
Fig. 45. Male and female genitalia of *Battus polydamus* (L.). For scale length and key to structures refer to figure 20.
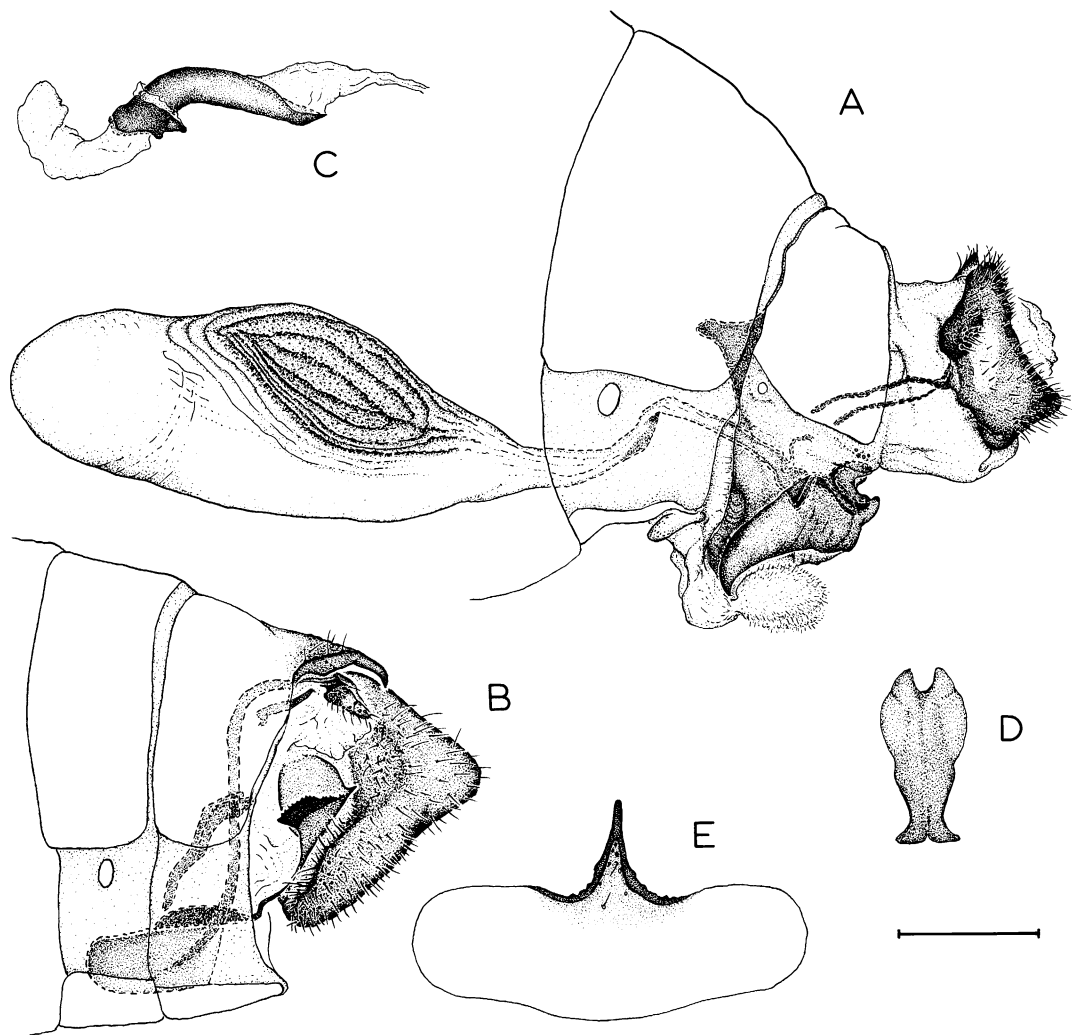
Fig. 46.   Male and female genitalia of *Battus belus* (Cramer). For scale length and key to structures refer to figure 20.
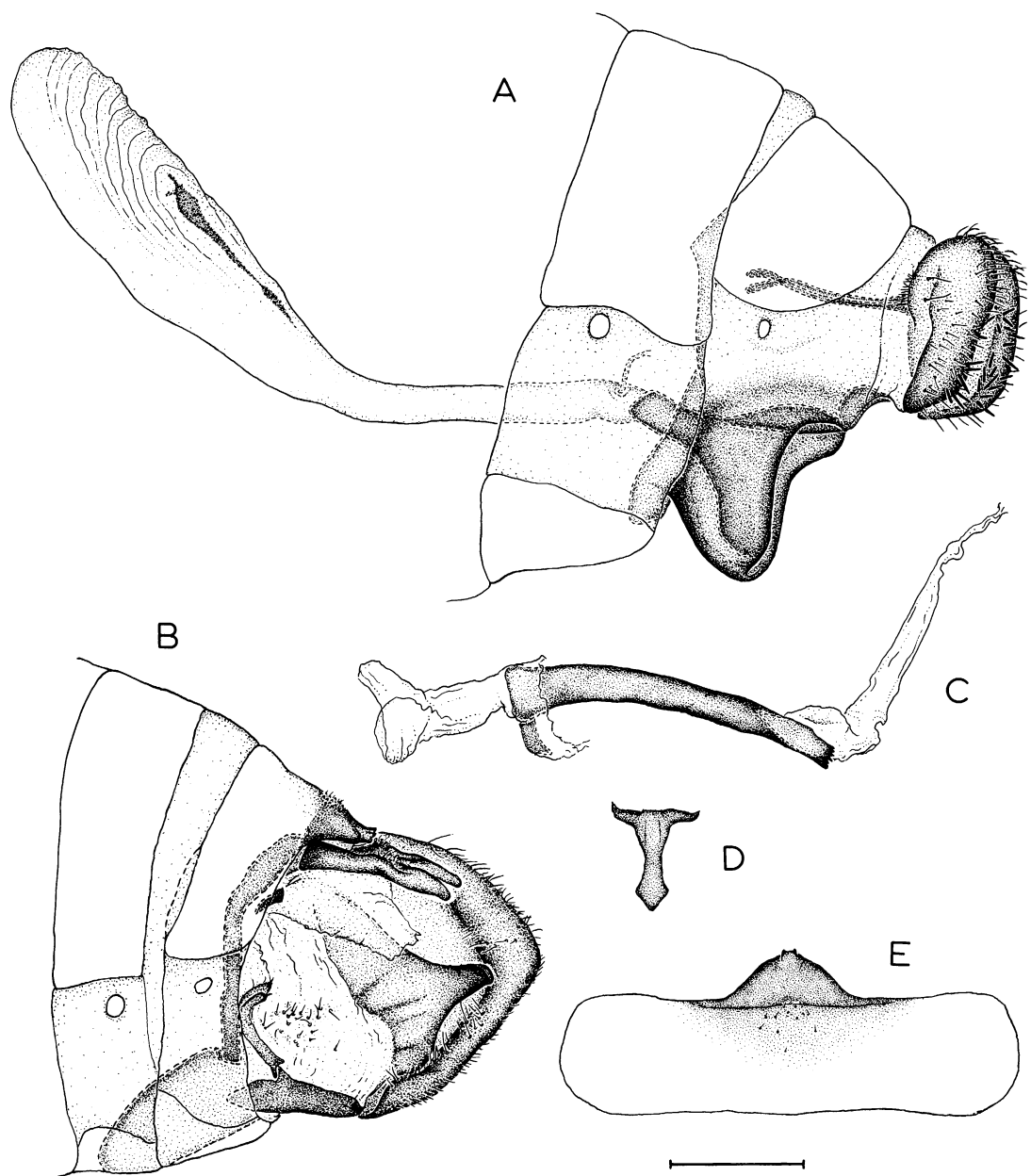
Fig. 47. Male and female genitalia of *Pharmacophagus antenor* (Drury). For scale length and key to structures refer to figure 20.
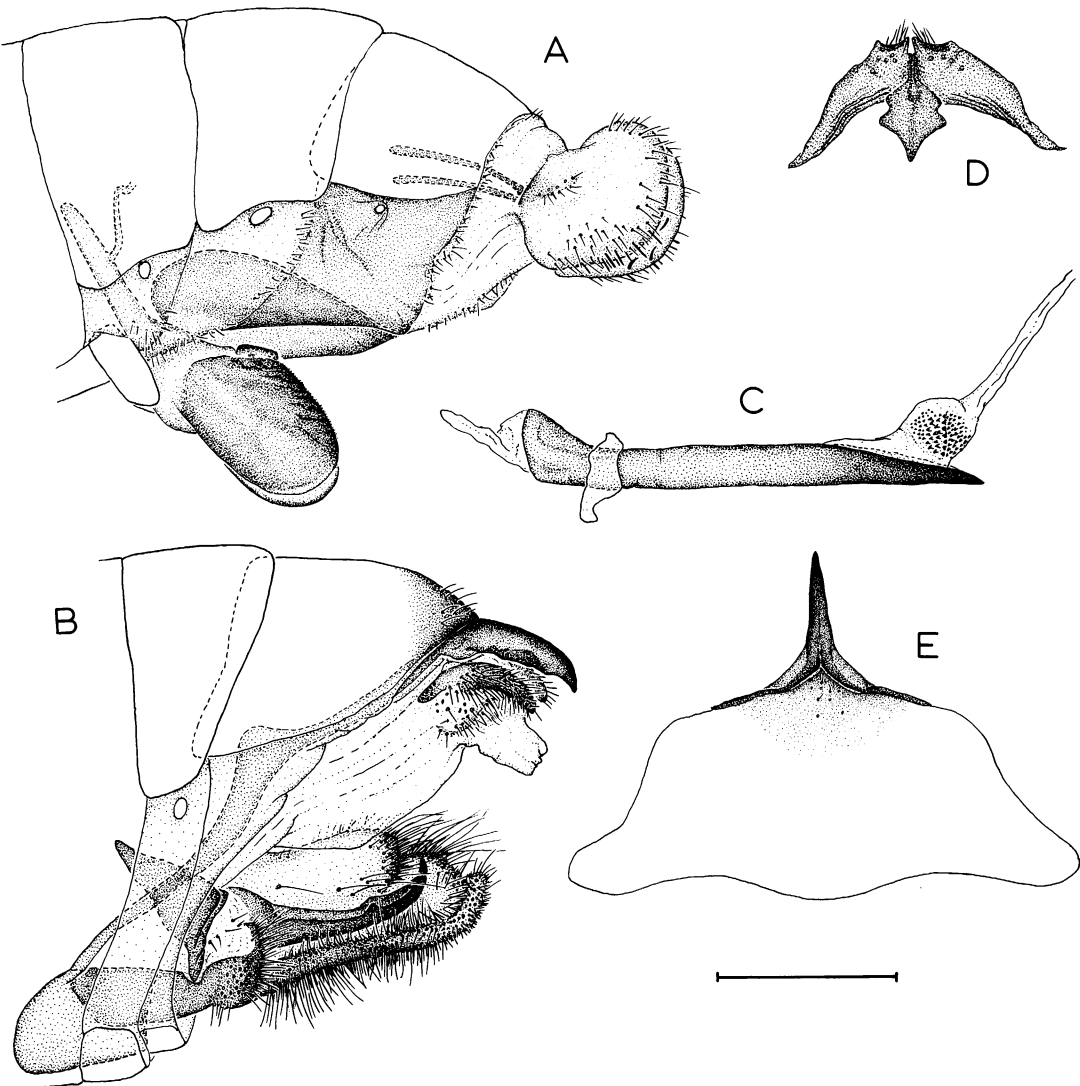
Fig. 48.   Male and female genitalia of *Cressida cressida* (Fabricius). For scale length and key to structures refer to figure 20.
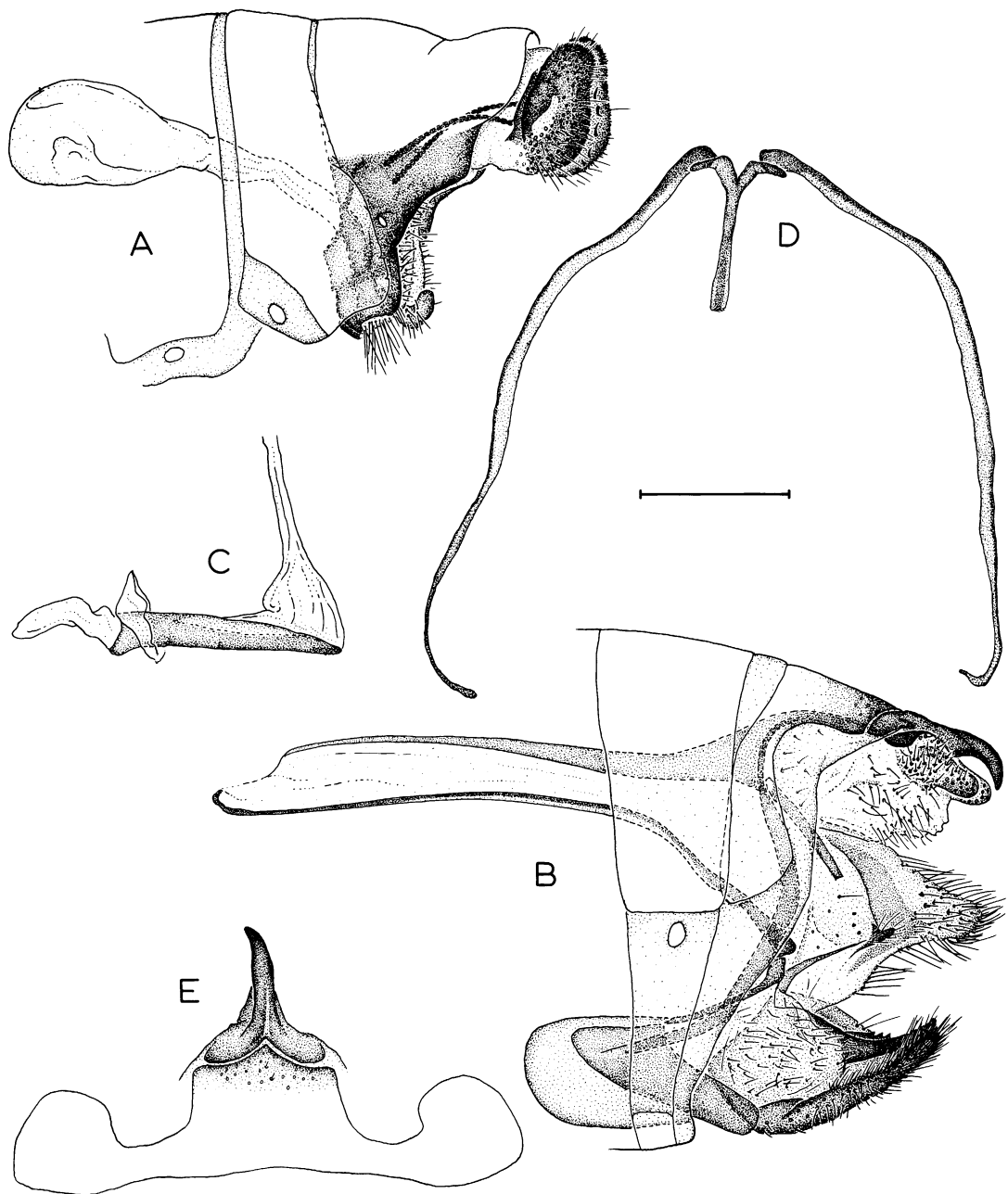
Fig. 49. Male and female genitalia of *Euryades corethrus* (Boisduval). For scale length and key to structures refer to figure 20.
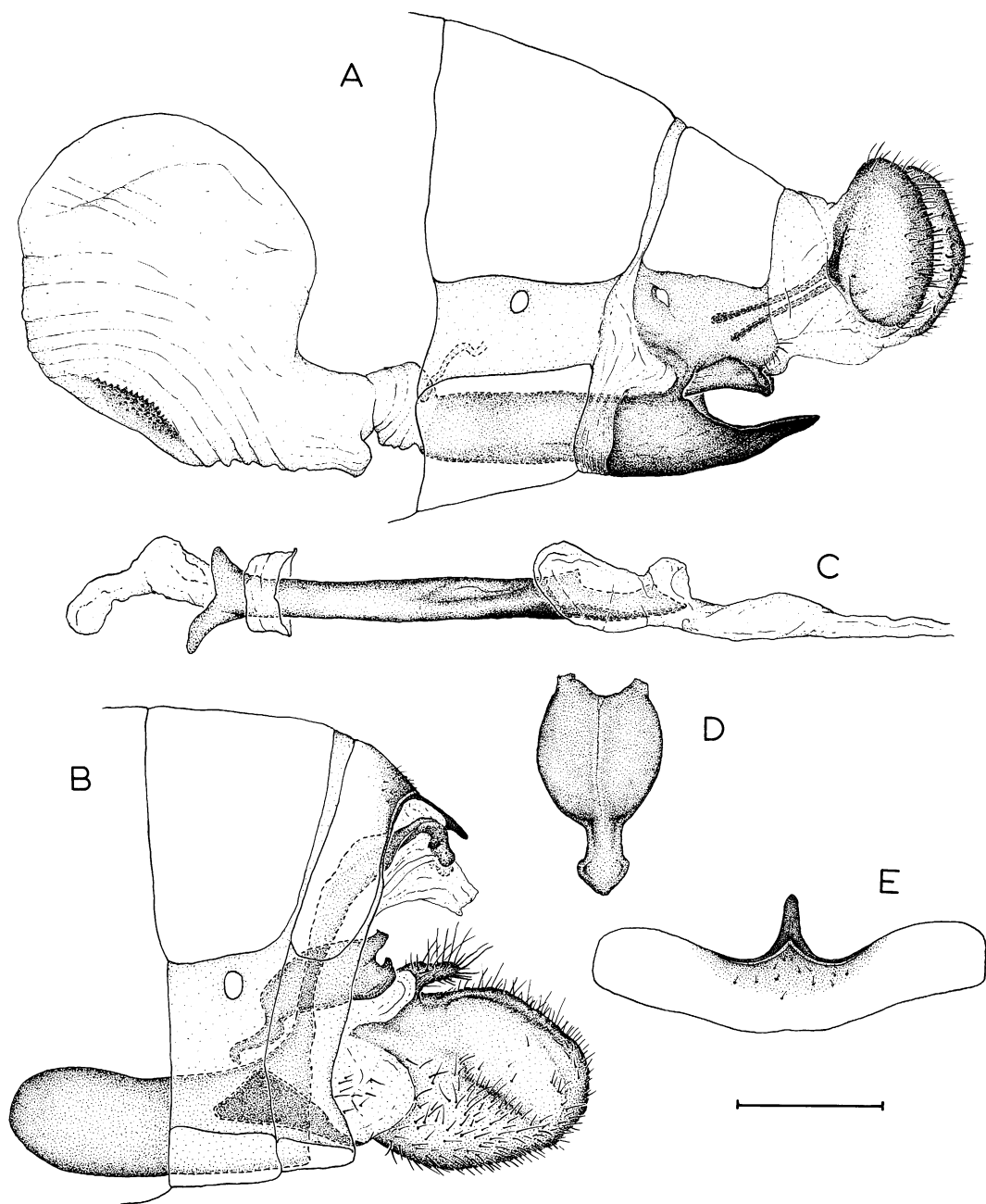
Fig. 50. Male and female genitalia of *Pachliopta* (*Losaria*) *neptunus* (Guérin-Méneville). For scale length and key to structures refer to figure 20.
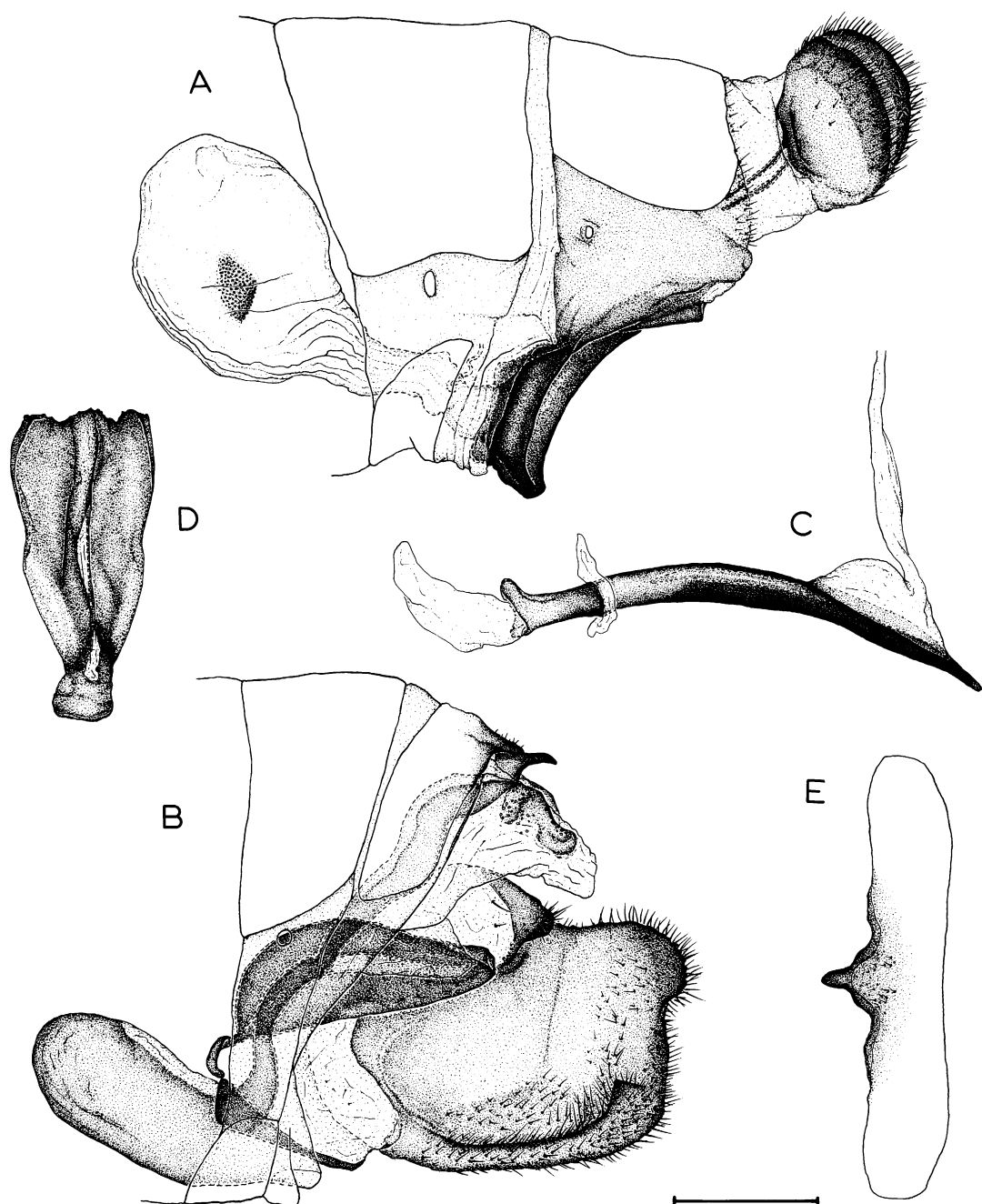
Fig. 51. Male and female genitalia of *Pachliopta* (*Losaria*) *palu* (Martin). For scale length and key to structures refer to figure 20.
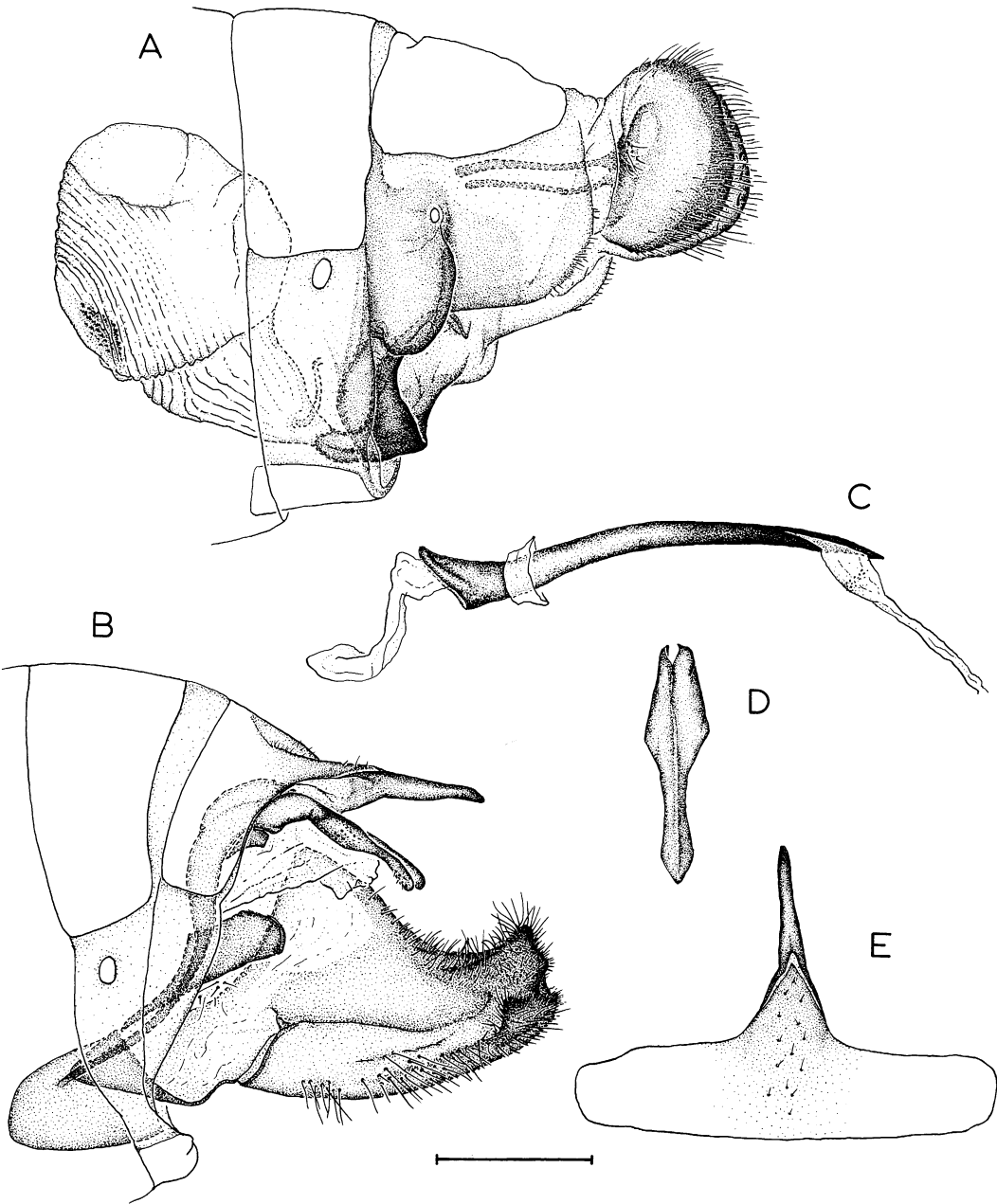
Fig. 52. Male and female genitalia of *Pachliopta* (*Losaria*) *coon* (Fabricius). For scale length and key to structures refer to figure 20.
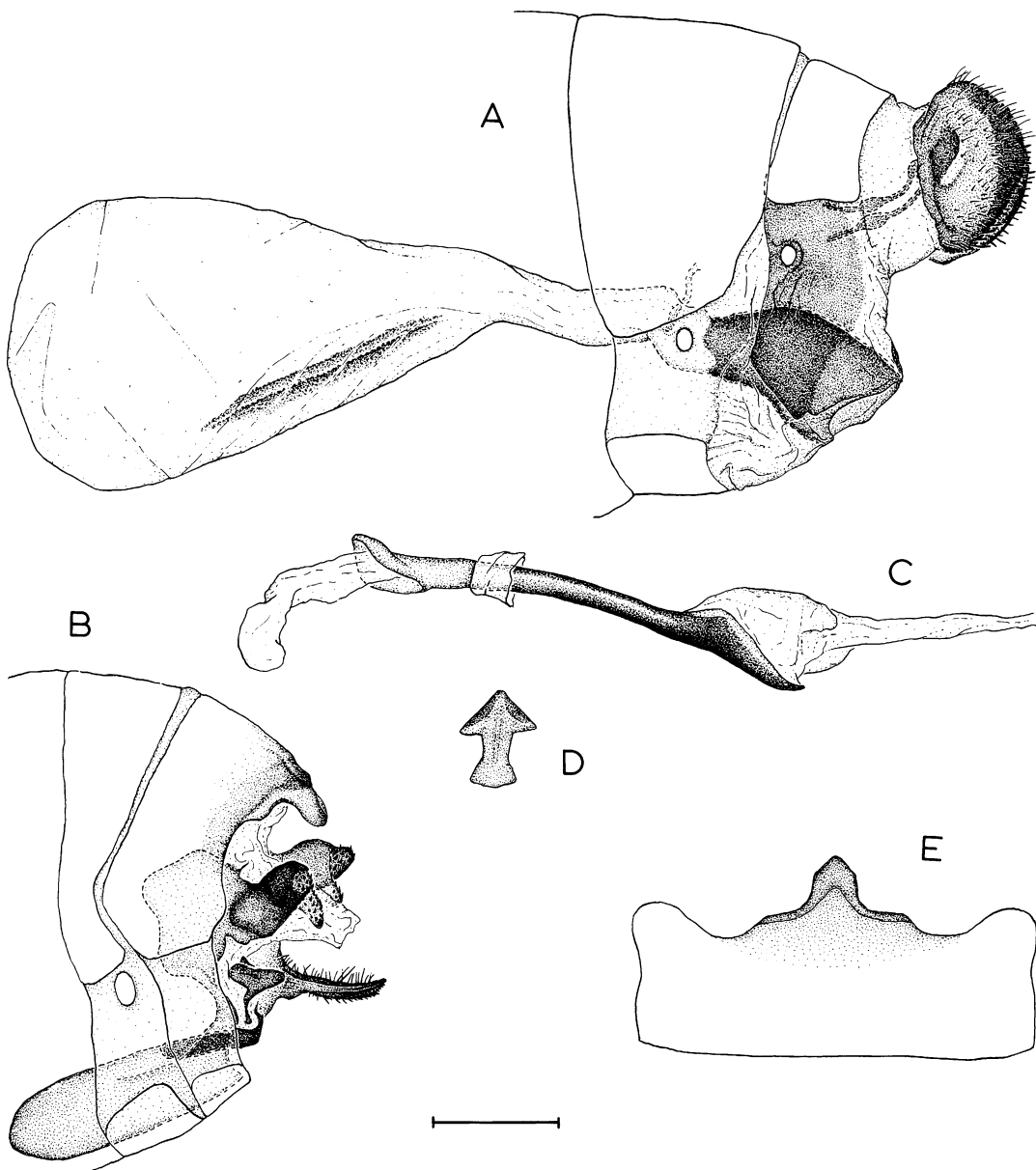
Fig. 53. Male and female genitalia of *Pachliopta* (*Pachliopta*) *hector* (L.). For scale length and key to structures refer to figure 20.
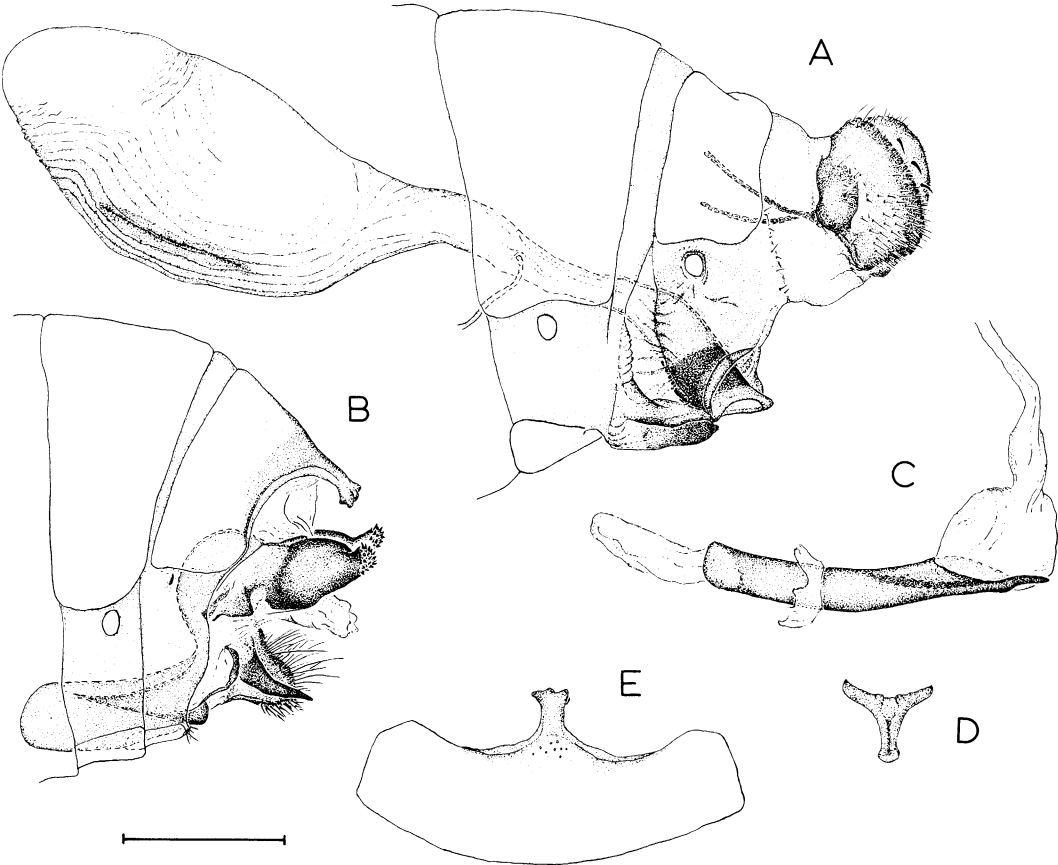
Fig. 54. Male and female genitalia of *Pachliopta* (*Pachliopta*) *aristolochiae* (Fabricius). For scale length and key to structures refer to figure 20.
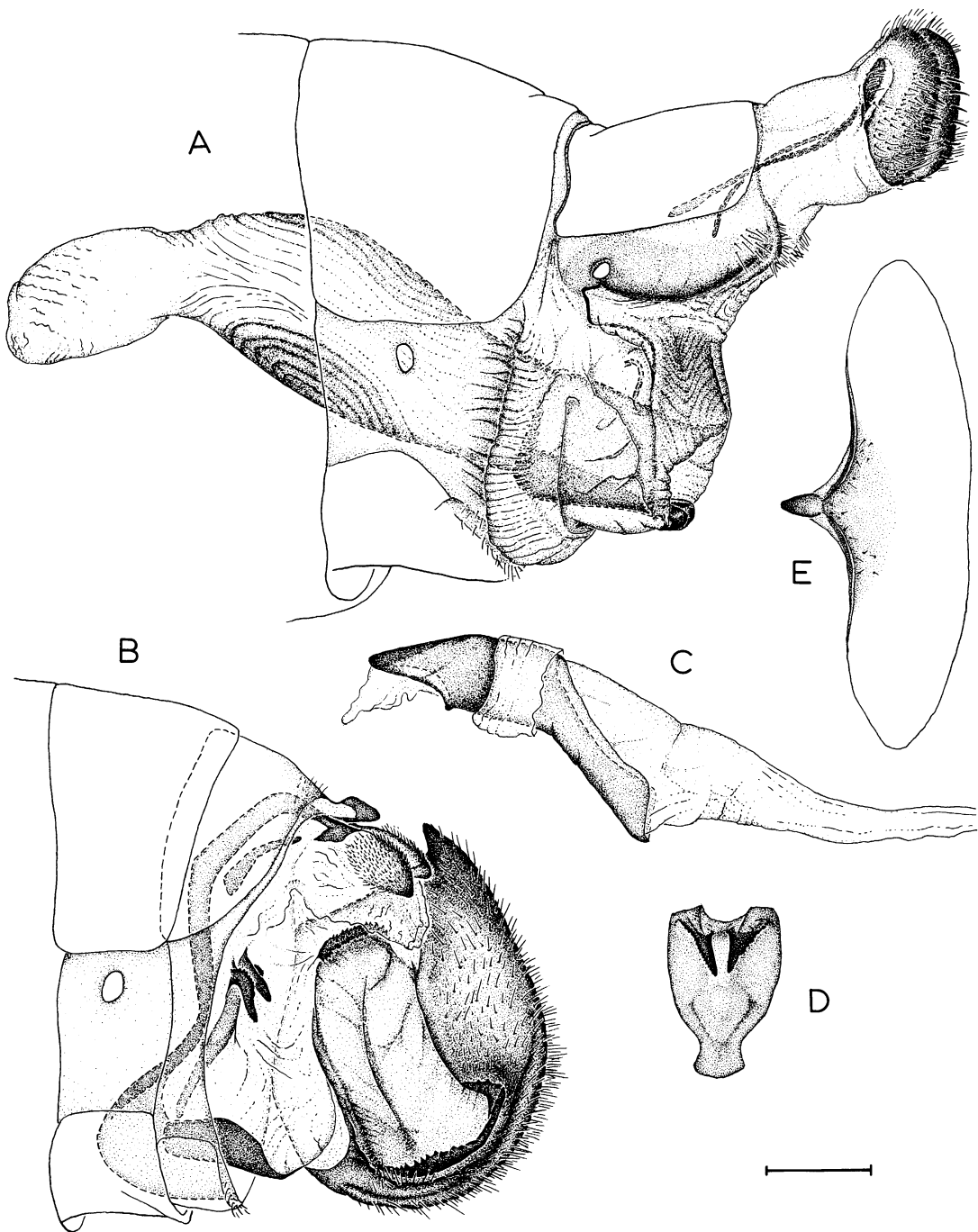
Fig. 55. Male and female genitalia of *Troides* (*Trogonoptera*) *brookiana* (Wallace). For scale length and key to structures refer to figure 20.
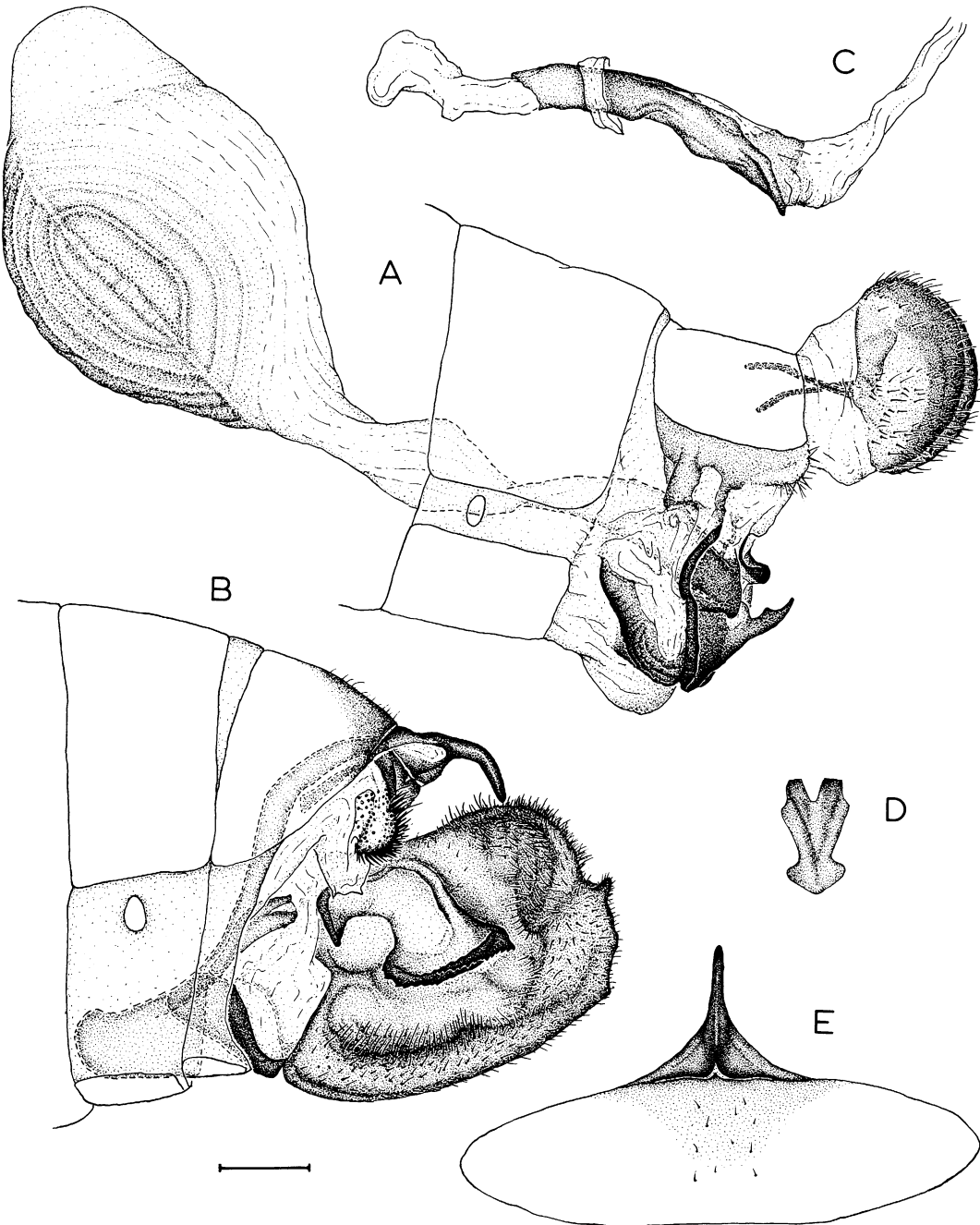
Fig. 56.   Male and female genitalia of *Troides* (*Troides*) *hypolitus* (Cramer). For scale length and key to structures refer to figure 20.
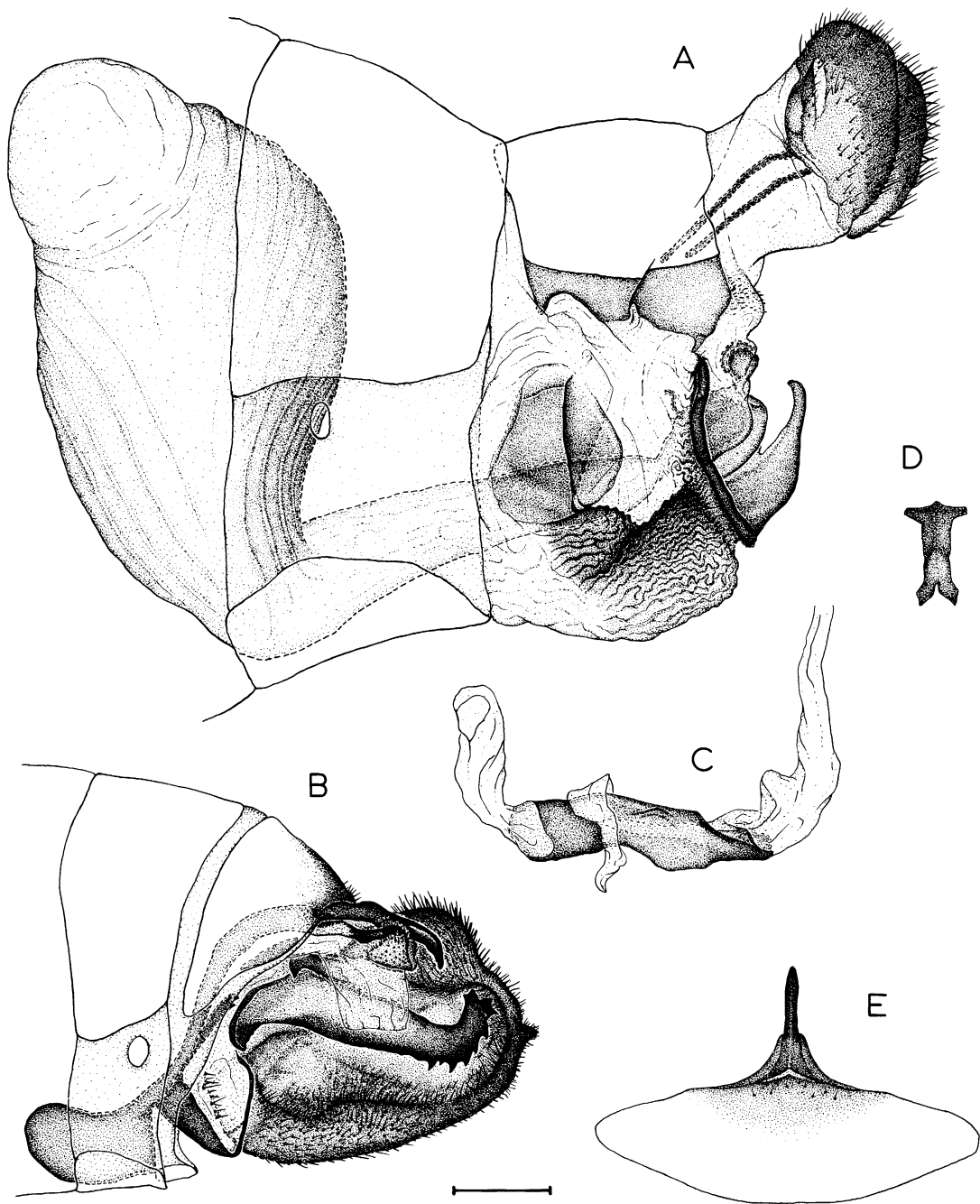
Fig. 57.   Male and female genitalia of *Troides* (*Troides*) *aeacus* (C. and R. Felder). For scale length and key to structures refer to figure 20.
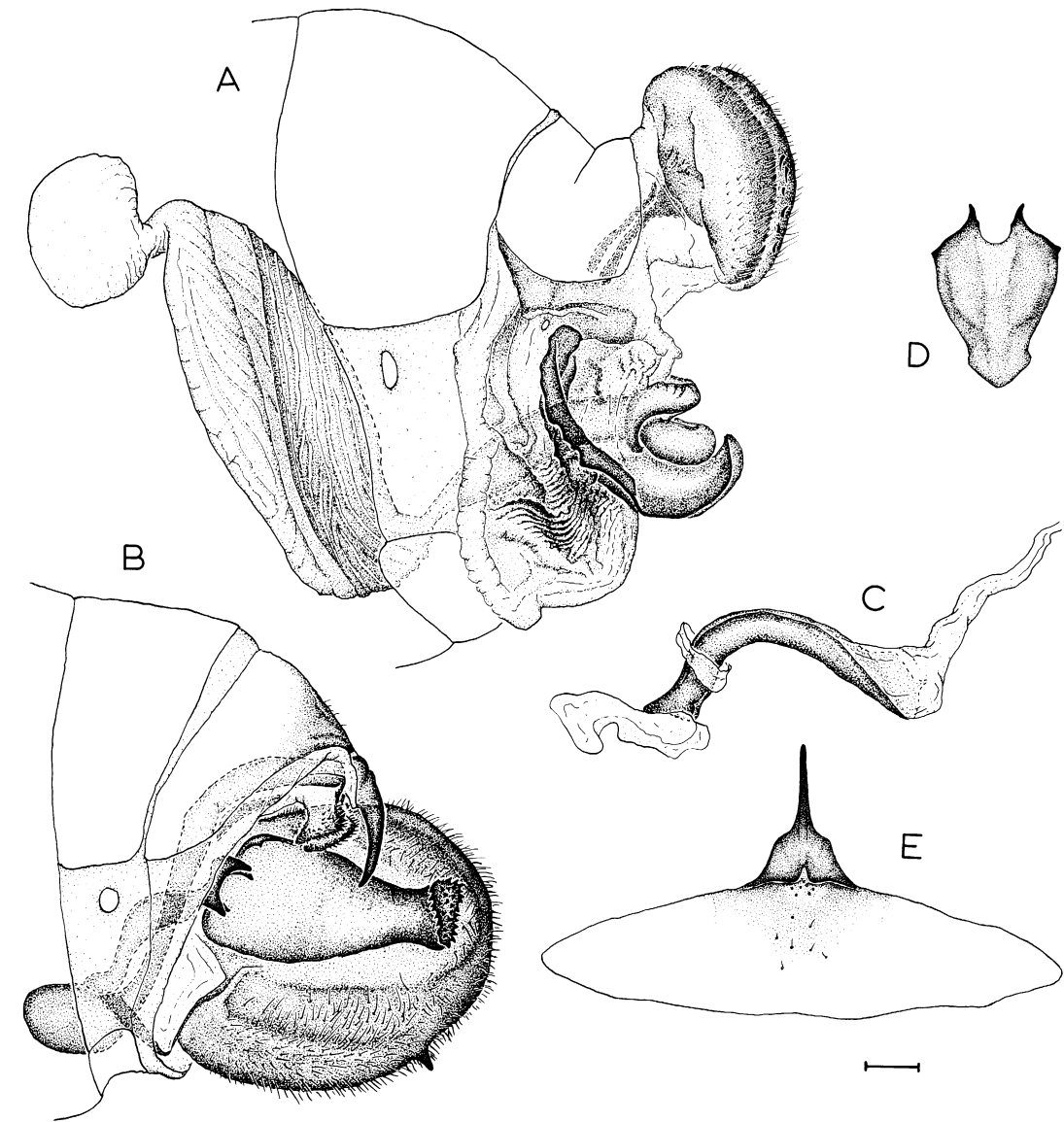
Fig. 58.   Male and female genitalia of *Troides* (*Troides*) *priamus* (L.). For scale length and key to structures refer to figure 20.
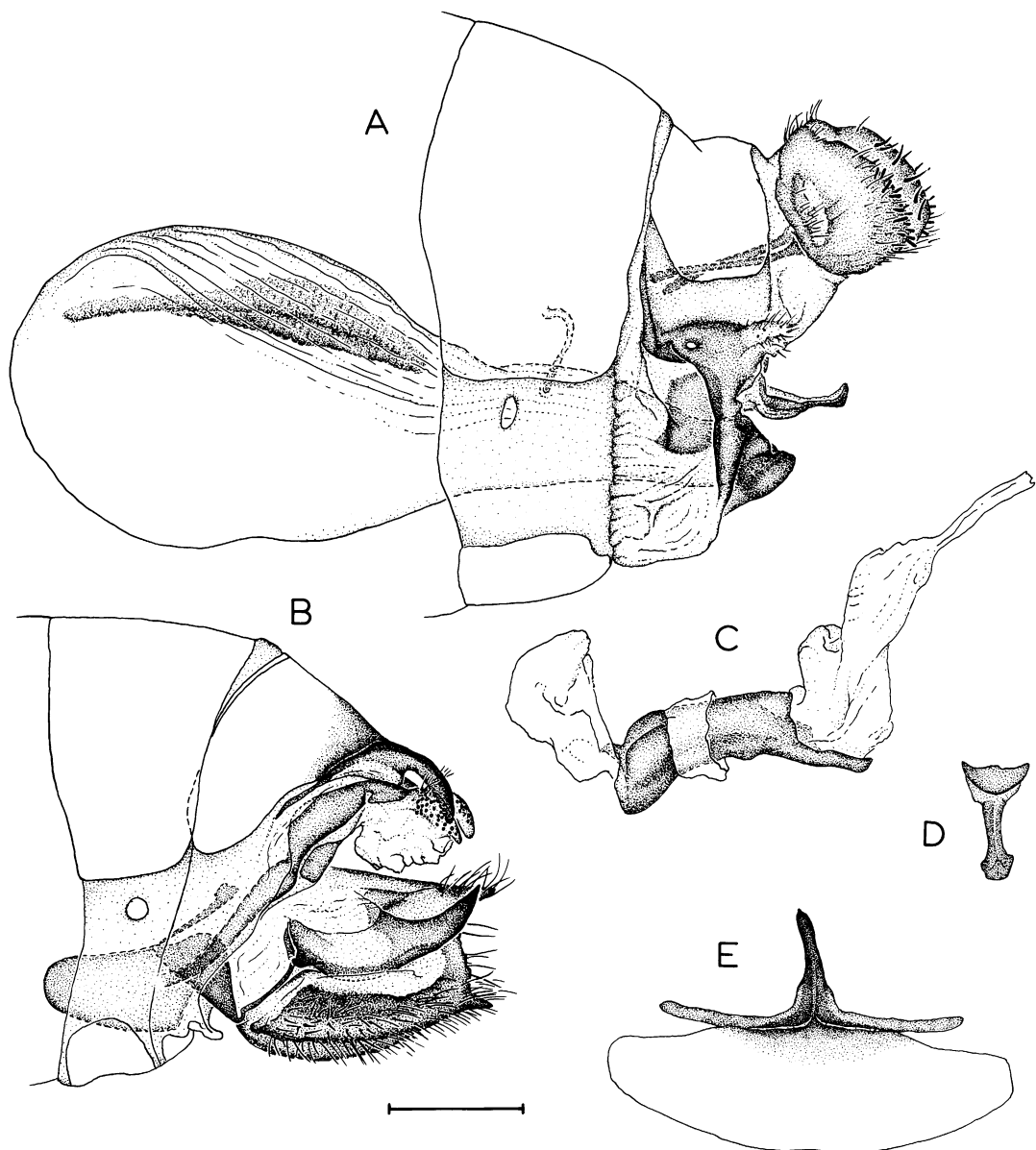
Fig. 59.   Male and female genitalia of *Parides* (*Atrophaneura*) *varuna* (White). For scale length and key to structures refer to figure 20.
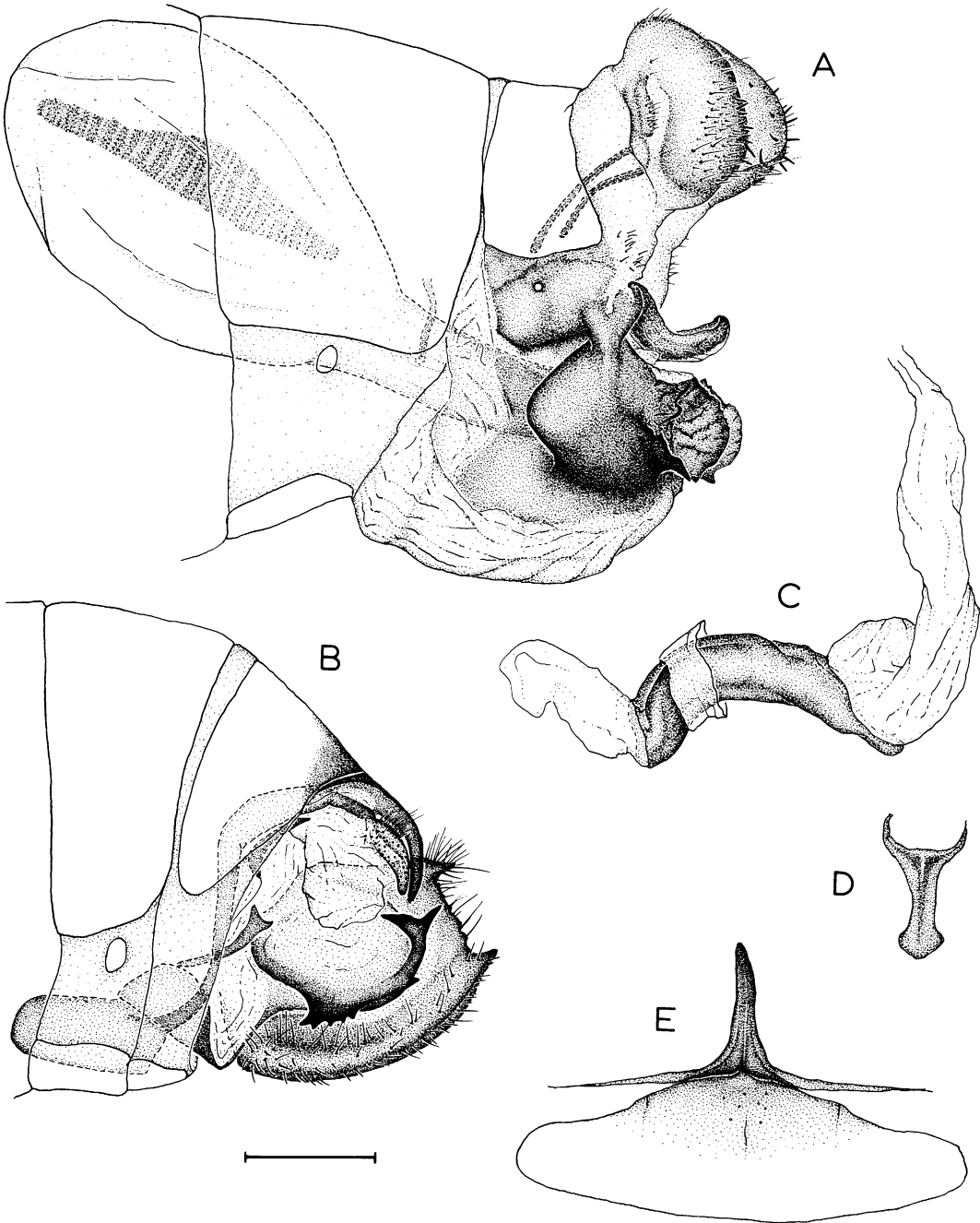
Fig. 60.   Male and female genitalia of *Parides* (*Atrophaneura*) *horishanus* (Matsumura). For scale length and key to structures refer to figure 20.
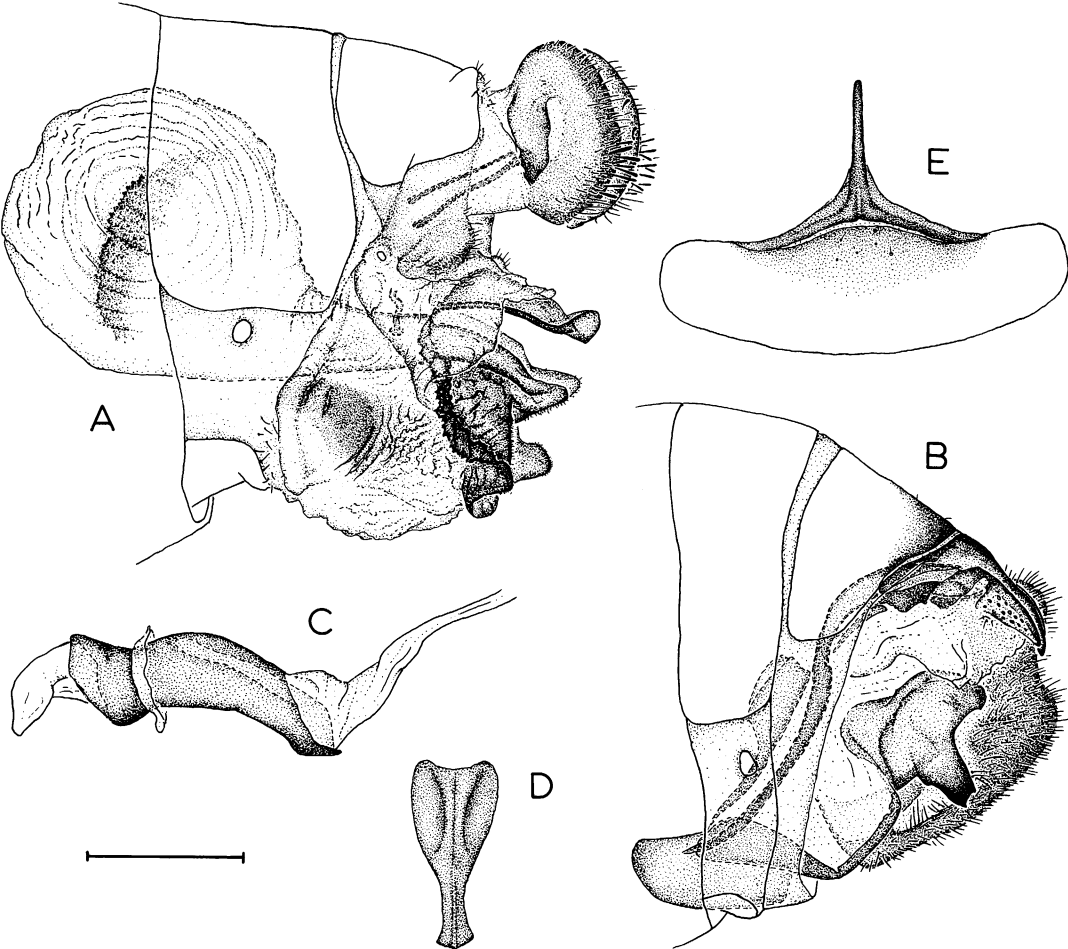
Fig. 61.   Male and female genitalia of *Parides* (*Parides*) *photinus* (Doubleday). For scale length and key to structures refer to figure 20.

Fig. 62.   Male and female genitalia of *Parides* (*Parides*) *lysander* (Cramer). For scale length and key to structures refer to figure 20.

Fig. 63. Male and female genitalia of *Parides* (*Parides*) *agavus* (Drury). For scale length and key to structures refer to figure 20.

Fig. 64.   Male and female genitalia of *Parides* (*Panosmia*) *latreillei* (Donovan). For scale length and key to structures refer to figure 20.

Fig. 65. Male and female genitalia of *Parides* (*Panosmia*) *polyeuctes* (Doubleday). For scale length and key to structures refer to figure 20.
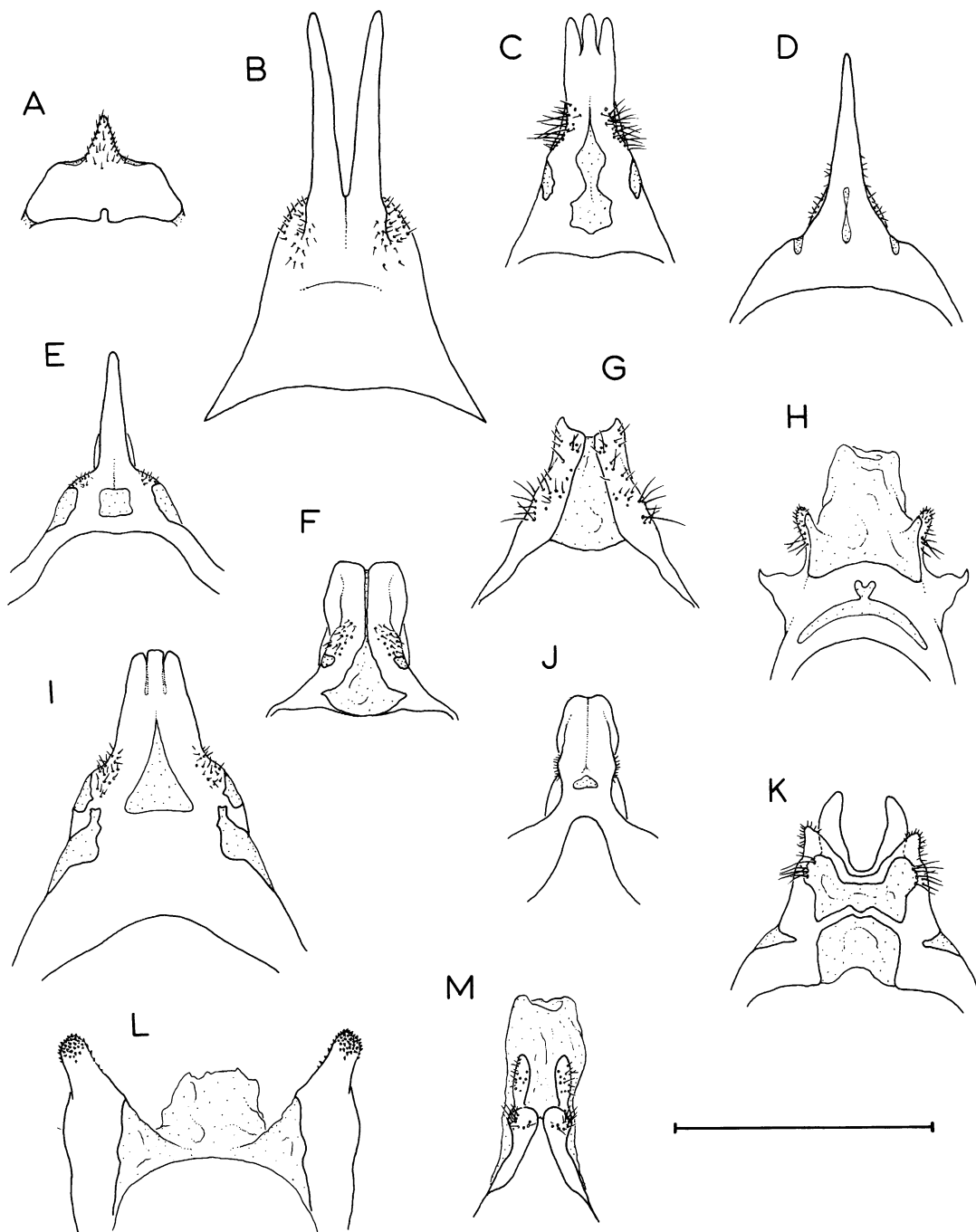
Fig. 66 [Characters 9, 140].   Dorsal view of tegumen (= 9th tergite) and uncus. (Anal tube shown in figs. H, L, and M.) A. *Baronia brevicornis*; B. *Luehdorfia japonica*; C. *Eurytides thyastes*; D. *Eurytides celadon*; E. *Protographium leosthenes*; F. *Iphiclides podalirius*; G. *Lamproptera curius*; H. *Graphium (Pazala) eurous*; I. *Teinopalpus imperialis*; J. *Meandrusa payeni*; K. *Papilio scamander*; L. *Pachliopta (Pachliopta) polyphontes*; M. *Battus polydamus*. Scale line = 2 mm.
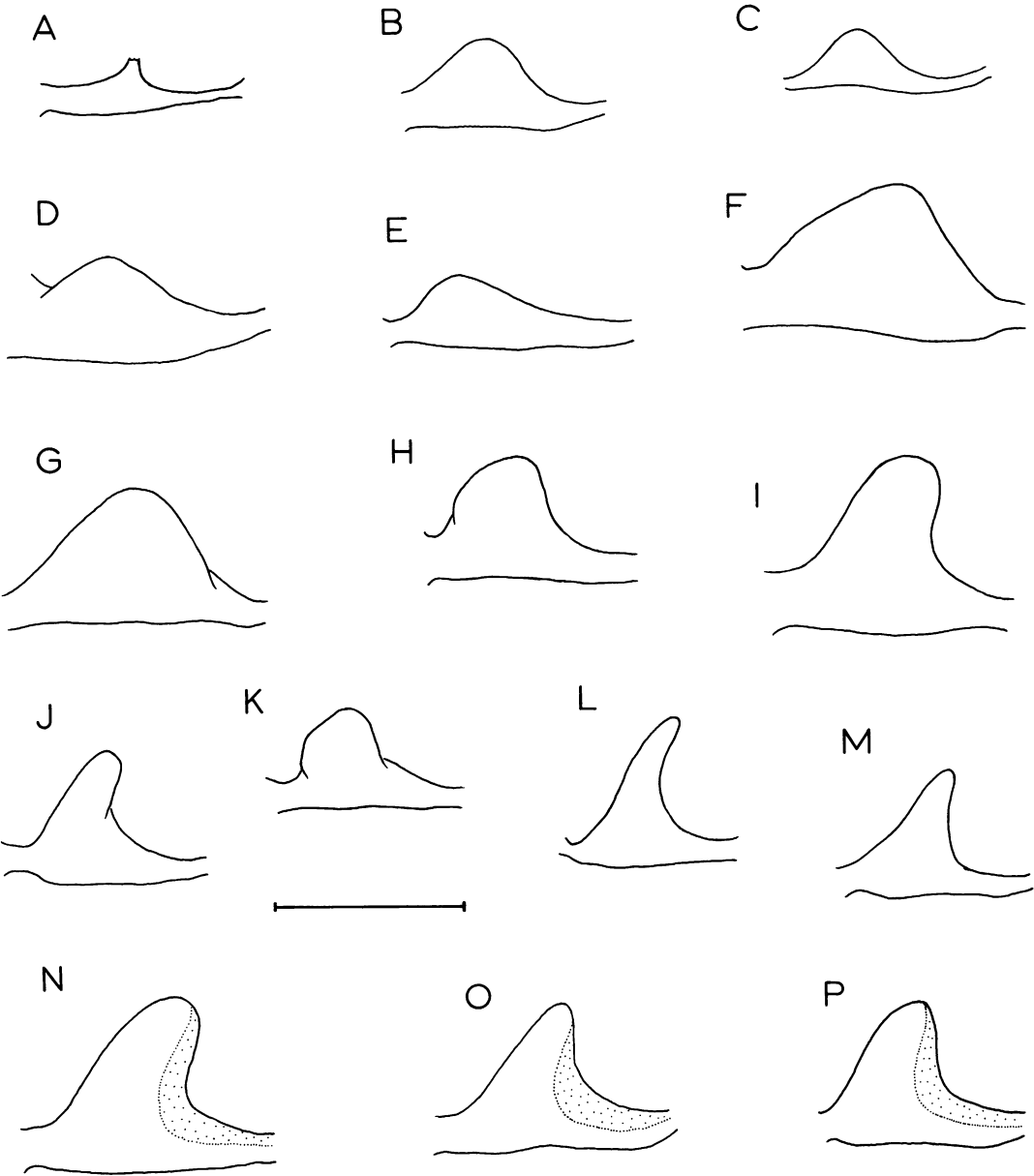
Fig. 67 [Characters 45, 95].   Left (female) tentorial crests of species in the Papilionidae; anterior at left. A. *Baronia brevicornis*; B. *Luehdorfia japonica*; C. *Archon apollinus*; D. *Papilio victorinus*; E. *Parides (Panosmia) latreillei*; F. *Meandrusa sciron*; G. *Teinopalpus imperialis*; H. *Eurytides epidaus*; I. *Eurytides telesilaus*; J. *Protographium leosthenes*; K. *Iphiclides podalirius*; L. *Lamproptera meges*; M. *Graphium (Pazala) mandarinus*; N. *Graphium (Graphium) euryplus*; O. *Graphium (Arisbe) philonoe*; P. *Graphium (Pathysa) nomius*. Scale line = 1 mm.
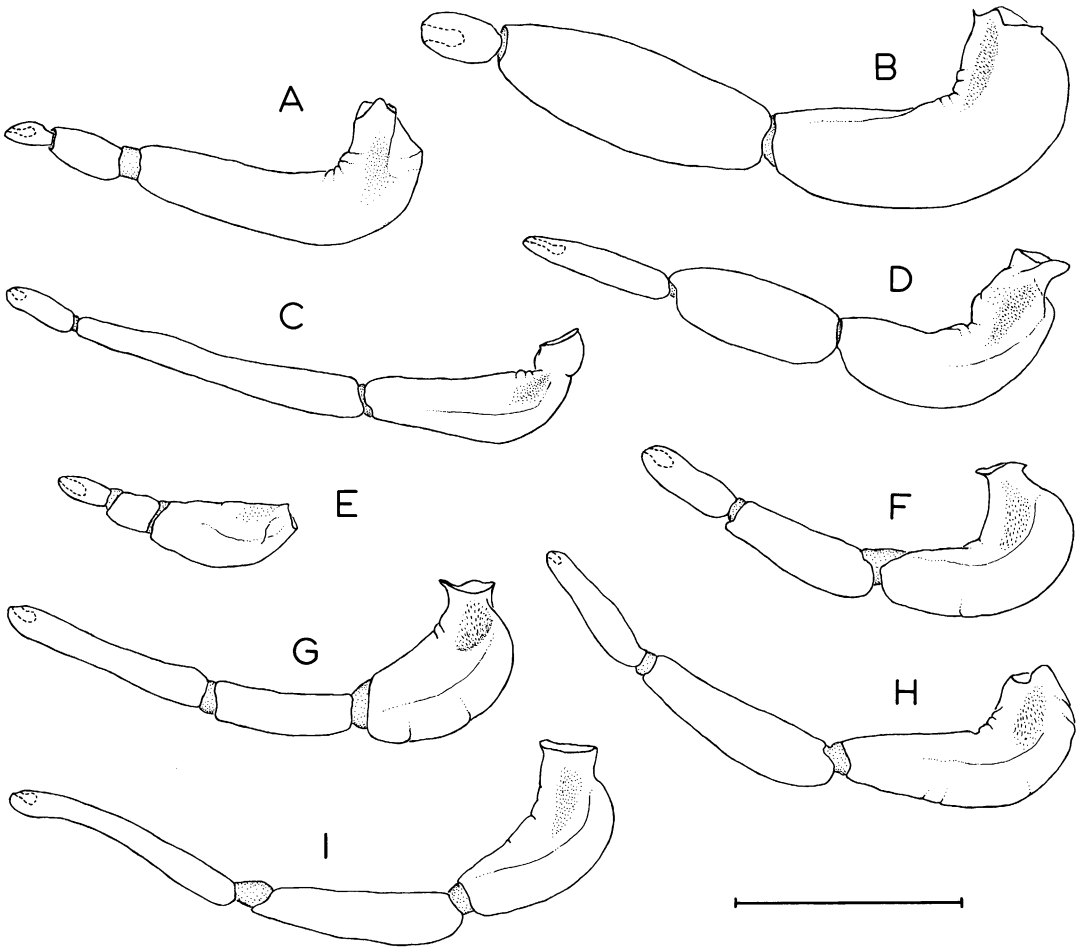
Fig. 68 [Characters 12, 35].   Right female labial palpus. A. *Dismorphia amphione*; B. *Colias philodice*; C. *Euchloe hyantis*; D. *Pieris rapae*; E. *Baronia brevicornis*; F. *Archon apollinus*; G. *Parnassius szechenyii*; H. *Luehdorfia japonica*; I. *Parnalius polyxena*. Scale line = 1 mm.
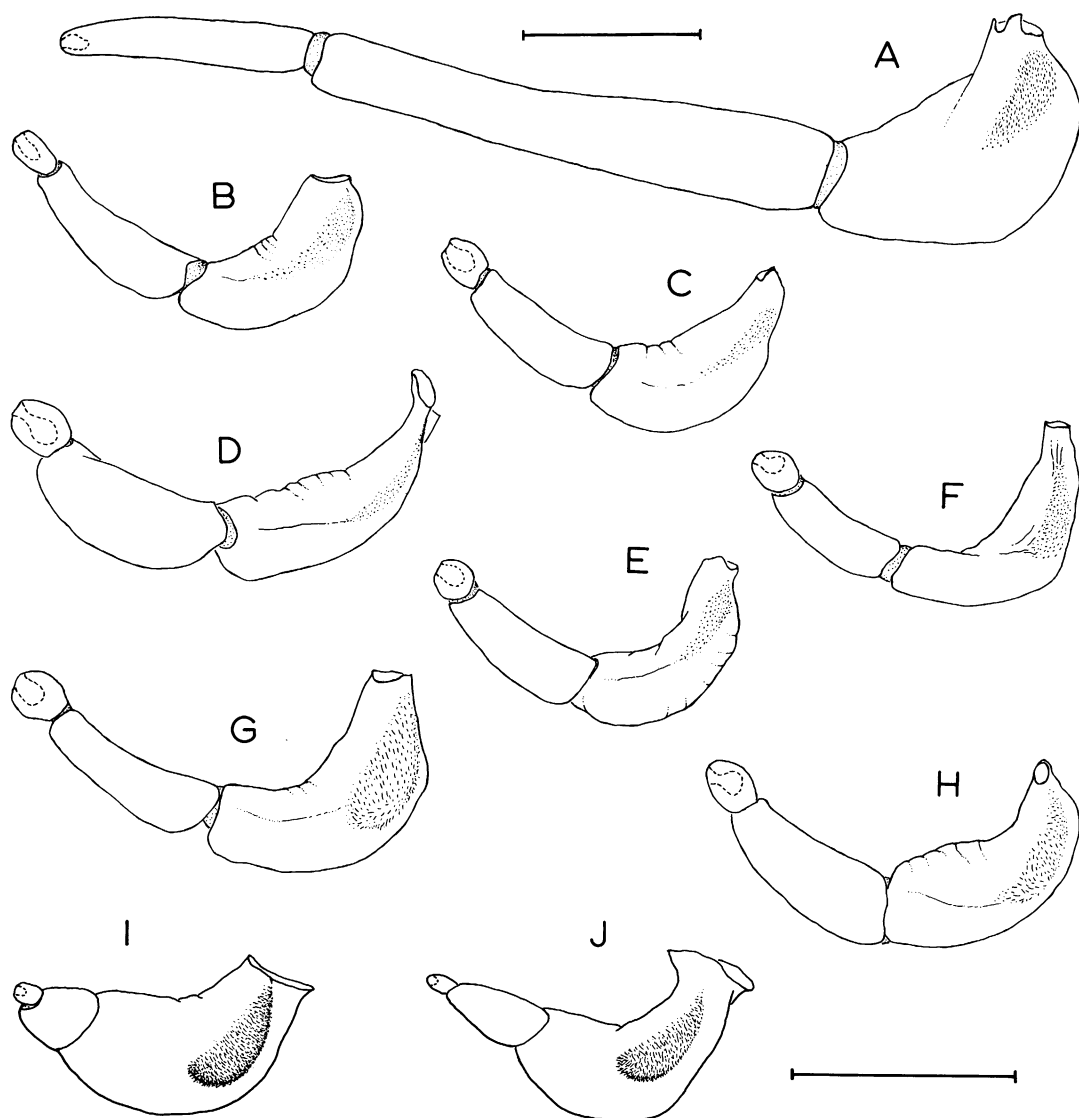
Fig. 69 [Characters 12, 35]. Right female labial palpus. A. *Teinopalpus imperialis* (scale line = 1 mm); B. *Iphiclides podalirius*; C. *Protographium leosthenes*; D. *Graphium (Graphium) euryplus*; E. *Graphium (Arisbe) philonoe*; F. *Graphium (Pathysa) nomius*; G. *Eurytides telesilaus*; H. *Eurytides epidaus*; I. *Lamproptera meges* (male); J. *Lamproptera meges* (female). Scale line = 1 mm.
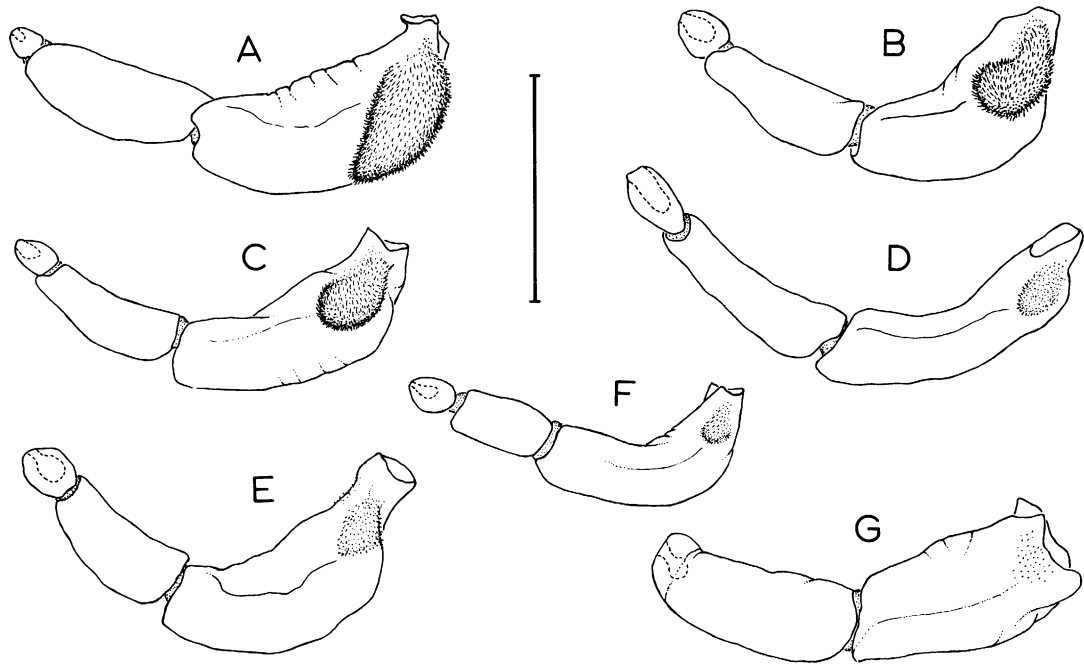
Fig. 70 [Character 35]. Right female labial palpus of Papilionini. A. *Meandrusa sciron*; B. *Papilio victorinus*; C. *Papilio troilus*; D. *Papilio thoas*; E. *Papilio protenor*; F. *Papilio anactus*; G. *Papilio toboroi*.
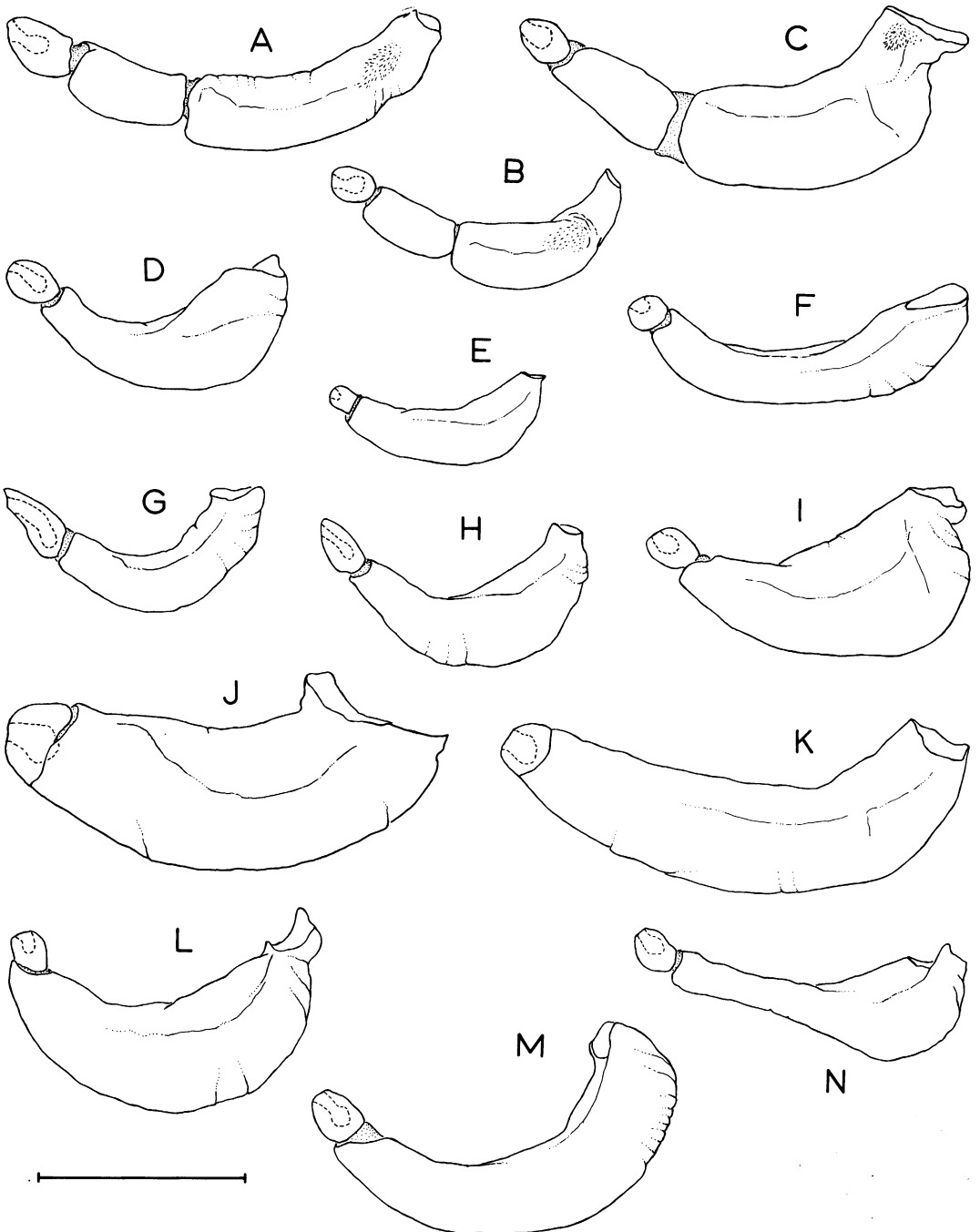
Fig. 71 [Character 113].   Right female labial palpus of Troidini. A. *Battus belus*; B. *Battus polydamus*; C. *Pharmacophagus antenor*; D. *Pachliopta (Pachliopta) aristolochiae*; E. *Pachliopta (Losaria) neptunus*; F. *Pachliopta (Losaria) coon*; G. *Cressida cressida*; H. *Euryades corethrus*; I. *Parides (Panosmia) latreillei*; J. *Troides (Troides) priamus*; K. *Troides (Trogonoptera) brookiana*; L. *Parides (Atrophaneura) varuna*; M. *Parides (Parides) photinus*; N. *Parides (Parides) lysander*. Scale line = 1 mm.
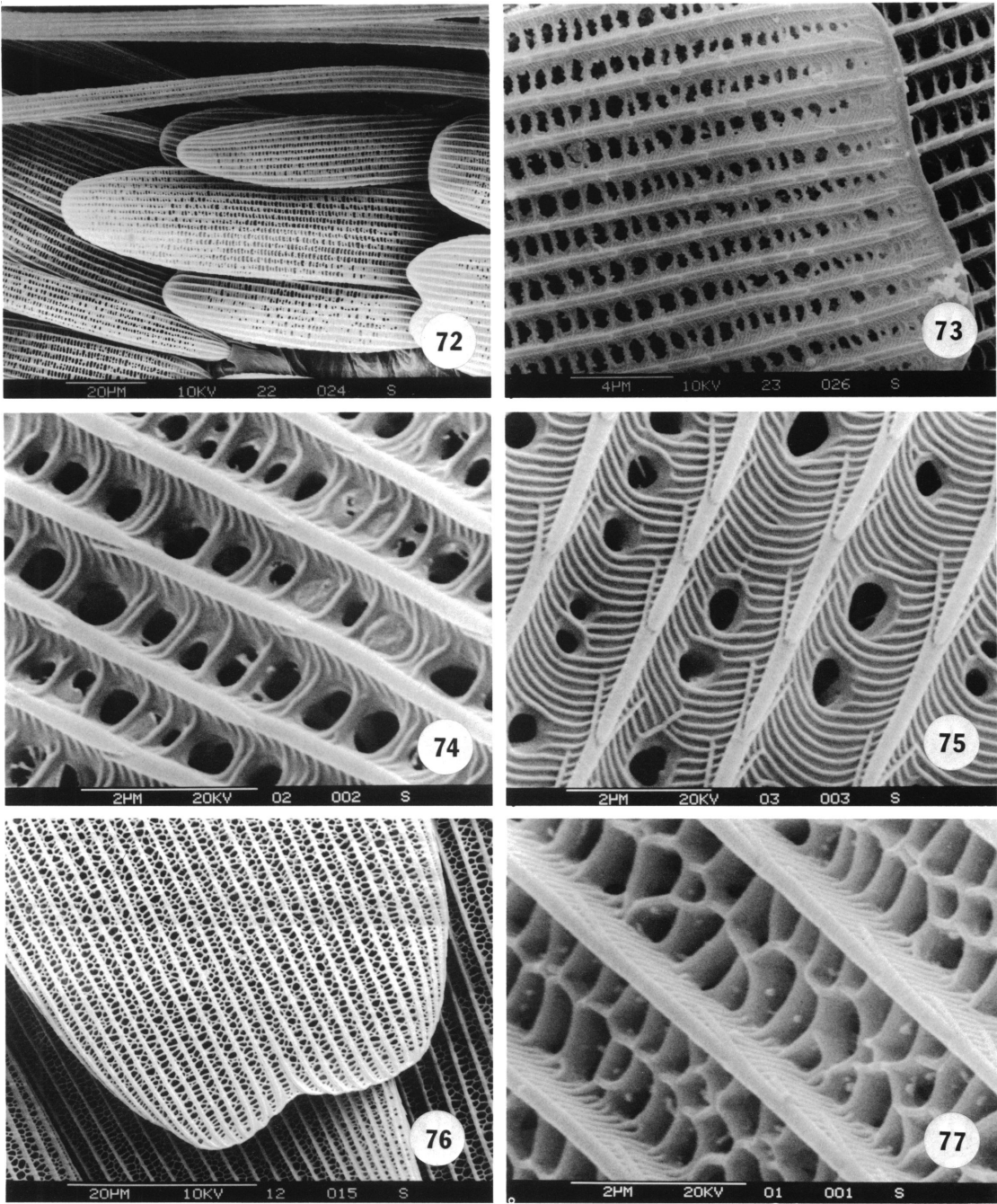
Figs. 72–77 [Character 23].   Male hind wing scales. 72, *Dismorphia amphione* (Pieridae), hind wing margin; 73, *Pieris rapae* (Pieridae), close-up of scale from hind wing margin; 74, *Graphium nomius,* close-up of typical hind wing scale; 75, *Eurytides telesilaus,* close-up of typical hind wing scale; 76, *Papilio troilus,* scales from hind wing margin; 77, *Meandrusa payeni,* close-up of typical hind wing scale.
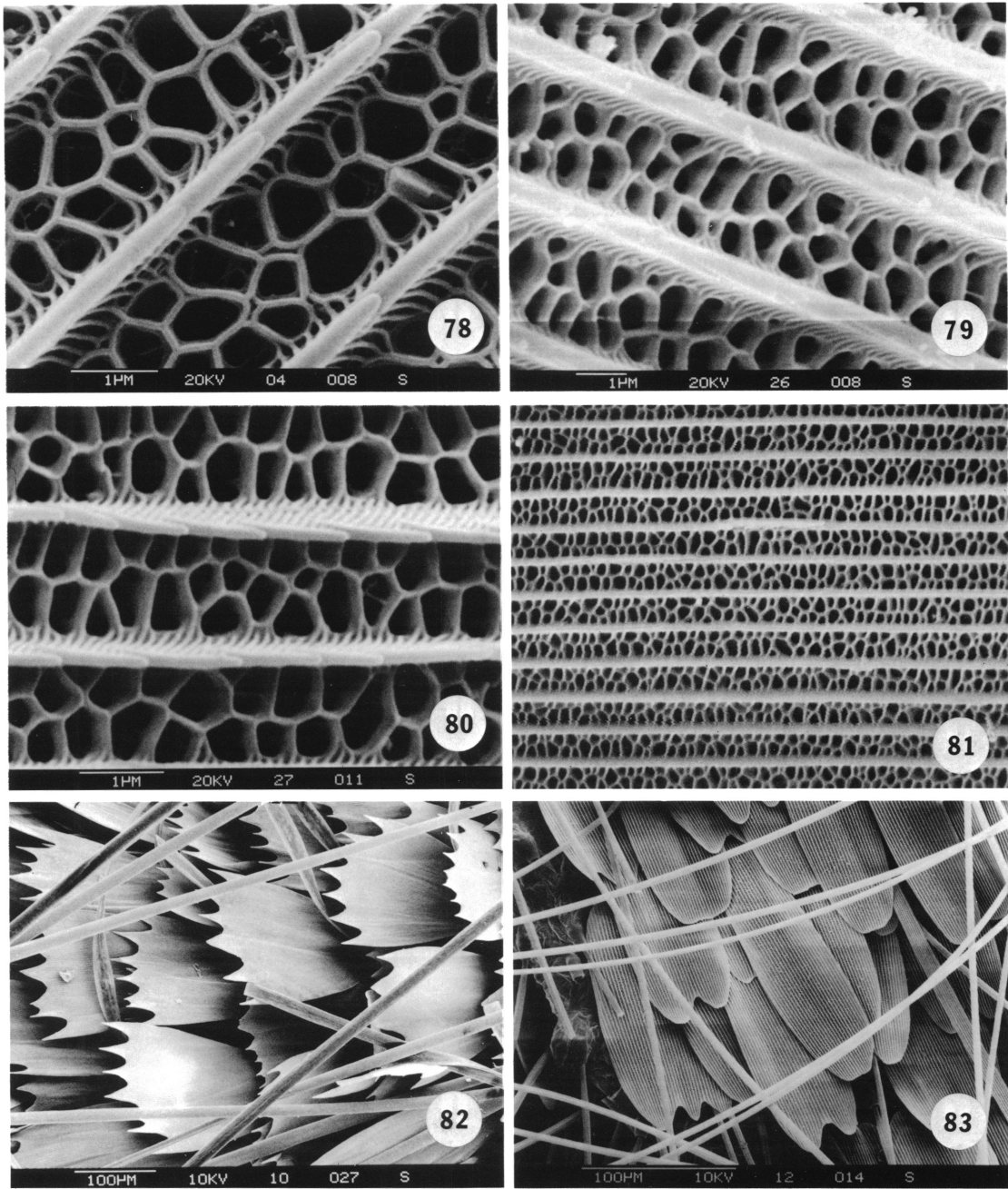
Figs. 78–81 [Character 23].   Typical male hind wing scales. 78, *Pachliopta* (*Losaria*) *neptunus*; 79, *Pachliopta* (*Pachliopta*) *hector*; 80, *Parides* (*Atrophaneura*) *horishanus*; 81, *Teinopalpus imperialis*.
Figs. 82, 83 [Character 18].   Male hind wing margin. 82, *Papilio scamander*; 83, *Papilio troilus*.
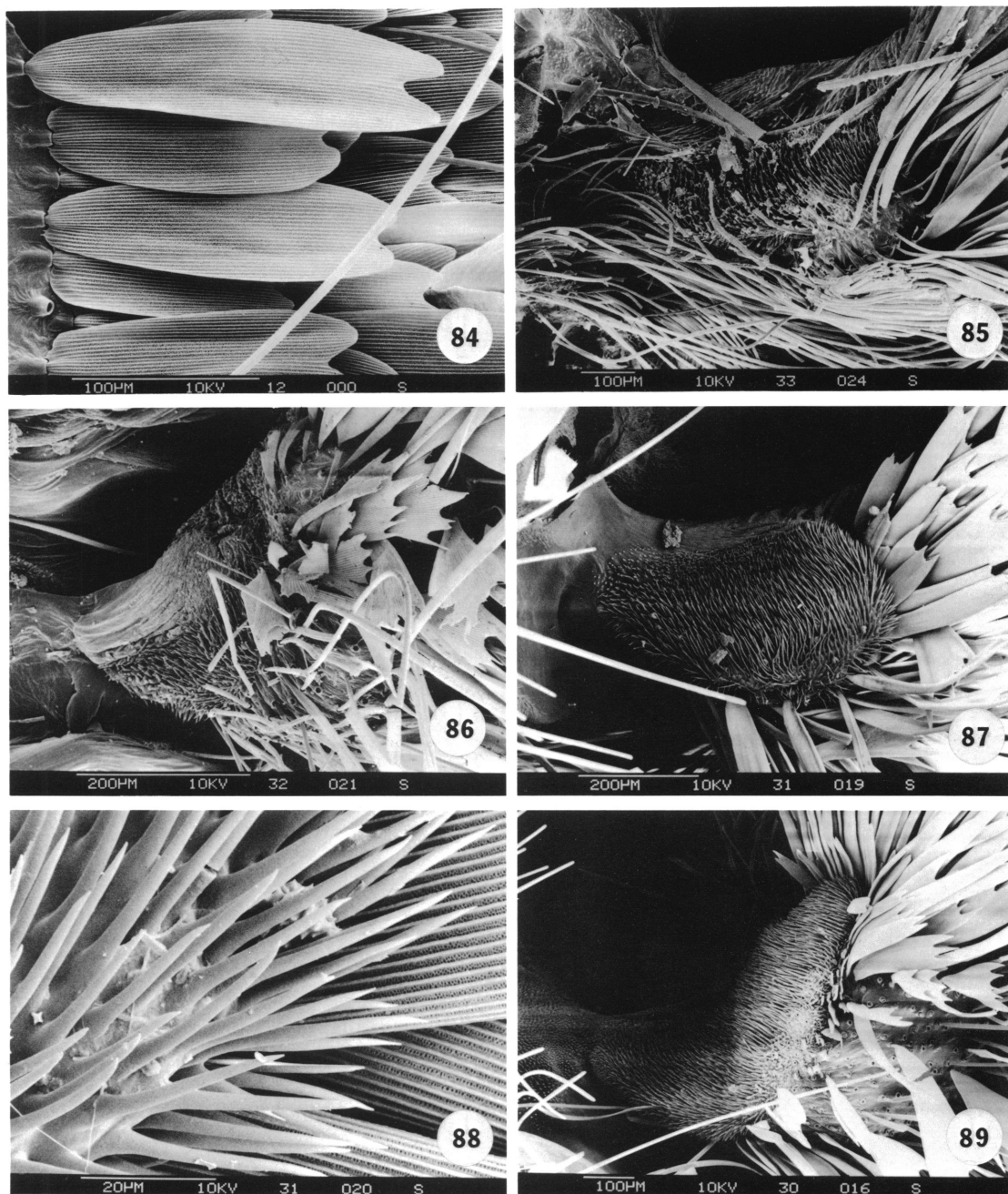
Fig. 84 [Character 18].   Close-up of scales in figure 83 (*Papilio troilus*).
Figs. 85–89 [Character 35].   Basal segment of male left labial palpi (with right palpus removed) showing the basal fleck (Reuter, 1896); proximal portion at right. 85, *Eurytides telesilaus*; 86, *Protographium leosthenes*; 87, *Papilio victorinus*; 88, *P. victorinus*, close-up of basal fleck; 89, *Meandrusa sciron*.
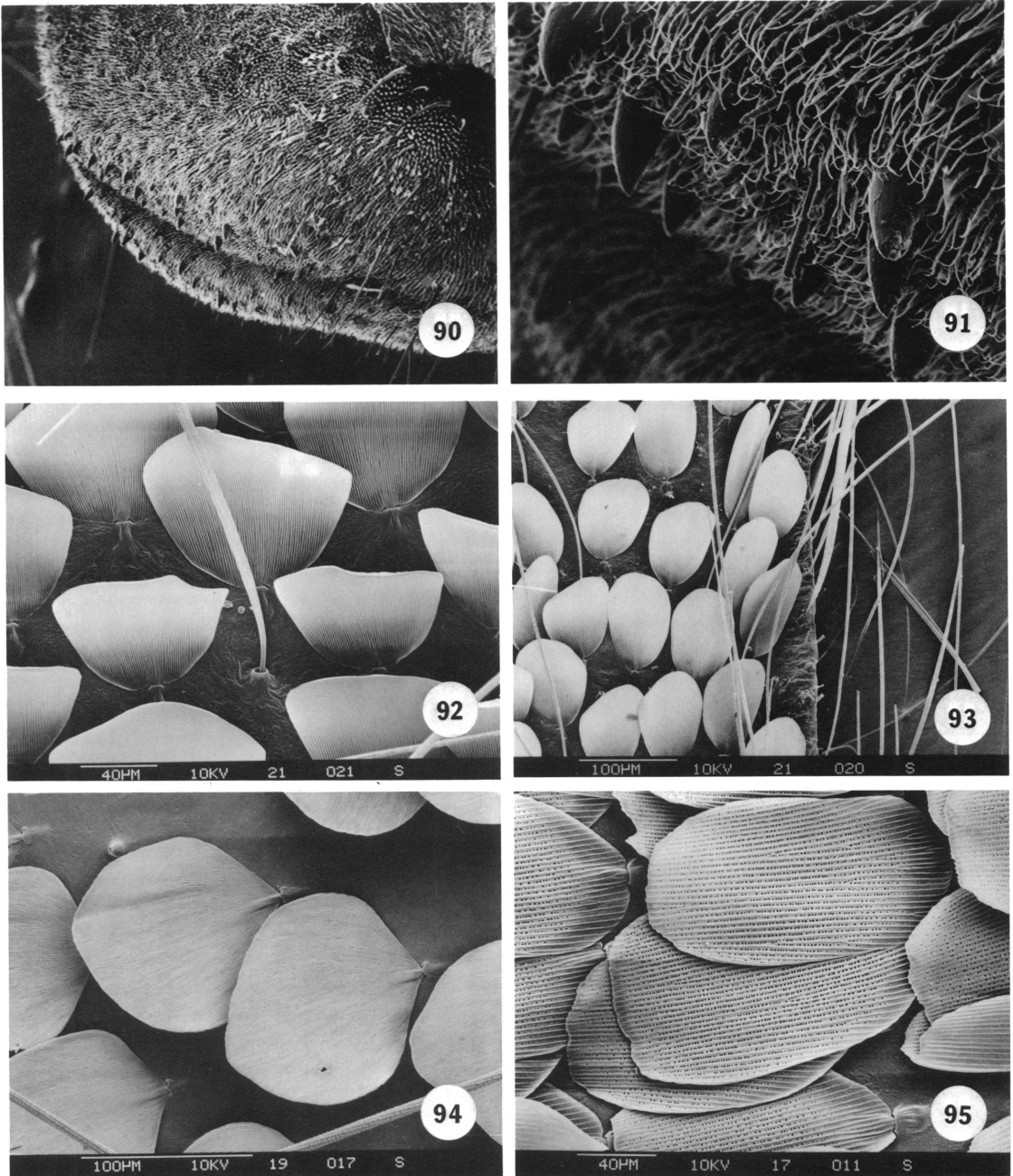
Figs. 90, 91 [Character 52]. Papillae anales of *Iphiclides podalirius*. 90, Both lobes, showing peglike setae characteristic of graphiines (anterior at right); 91, same with close-up of peglike setae and blunt hairlike setae.

Figs. 92–95 [Character 57]. Male hind wing scales. 92, *Baronia brevicornis,* showing typical scales from near center of hind wing; 93, *B. brevicornis,* hind wing margin; 94, *Archon apollinus,* scales from near center of hind wing; 95, *Iphiclides podalirius,* modified scales from hind wing margin.
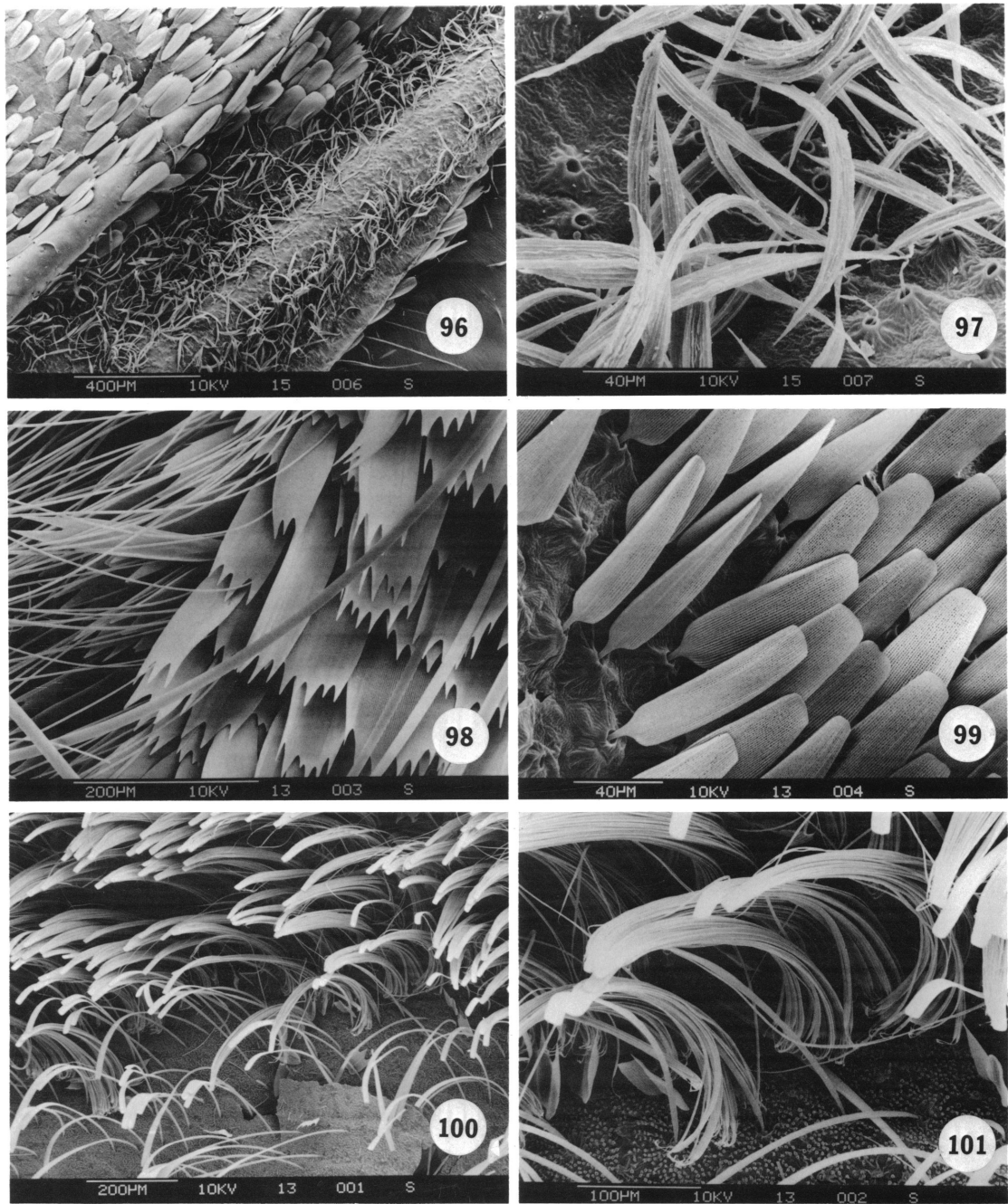
Figs. 96, 97 [Character 58].   Androconia from the hind wing of graphiine species. 96, *Eurytides epidaus,* hind wing margin; 97, *E. epidaus,* close-up of curly deciduous scales.

Figs. 98–101 [Character 91].   Androconia from the hind wing showing three types of scales found in *Graphium.* 98, *Graphium (Graphium) agamemnon,* hind wing margin at posterior edge; 99, *Graphium (Pathysa) nomius,* showing type 2 scales; 100, *G. agamemnon,* deciduous androconia showing scale packets; 101, close-up of scales in figure 100.
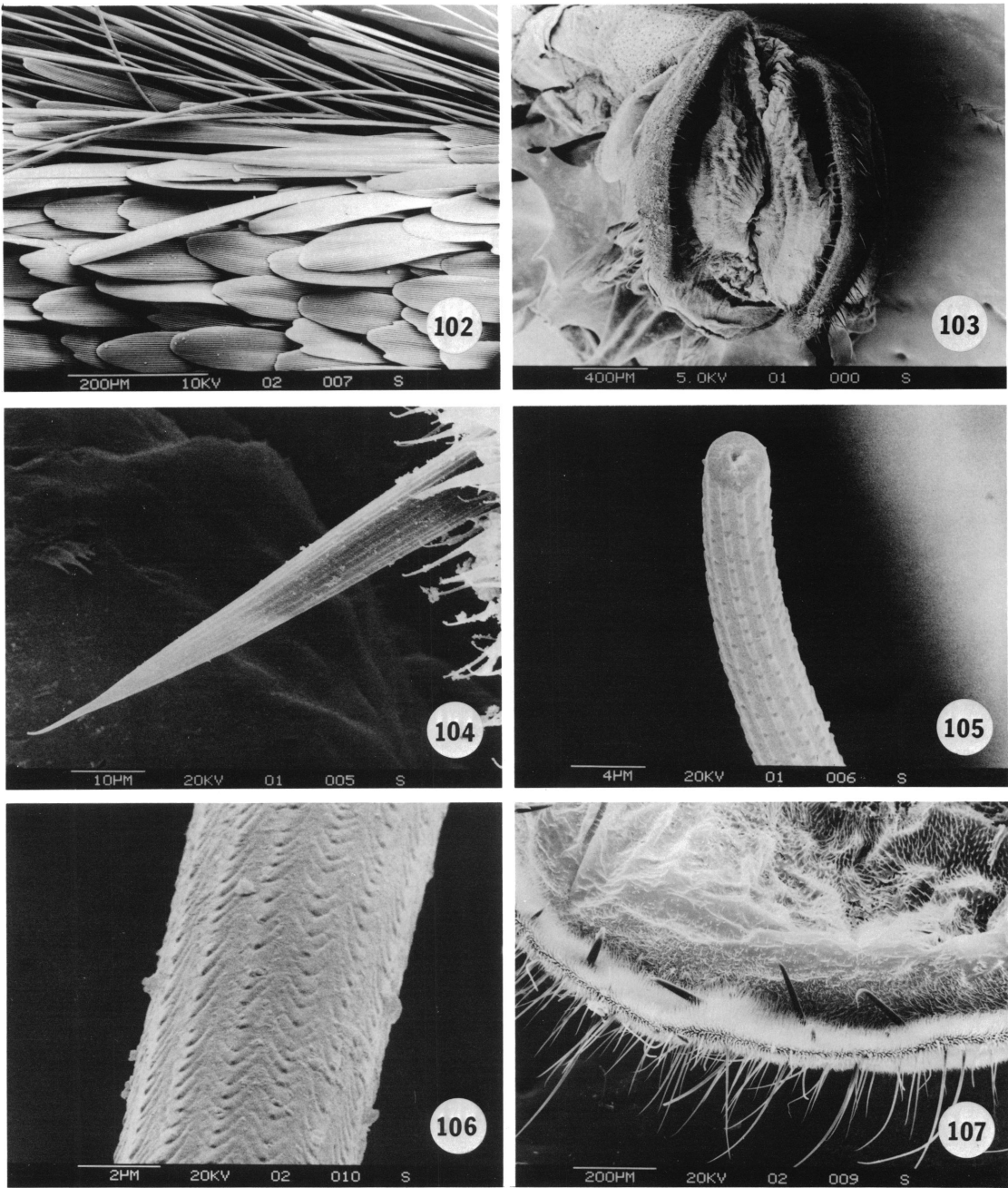
Fig. 102 [Character 101].   Male hind wing margin of *Pharmacophagus antenor.*
Figs. 103–107 [Character 102].   Papillae anales (ovipositor lobes). 103, *Papilio troilus,* both lobes in anal view; 104, *P. troilus,* seta on lateral surface of lobe; 105, *P. troilus,* broken seta from lateroventral portion of lobe; 106, *Pachliopta (Losaria) coon,* seta from lateral portion of lobe; 107, *P. coon,* anal view of a single lobe showing medial hook-shaped setae.
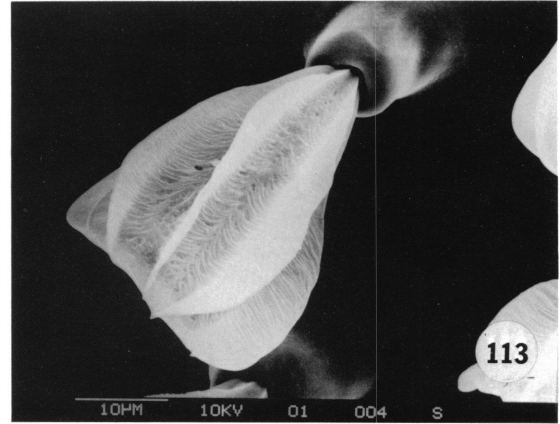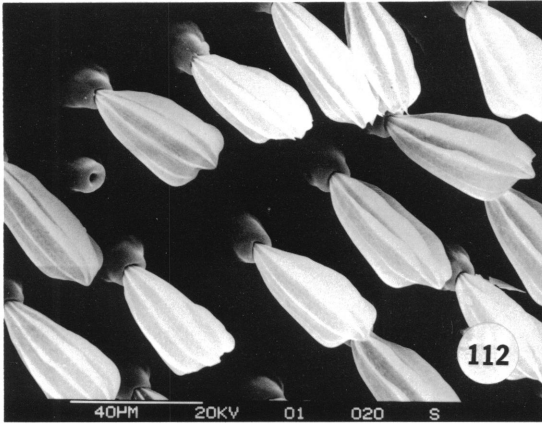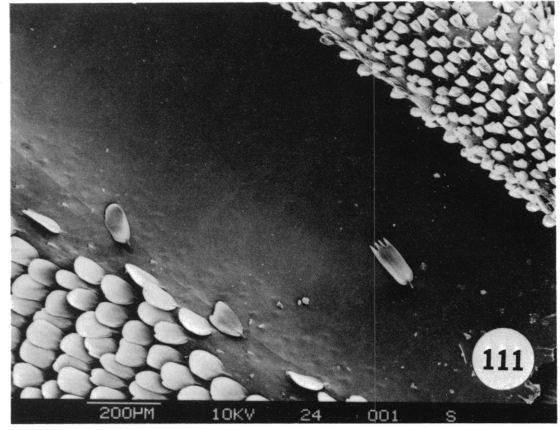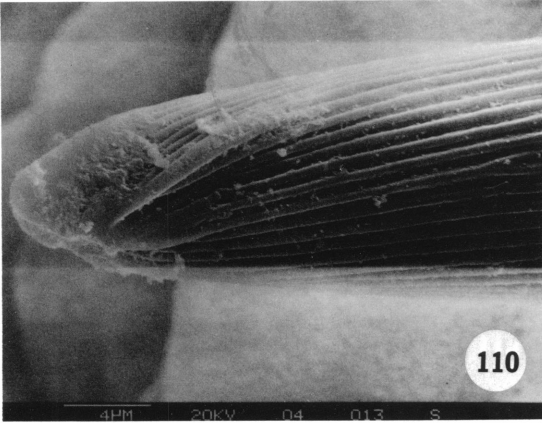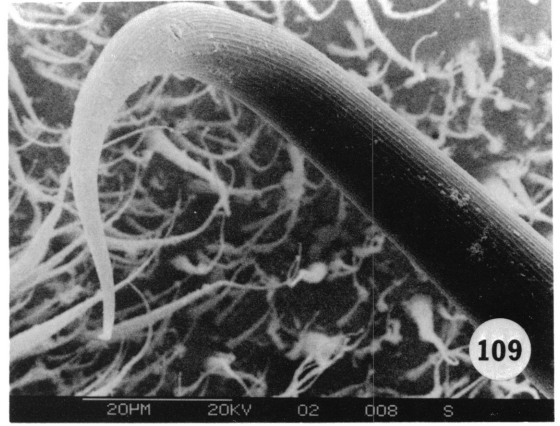
Figs. 108–110 [Character 102].   Setae on the papillae anales. 108, *Parides (Panosmia) latreillei,* posterolateral view of the edge of a single lobe showing club-shaped setae; 109, *Pachliopta (Losaria) coon,* close-up of hook-shaped seta from figure 107; 110, close-up of the tip of a club-shaped seta from figure 108.

Figs. 111–113 [Character 105].   Anal region of the male hind wing of *Battus* species. 111, *B. philenor,* showing naked streak (center), typical wing scales (bottom left), and fluted scales (top right); 112, *B. polydamus,* fluted scales distal to naked streak; 113, *B. polydamus,* close-up of fluted scale.
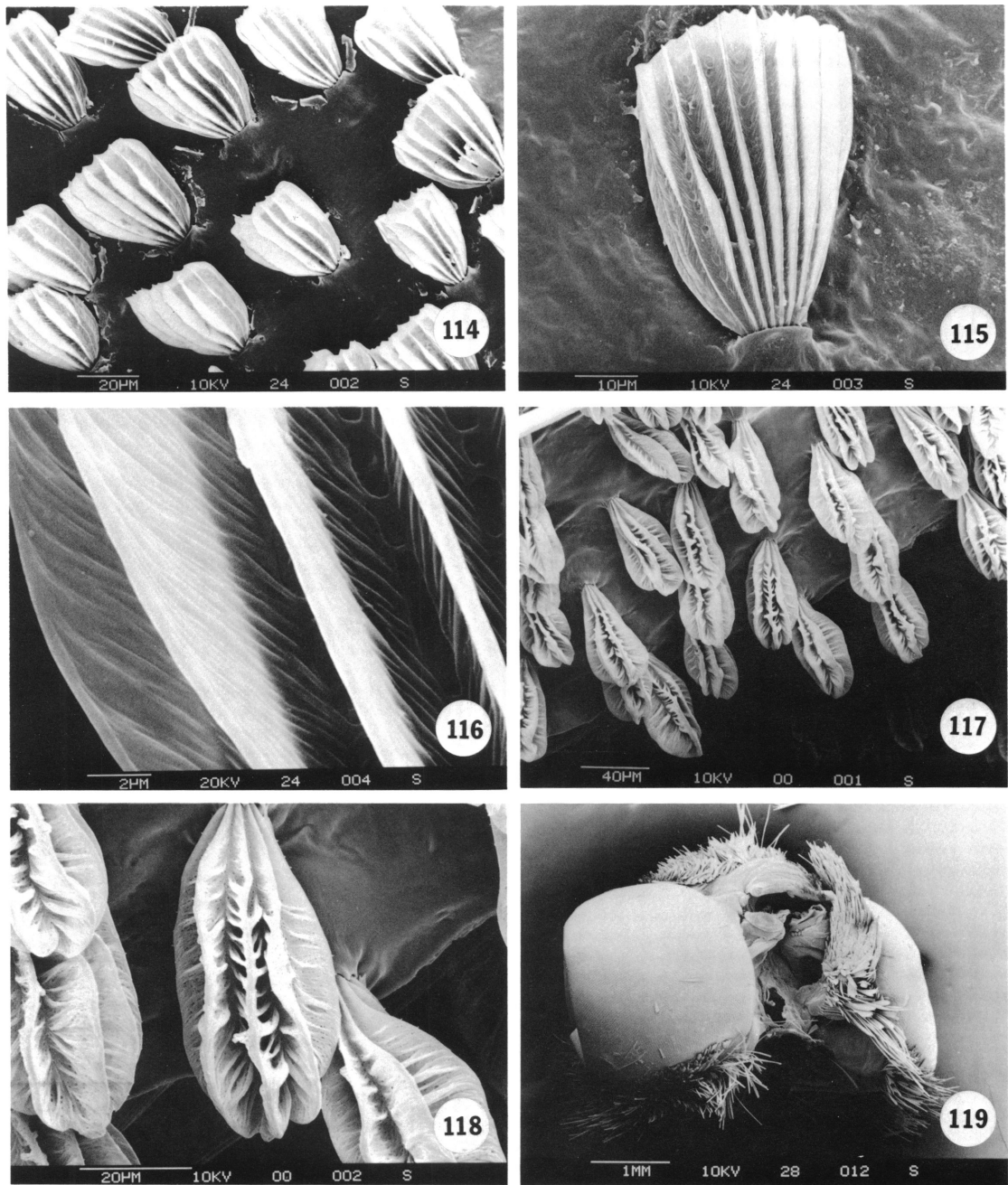
Figs. 114–118 [Character 105].   Fluted scales from the male hind wing margin of *Battus* species. 114, *B. philenor*; 115, *B. philenor,* single fluted scale; 116, *B. philenor,* surface of scale in figure 115; 117, *B. belus*; 118, *B. belus,* single fluted scale.

Fig. 119 [Character 113].   Anteroventral view of head of *Pharmacophagus antenor* with right palpus and tongue removed.
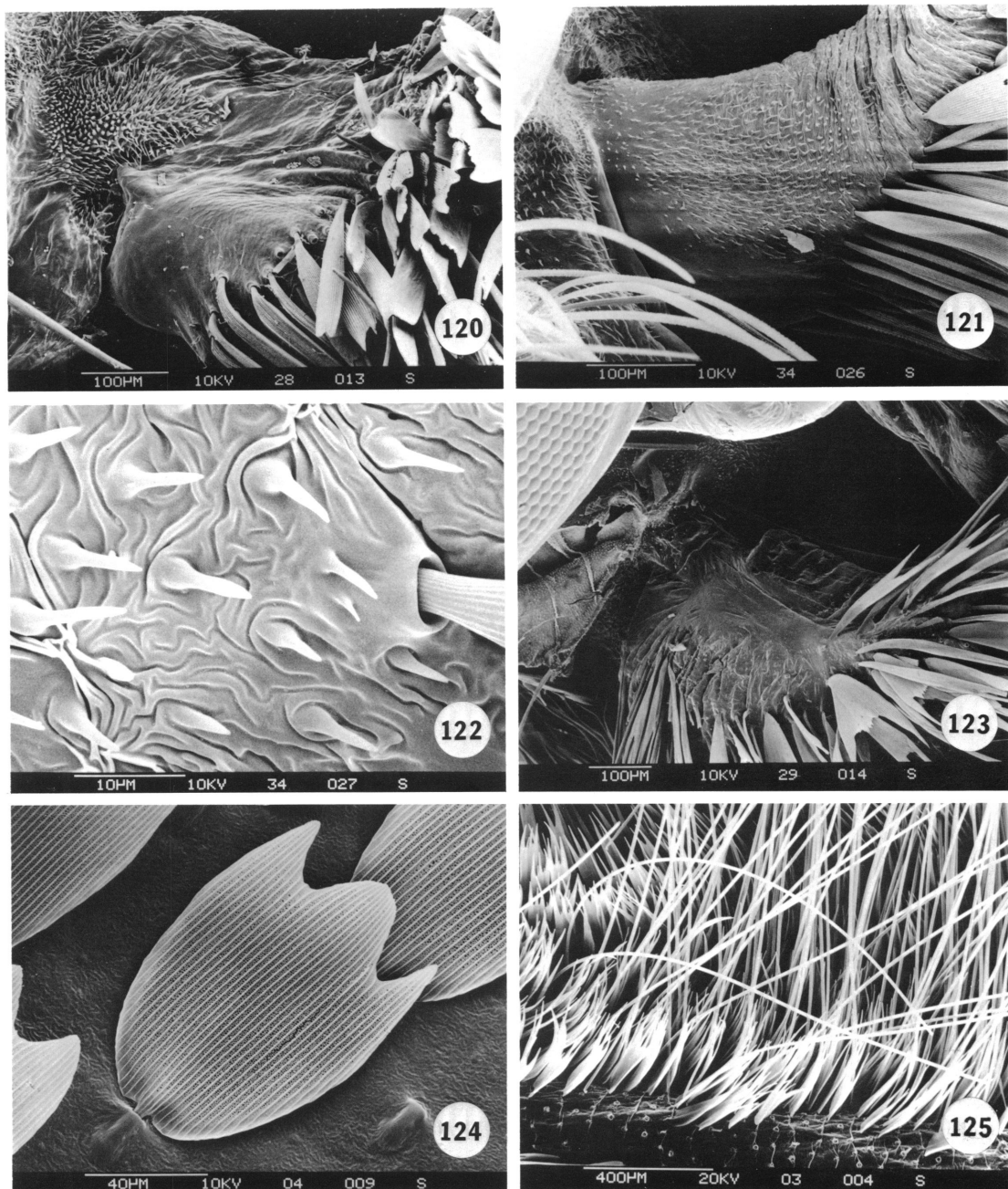
Figs. 120–123 [Character 113]. Basal segment of left male labial palpus (right palpus removed); proximal portion at left. 120, *Pharmacophagus antenor*; 121, *Battus philenor*; 122, *B. philenor*, close-up of basal fleck; 123, *Parides* (*Panosmia*) *latreillei*.

Figs. 124, 125 [Character 118]. Scales on the male hind wing. 124, *Pachliopta* (*Losaria*) *neptunus*, typical scale; 125, *P. neptunus*, two types of androconia found on the anal margin (bristlelike scales on anal vein and broad scales).
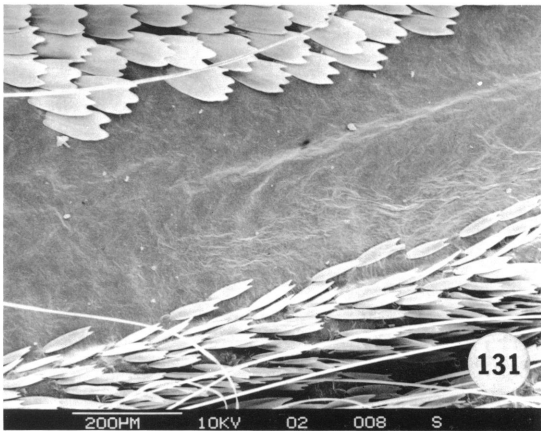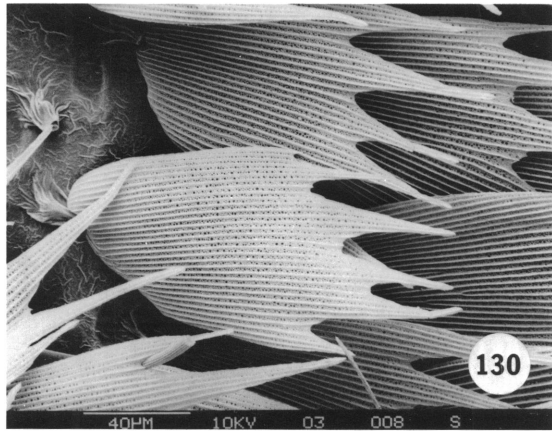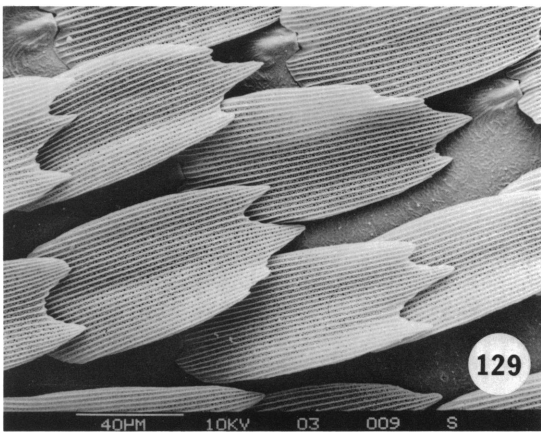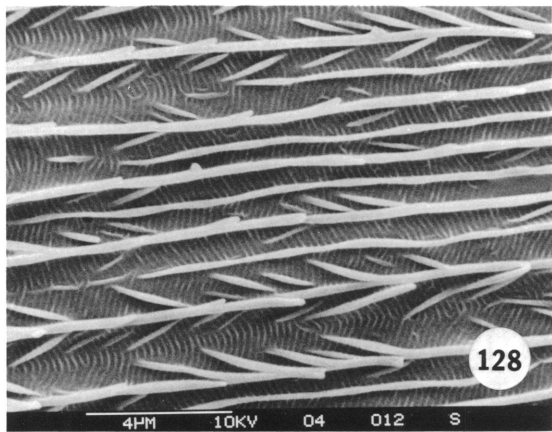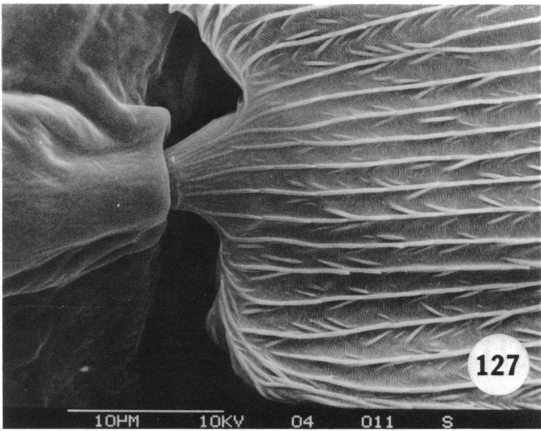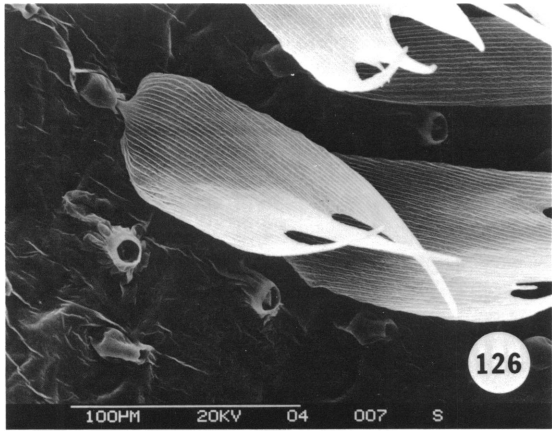
Figs. 126–131 [Character 118].　Scales on the male hind wing. 126, *P. neptunus,* broad scales (in fig. 125); 127, *P. neptunus,* base of broad scale (in figs. 125, 126); 128, *P. neptunus,* surface of scale in figures 126, 127; 129, *Pachliopta (Losaria) coon,* typical scale; 130, *P. coon,* scale from anal region; 131, *Cressida cressida,* scent organ with hind wing margin at bottom, showing typical scales (top), naked streak (center), and androconia (bottom).
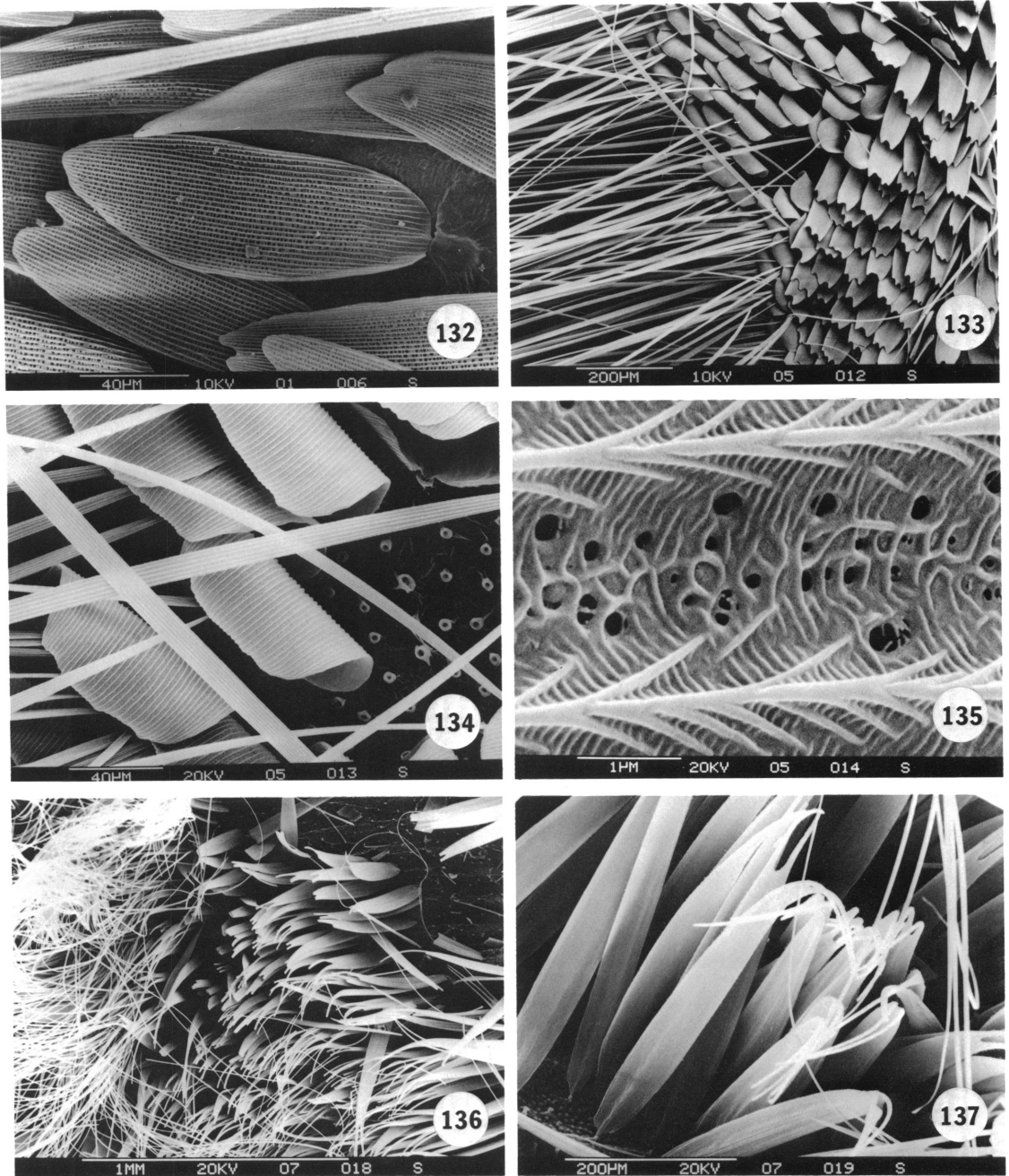
Fig. 132 [Character 118].   Scales on the male hind wing margin of *Euryades corethrus.*
Figs. 133–137 [Characters 143, 167].   Androconia on the hind wing margin. 133, *Parides (Parides) photinus,* three types of scales (typical at right, deciduous at left, lower-level at center); 134, *P. photinus,* lower-level scale; 135, *P. photinus,* close-up of scale in figure 134; 136, *Troides (Troides) hypolitus,* deciduous and lower-level scales; 137, *T. hypolitus,* lower-level scales.
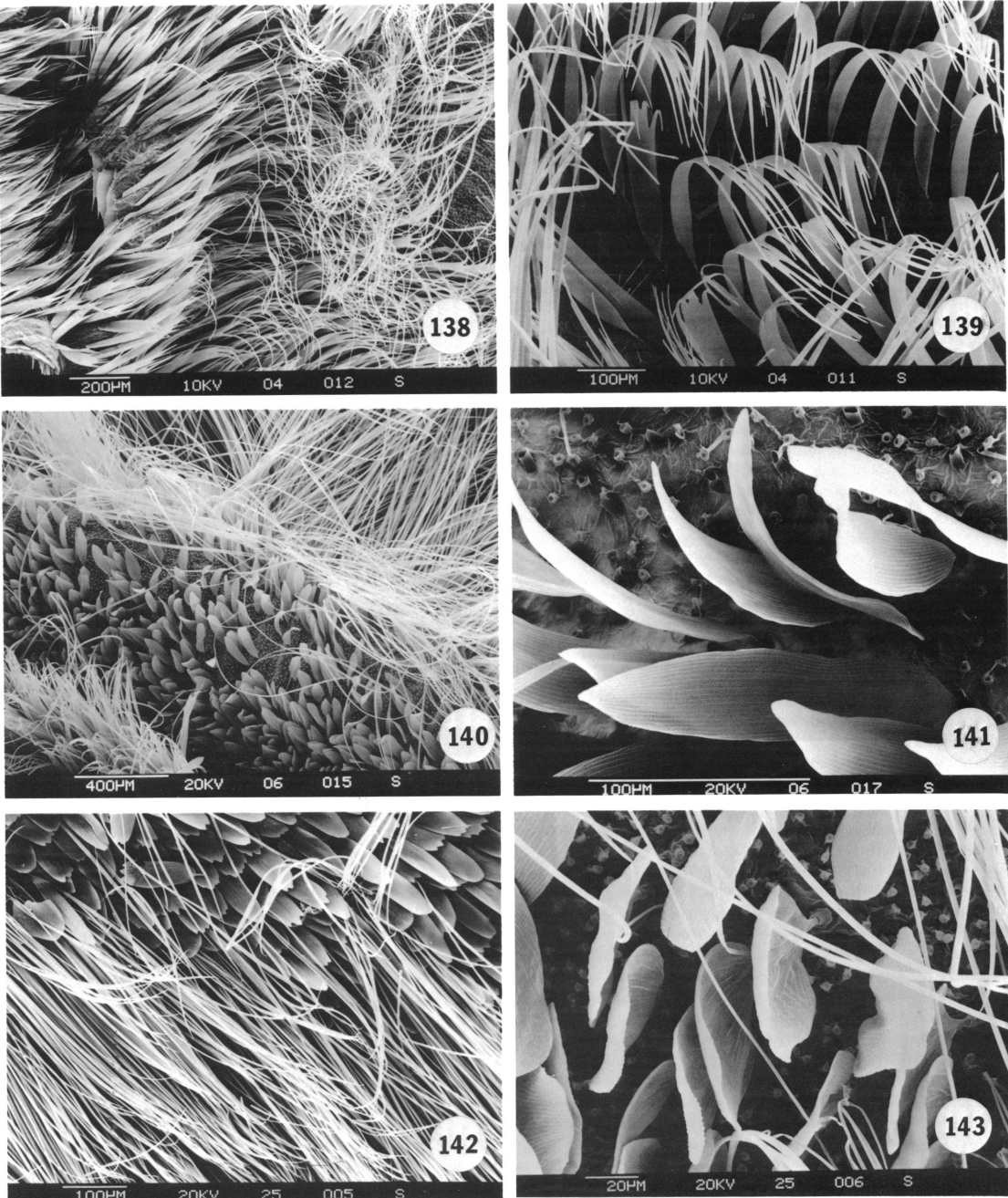
Figs. 138–143 [Character 143].   Androconia on the hind wing margin. 138, *Troides (Trogonoptera)*
brookiana, deciduous and lower-level scales (with some deciduous scales removed); 139, *T. brookiana,*
lower-level scales; 140, *Parides (Panosmia) latreillei*; 141, *P. latreillei,* lower-level scales, showing sockets
of both lower-level and deciduous scales (smaller sockets); 142, *Parides (Atrophaneura) alcinous*; 143,
P. alcinous, lower-level scales (some deciduous scales removed).
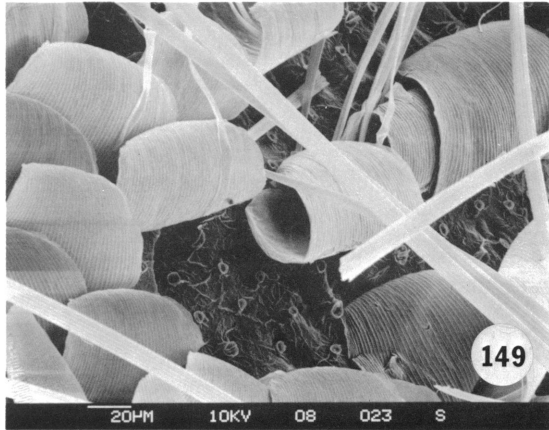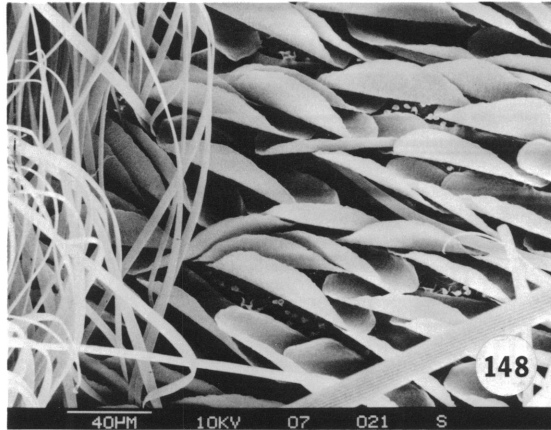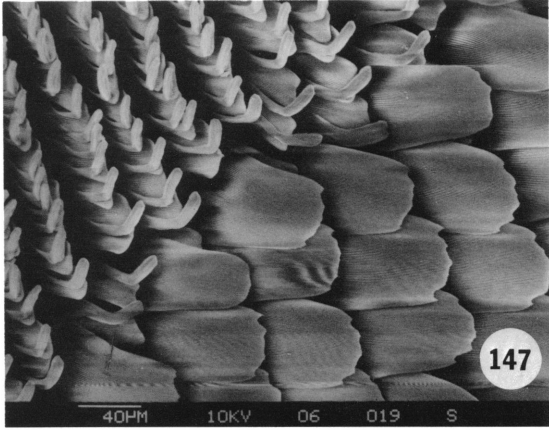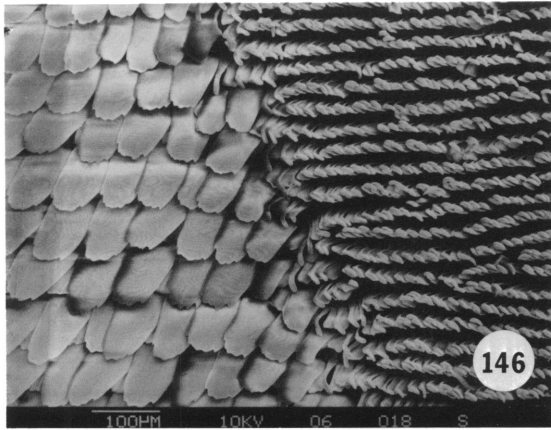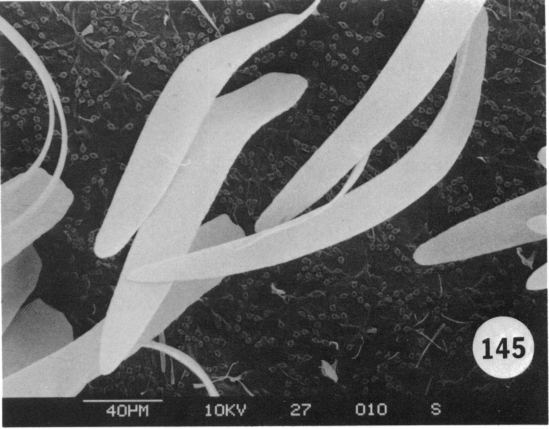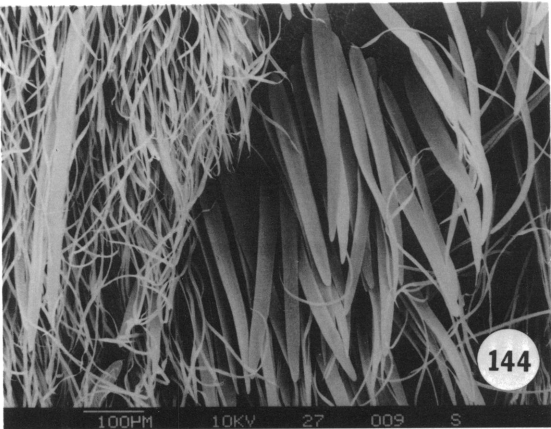
Figs. 144, 145 [Character 143].   Androconia on the hind wing margin. 144, *Parides* (*Atrophaneura*) *horishanus*; 145, *P. horishanus,* lower-level scales showing sockets of both lower-level and deciduous scales.

Figs. 146, 147 [Character 143].   Androconia on the forewing of *Troides* (*Troides*) *priamus*.

Figs. 148, 149 [Character 167].   Lower-level androconia. 148, *Parides* (*Parides*) *lysander*; 149, *P.* (*Parides*) *nephalion*.
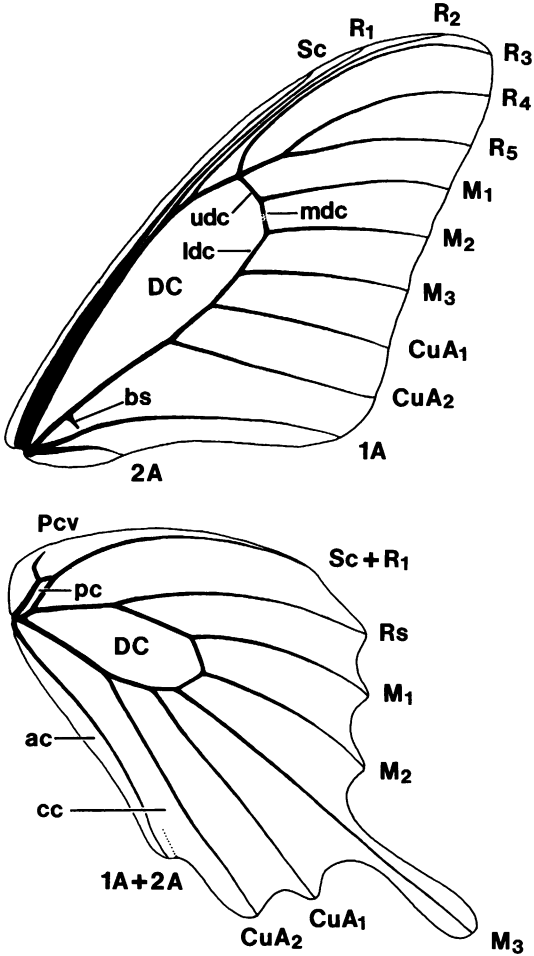
Fig. 150. Wing venation of *Papilio thoas* showing the nomenclature used in this study (from Forbes, 1923; Ackery and Vane-Wright, 1984). **A** = anal vein; **ac** = anal cell; **bs** = basal spur (Munroe, 1961); **cc** = cubital cell; **CuA** = cubitoanal vein; **DC** = discal cell; **ldc** = lower discocellular vein; **M** = medial vein; **mdc** = middle discocellular vein; **pc** = precostal cell; **Pcv** = precostal vein; **R** = radial vein; **Rs** = radial sector; **Sc** = subcostal vein; **udc** = upper discocellular.
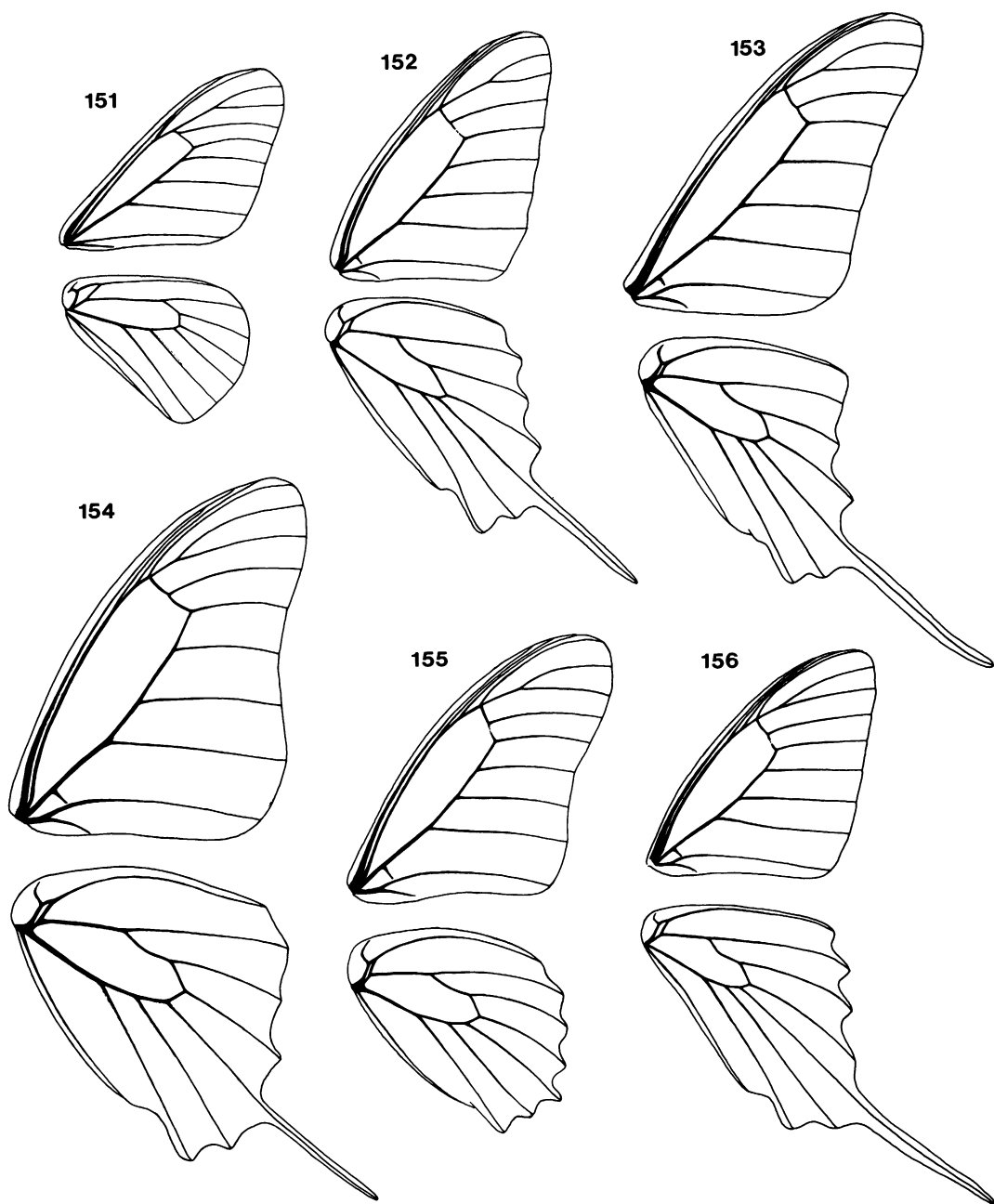
Figs. 151–156 [Characters 6, 7, 19, 46, 79]. Wing venation. 151, *Baronia brevicornis,* male; 152, *Eurytides marcellus,* male; 153, *E. thyastes,* male; 154, *E. dolicaon,* male; 155, *E. phaon,* male; 156, *Protographium leosthenes,* female.
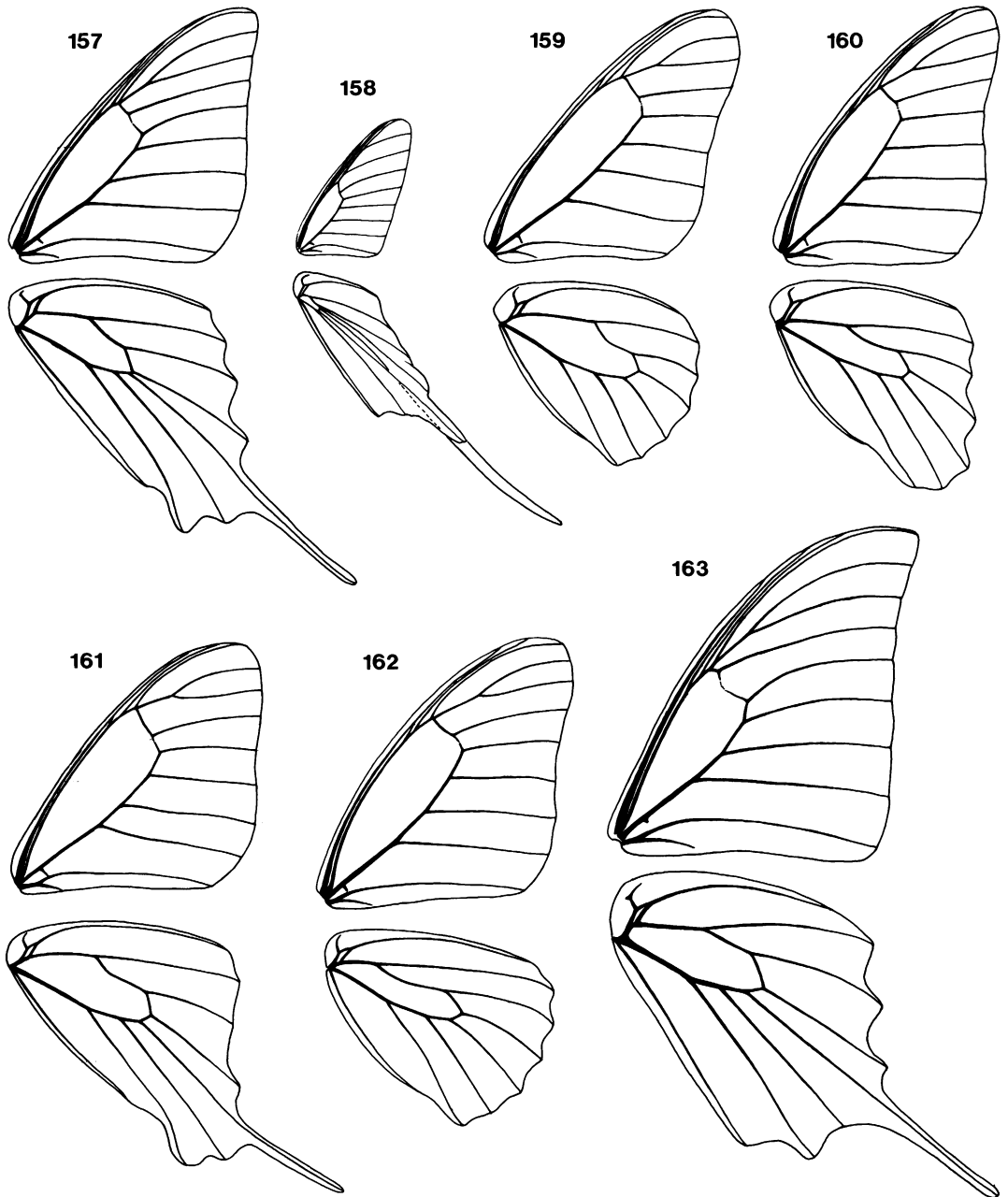
Figs. 157–163 [Characters 13, 19, 25, 26, 46, 71, 73, 74, 75, 79].   Wing venation. 157, *Iphiclides podalirius,* female; 158, *Lamproptera meges,* male; 159, *Graphium (Arisbe) taboranus,* male; 160, *Graphium (Graphium) euryplus,* male; 161, *Graphium (Pazala) eurous,* male; 162, *Graphium (Pathysa) macareus,* male; 163, *Teinopalpus imperialis,* Hope, male.
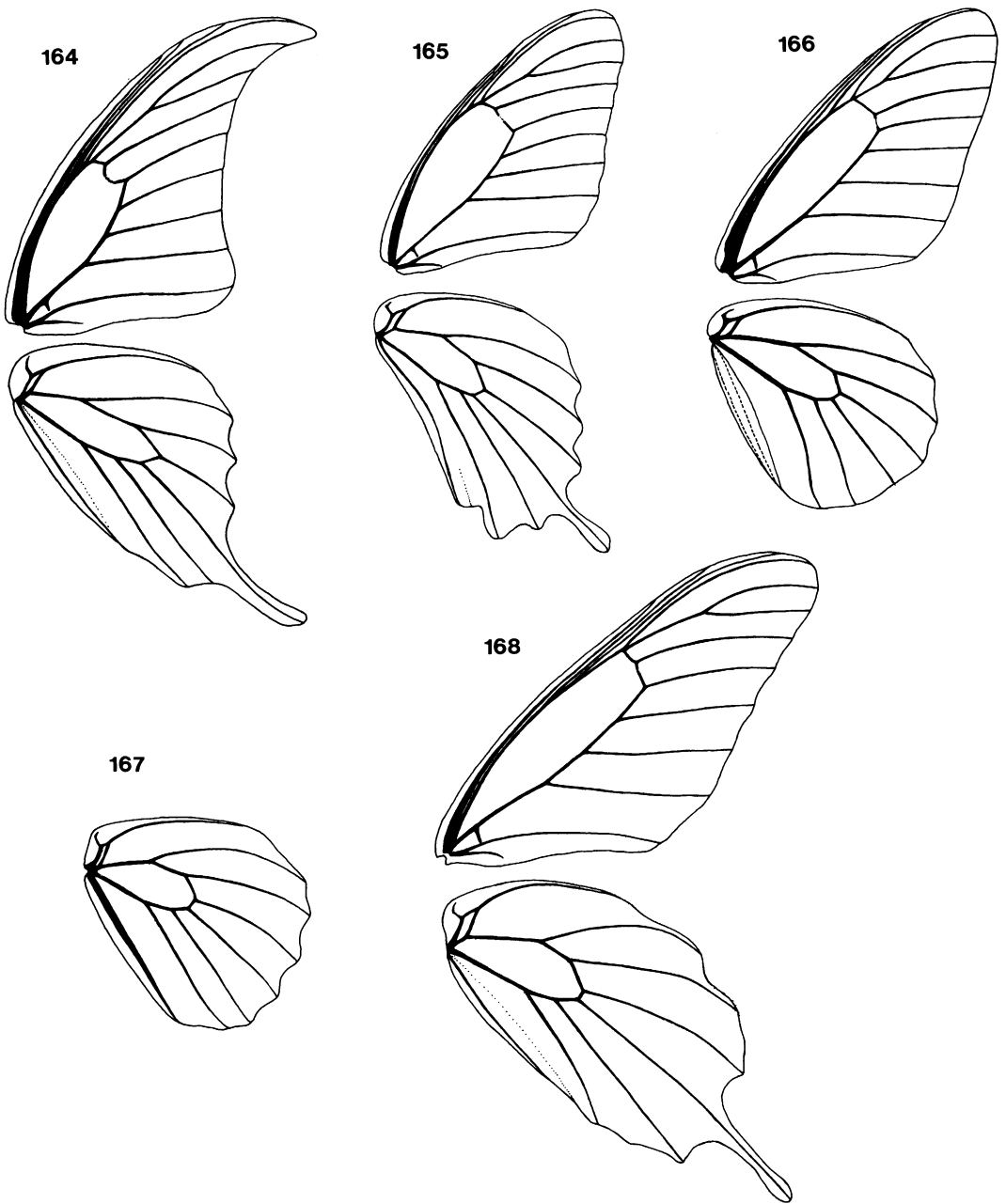
Figs. 164–168 [Characters 13, 19, 25, 71, 106]. Wing venation; except where noted the anal margin has been unrolled during preparation of the mount. 164, *Meandrusa payeni,* male; 165, *Papilio troilus,* male; 166, *Battus belus,* male (anal margin of hind wing in typical rolled position); 167, *Battus polydamus,* male; 168, *Pharmacophagus antenor,* male.

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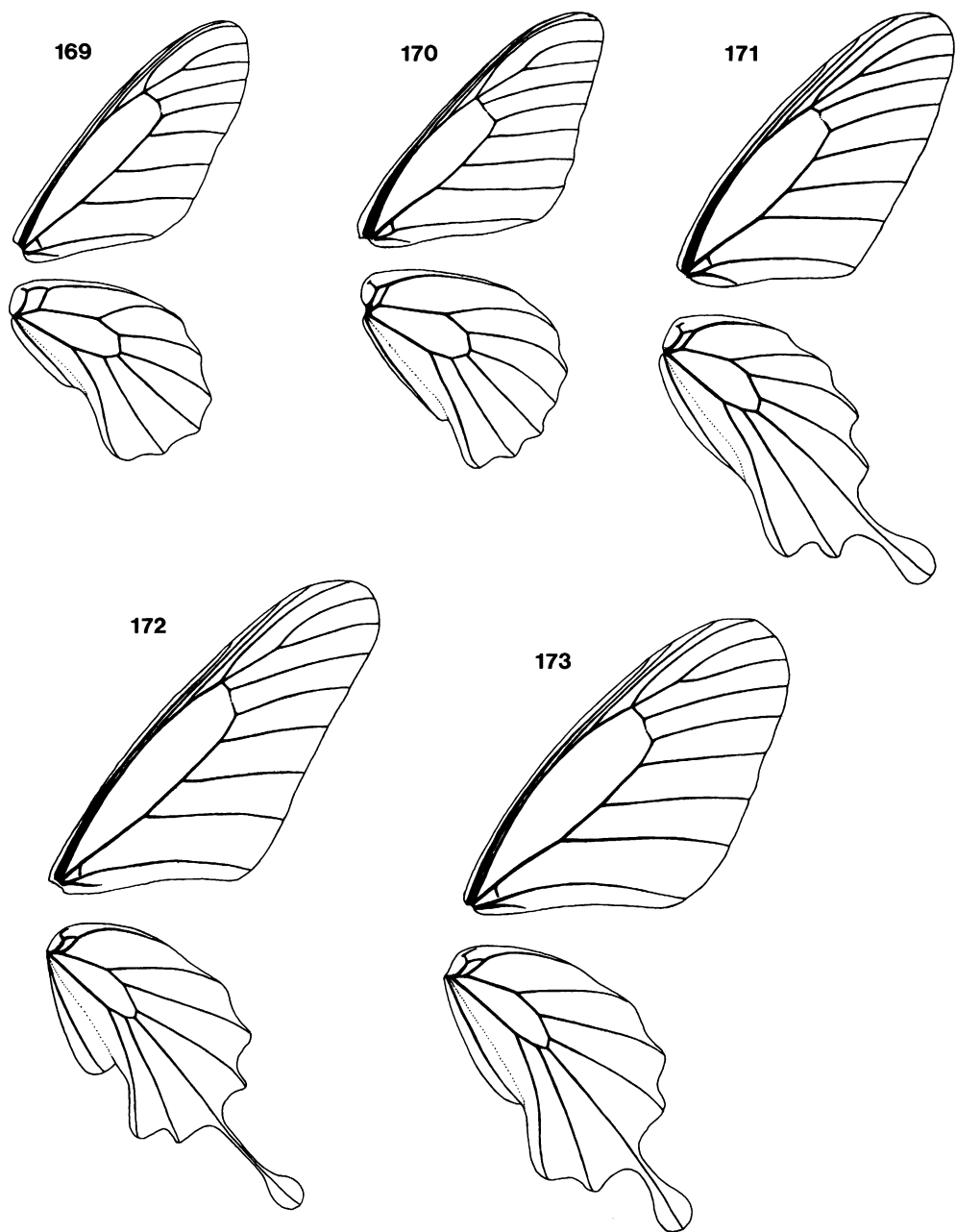
Figs. 169, 170 [Characters 117, 127].   Wing venation with anal margin of hind wing unrolled. 169, *Cressida cressida,* male; 170, *Euryades corythrus,* male.

Figs. 171–173 [Characters 117, 135, 136].   Wing venation with anal margin of hind wing unrolled. 171, *Pachliopta (Pachliopta) aristolochiae,* male; 172, *P. (Losaria) neptunus,* male; 173, *P. (Losaria) neptunus,* female.
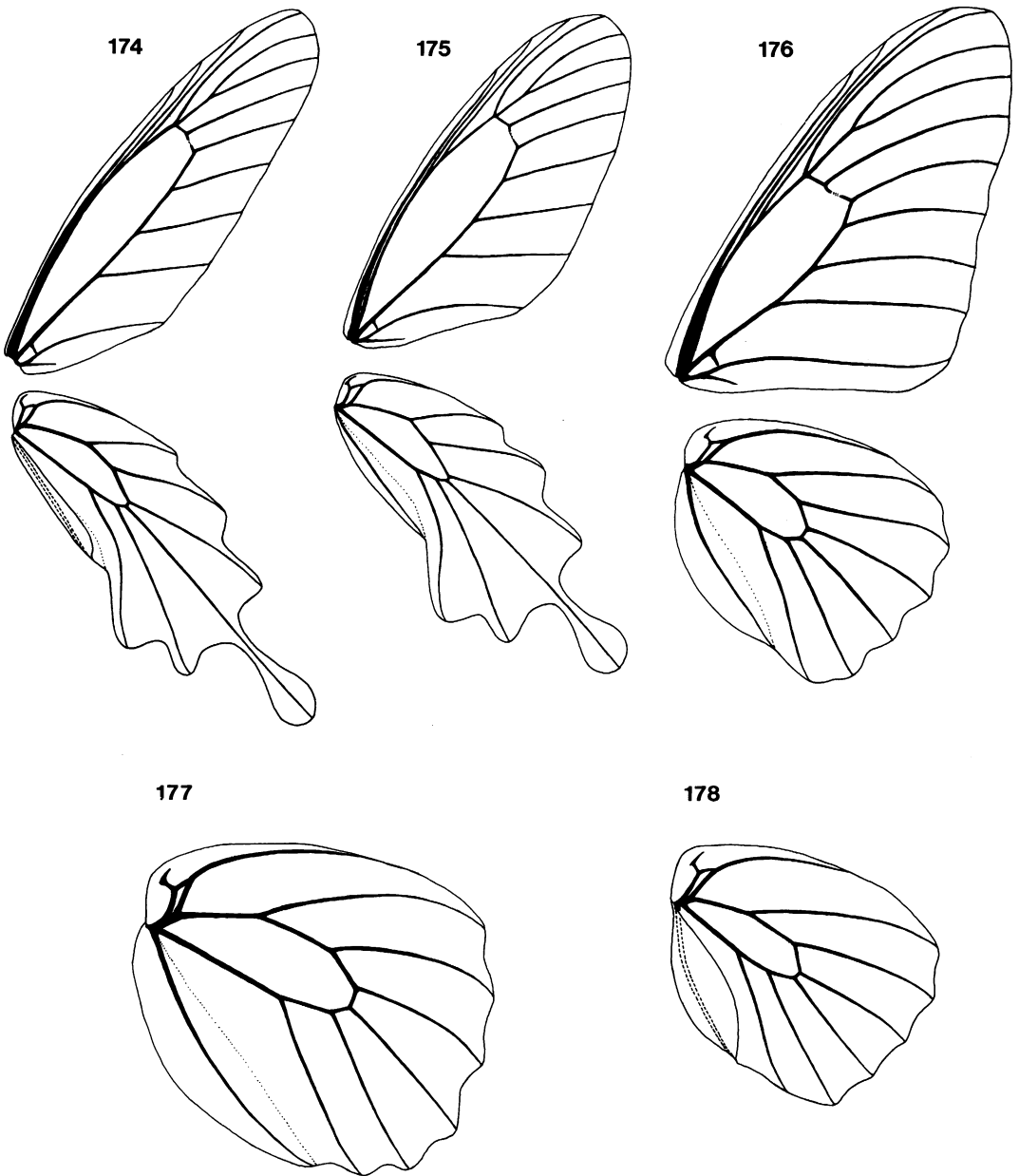
Figs. 174, 175 [Characters 117, 135, 136].   Wing venation with anal margin of hind wing unrolled (except where noted). 174, *Pachliopta* (*Losaria*) *coon,* male (anal margin in typical rolled position); 175, *P. coon,* female.

Figs. 176–178 [Characters 144, 146, 147].   Wing venation with anal margin of hind wing unrolled (except where noted). 176, *Troides* (*Troides*) *helenus,* male; 177, *Troides* (*Troides*) *priamus,* male hind wing; 178, *Troides* (*Trogonoptera*) *brookiana,* male hind wing (anal margin in the typical rolled position).
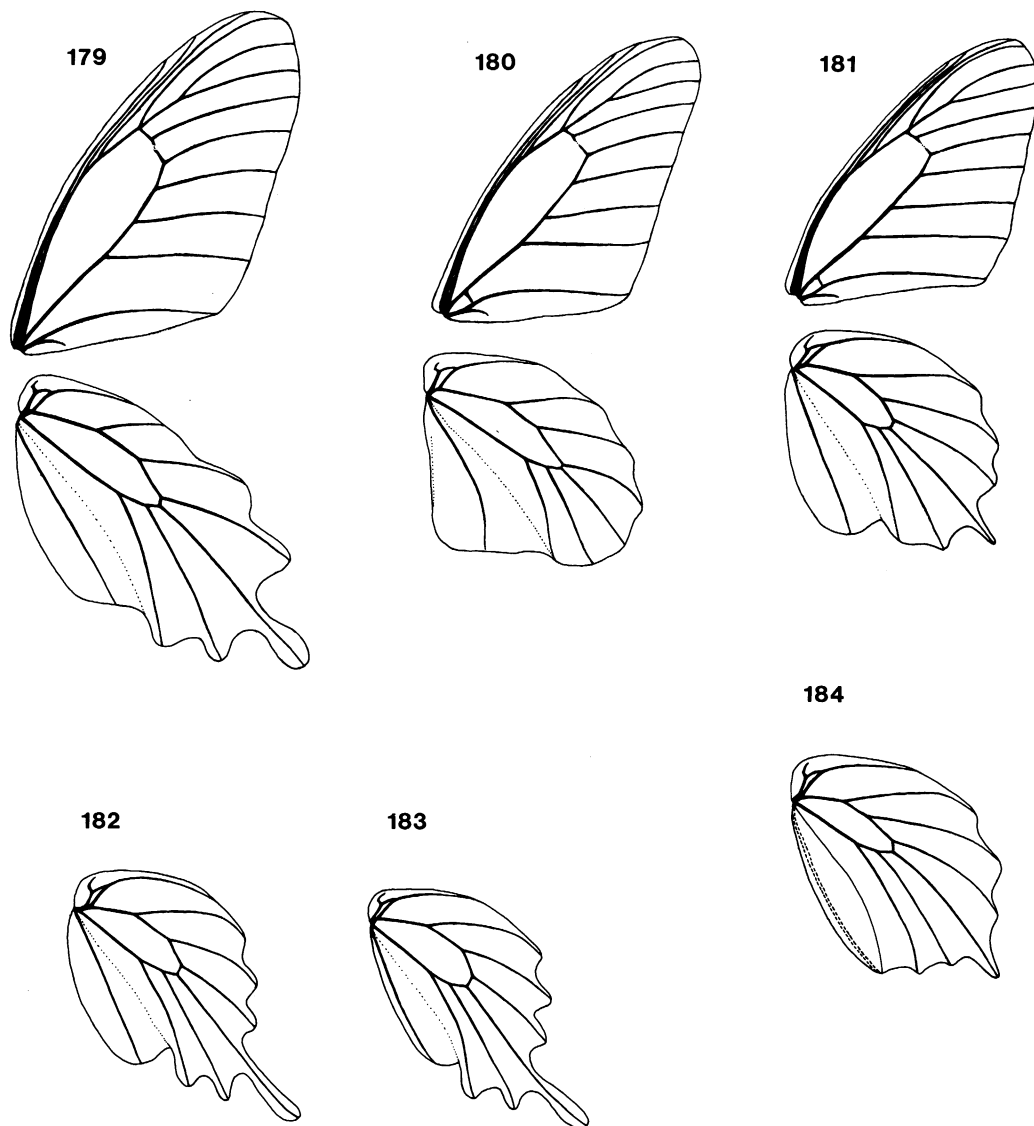
Figs. 179–184 [Characters 144, 164]. Wing venation with anal margin unrolled (except where noted). 179, *Parides (Panosmia) latreillei,* male; 180, *Parides (Atrophaneura) varuna,* male; 181, *Parides (Parides) photinus,* male; 182, *Parides (Parides) ascanius,* male hind wing; 183, *P. ascanius,* female hind wing; 184, *Parides (Parides) lysander,* male hind wing in typical rolled position.
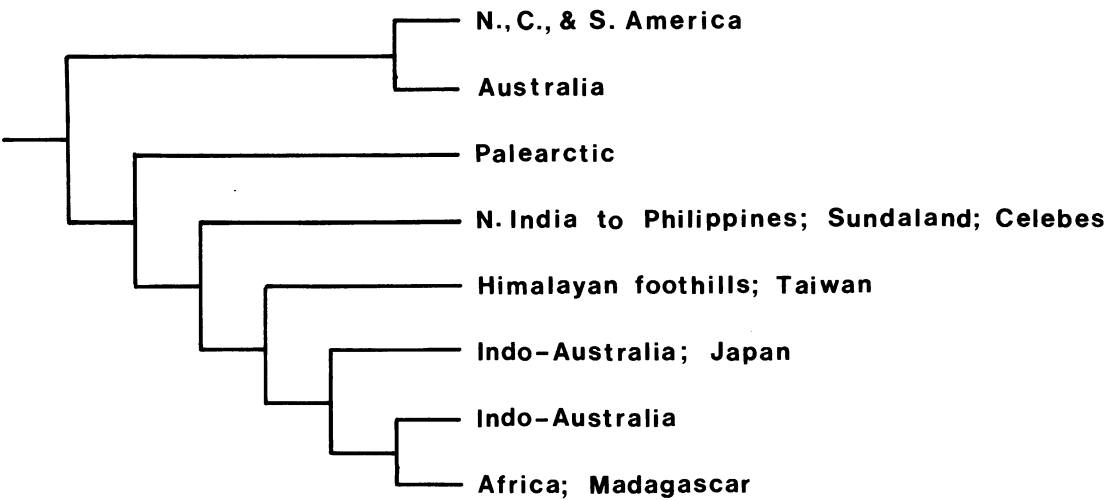
N., C., & S. America

Australia

Palearctic

N. India to Philippines; Sundaland; Celebes

Himalayan foothills; Taiwan

Indo-Australia; Japan

Indo-Australia

Africa; Madagascar

Fig. 185. Area cladogram for the Graphiini.

N., C., & S. America; Caribbean

Madagascar

N. & E. Australia; S. Papua

Patagonia

S.E. Asia S. to Sulawesi

Pakistan to S.E. Asia; Solomons; E. Australia

Sundaland; Palawan

India E. to New Guinea

New Guinea; Solomons; E. Australia

N. India to Philippines; Sundaland; Celebes

C. & S. America; Cuba

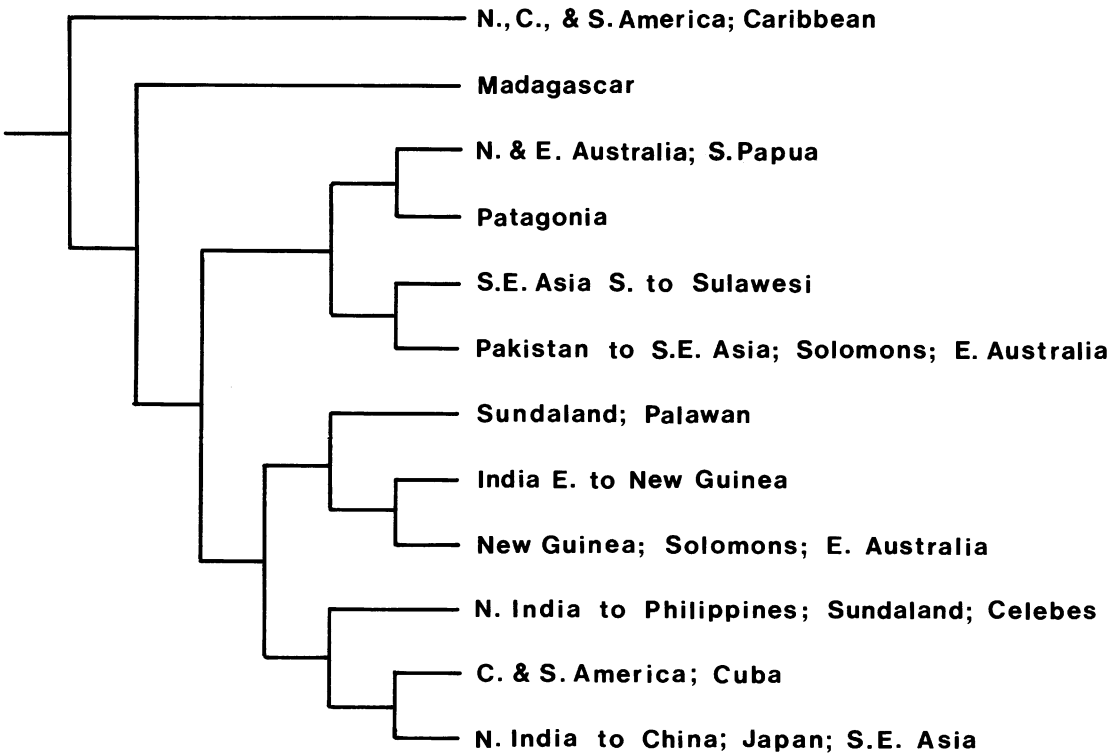N. India to China; Japan; S.E. Asia

Fig. 186. Area cladogram for the Troidini.

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