Systematics and Evolution of the Genera in the Subfamilies Usiinae and Phthiriinae (Diptera: Bombyliidae) of the World

by

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Abstract

A comprehensive phylogenetic and comparative morphological study at the generic level of taxa constituting the bombyliid subfamilies Usiinae and Phthiriinae is presented. Keys are given to the subfamilies of the bombyliid 'section' Homoeophthalmae and to the genera of the subfamilies Usiinae and Phthiriinae. A close phylogenetic relationship of the two subfamilies is shown through cladistic analysis. Two new tribes are proposed for the genera in the Usiinae: Apolysini (for Apolysis Loew) and Usiini (for Usia Latreille and Parageron Paramonov). Oligodranes Loew is shown not to belong to either the Usiinae or Phthiriinae and is restricted to five known species from south and central Asia and the Middle East. Remaining species previously misidentified as Oligodranes, especially those from the Nearctic and Afrotropical regions, are transferred to Apolysis. New junior synonyms of Apolysis are Rhabdopselaphus Bigot, Pseudogeron Cresson, and Dagestania Paramonov. New replacement names for junior secondary homonyms in Apolysis proposed herein are Apolysis crisis, for A. cinerea Evenhuis, 1983 (preoccupied by Séguy, 1926); A. hesseana, for A. namaensis Hesse, 1975 (preoccupied by Hesse, 1938); A. melanderella, for A. cinerea Melander, 1946 (preoccupied by Séguy, 1926); and A. zaitzevi, for A. montana Zaitzev, 1972 (preoccupied by Melander, 1946). Parageron, previously considered a junior synonym or subgenus of Usia, is shown to be a valid genus. Many species previously placed in Usia are transferred to Parageron. Usia is separated into two subgenera, one of which is new (Micrusia), primarily based on the presence or absence of a scrobiculate integument. The genera of the Phthiriinae are retained in two tribes:

Phthiriini (for Acreophthiria Evenhuis, Acreotrichus Macquart, Australiphthiria Evenhuis, Neacreotrichus Cockerell, Phthiria Meigen, and Pvgocona Hull) and Poecilognathini (for Euryphthiria Evenhuis, Poecilognathus Jaennicke, Relictiphthiria Evenhuis, and Tmemophlebia Even-Neacreotrichus is resurrected huis). from synonymy with Phthiria to accommodate Nearctic and northern Neotropical species previously placed in Phthiria. The fossil genus Geronites Cockerell is found to be a new junior synonym of Poecilognathus. A list of genera removed from the Usiinae and Phthiriinae is given, with brief discussions on reasons for their removal and present subfamilial placement. Newly removed genera include: Mallophthiria Edwards (to Bombyliinae, tribe Crocidiini), Timiomyia Evenhuis (to Bombyliinae, tribus inquirendus), Oligodranes (to new subfamily Oligodraninae), and the amber fossil genus Zarzia Zaitzev (tentatively to the Rhagionidae). The Corsomyza-group of genera is placed in the new tribe Mariobezziini. New generic synonymies include: Apatomyza Henning, 1832 (= Apatomyza Wiedemann, 1819); Corsomyza 1832 (= Corsomyza Wiedemann, Henning. 1819); and the fossil genus Acreotrichites Cockerell, 1917 (= Desmatomyia Williston, 1895). Corsomyza simplex Henning, 1832 (= Corsomyza simplex Wiedemann, 1819) is designated as the type species of Corsomyza Henning. New combinations of species outside the Usiinae and Phthiriinae proposed herein include: Bombylius singularis Macquart to Legnotomyia, and Acreotrichites scopulicornis Cockerell and Psilocephala scudderi Cockerell to Desmatomyia.

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Fig. 1. Habitus of Poecilognathus sp. from Brazil.

Introduction

The family Bombyliidae, whose members are commonly called bee flies, constitutes one of the largest families of orthorrhaphous Brachycera. Over 5,00 nominal species are known worldwide (Evenhuis, 1983), and many undescribed taxa await description, especially from lesser-studied areas of the world including Australia, South America, and southern and eastern Asia. The family is distributed worldwide, but is most diverse and abundant in arid and semi-arid areas. Larval stages are parasitic or predaceous on various orders of insects, primarily ground-dwelling species (DuMerle, 1975). Adults commonly frequent wildflowers in search of nectar and pollen and are primary pollinators of some plant species (Schmitt, 1983).

Two 'sections' of the family have been proposed (Bezzi, 1924) to group like elements of the family: essentially these are taxa possessing tubular proboscides and lacking a bisected hind margin of the compound eyes (Homoeophthalmae), and taxa with fleshy proboscides and an indented, bisected hind margin of the eyes (Tomophthalmae). These sections correspond roughly to the early concepts of Bombyliidae and Anthracidae, respectively. These two families were considered distinct by authors such as Latreille, Fallén, Zetterstedt, and Macquart, but were united into the Bombyliidae by Meigen (1820) and have been treated as such by most workers since then. Though recent workers contend that these two sections do not correspond to true phylogenetic lineages in the family (Mühlenberg, 1971; Theodor, 1983) (i.e., the section Homoeophthalmae probably represents a polyphyletic group), they are retained in this study as convenient points of reference. Preliminary cladistic analysis (Evenhuis, unpubl.) shows that the section Tomophthalmae is monophyletic and that the Homoeophthalmae is polyphyletic. However, a more detailed phylogenetic analysis at the subfamily level (beyond the scope of this study), comprising groups within and outside of the Bombyliidae, including the Therevidae, Empididae (s. lat.), Hilarimorphidae, Scenopinidae, and Acroceridae, is needed before any conclusions can be drawn as to phylogenetic relationships among the subfamilies of Bombyliidae.

The Cythereinae, formerly treated in the Homoeophthalmae, are placed in the Tomophthalmae following the findings of Theodor (1983). His study showed that members of the Tomophthalmae have a double-chambered occipital foramen, whereas taxa belonging to the Homoeophthalmae have a single-chambered occipital foramen. The double chamber is most likely correlated with the articulation of the head with the second cervical sclerite of the prothorax, resulting in a more maneuverable head in tomophthalmines versus a tightly fitting head in homoeophthalmines. The subfamily Oniromyiinae, previously considered to be a member of the Homoeophthalmae (Hull, 1973), is here transferred to the Tomophthalmae based on the presence of a double-chambered occipital foramen.

The subfamilies treated in this study, Phthiriinae and Usiinae, constitute a fairly homogeneous group of genera in the Homoeophthalmae that are easily distinguished from other bombyliids by the attachment of the clypeus to the bases of the antennae (i.e., the antennae are placed at the upper portion of the oral margin, resulting in the absence of a face below the antennae) and by the presence of an apical or subapical sulcus on the third antennal segment containing a sensillum. Despite the relative homogeneity of the two subfamilies, their generic composition has varied considerably from author to author. Further complicating the taxonomic and phylogenetic status of the two subfamilies is Rohdendorf's (1964, 1977) proposal that the Usiinae be treated as a separate family.

The Usiinae and Phthiriinae were chosen for study to clarify their generic composition, determine the validity and scope of their subfamilial status, and examine Rohdendorf's (1964, 1977) proposal mentioned above. The relative homogeneity of many of the genera in these subfamilies provide a challenge for cladistic analysis to determine their phylogenetic relationships. Results obtained herein will augment observations reported in an ongoing monographic treatment of the family in the Nearctic Region by Hall & Evenhuis (1980–1987) and should be useful in future revisions of the genera of the Phthiriinae in the New World.

Materials and Methods

Over 30,000 specimens belonging to genera treated at one time or another in either the subfamily Phthiriinae or Usiinae were examined. Species examined during this study are listed below under each genus considered. Specimens were borrowed from or examined in the following institutions and private collections (abbreviations of institutions in parentheses are used henceforth in the text): American Museum of Natural History, New York (AMNH); Australian National Insect Collection, CSIRO, Canberra (ANIC); Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London (BMNH); Neal L. Evenhuis, Honolulu (NLE); J.C. Hall, Riverside, California (JCH); Humboldt Museum, Humboldt Universität, Berlin (HMB); Museum National d'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Natal Museum, Pietermaritzburg (NATAL); Snow Museum, University of Kansas, Lawrence (SNOW); South African Museum, Cape Town (SAFR); Texas A & M University, College Station (TEX); United States National Museum of Natural History, Washington, D.C. (USNM); Universidade de São Paulo, São Paulo (USP); University of California, Berkeley (UCB); University of California, Riverside (UCR); University of Minnesota, St. Paul (MINN); University of Tel Aviv, Ramat Aviv (ISRAEL); Zoological Institute, Academy of Sciences of the USSR, Leningrad (ZIL); Zoological Museum, Lund University, Lund, Sweden (LUND); Zoologisk Museum, Copenhagen (ZMC).

Adult specimens were critically examined for morphological characters using a stereo dissecting microscope. Antennae, mouthparts, and male and female genitalia were prepared for illustration by dissecting in 10% KOH and rinsing in 5% acetic acid. Male genitalia were then placed in a spot plate with glycerine for illustration and detailed examination. Antennae, mouthparts, and female genitalia were mounted on slides and examined under compound microscope. Illustrations were made using a camera lucida.

Immature stages are known only for a few species of Phthiriinae and Usiinae (DuMerle, 1975) and no new information on the biology or morphology of the immatures was found in this study. Owing to the paucity of immature material available for study, characters based on pre-imaginal stages could not be used in this study.

Adult morphological terminology follows that of Hull (1973) and Hall & Evenhuis (1980). Female genitalic terminology follows Theodor (1983), except that what Theodor termed the vaginal furca is here interpreted as the vaginal apodeme of Emden & Hennig (1970). The reader is referred to Figures 4–9 for general morphological features and associated terminology used in this work.

Cladistic analyses using the principle of maximum parsimony were performed on the genera of the subfamilies Usiinae and Phthiriinae to estimate phylogenetic relationships of the taxa involved. The program used was PAUP (Phylogenetic Analysis Using Parsimony), PC version 2.4.1 (Swofford, 1985). Options employed during the analyses included MULPARS, SWAP=GLOB-AL, and HOLD=10. These allowed for global branch swapping among ten initial trees in a search for equally parsimonious trees. Character state polarities were determined using outgroups (Watrous & Wheeler, 1981; Maddison et al., 1984; Clark & Curran, 1986).

Two separate data sets were analyzed: (1) on the genera of the Usiinae, and (2) on the genera of the Phthiriinae. Twelve terminal taxa based on 22 characters were used in the analysis of the genera of the Usiinae, and 10 terminal taxa based on 29 characters were involved in the Phthiriinae analysis.

List of Abbreviations

Α	_	anal vein(s) of wing (1, 2, 3)	Μ	-	medial vein(s) of wing (1, 2, 3)
ADC	-	apical spermathecal duct	MEN	-	mentum
AED	-	aedeagus	MES		mesonotum
al	-	alula of wing	MSP	-	mesopleuron
an	_	anal lobe of wing	MTN		metanotum
ANI	-	antennal segment I	MTP	-	metapleuron
ANII	-	antennal segment II	MTS	_	metasternum
ANIII	-	antennal segment III	MXP	-	maxillary palpus
ANT	_	anterodorsal extension (ramus) of	NOT	-	notch of epandrium
		epiphallus	OCC	_	occiput
ANP	-	pronotum, pronotal collar	OCF	-	occipital foramen
API	-	apicomesal lobe of basistylus	OCT	-	ocellar tubercle
APV	-	apical valve of ejection apparatus	PAC		post alar callus
BAP	-	basal aedeagal apodeme	PEN	-	penial guide (of epiphallus)
BAS	_	basistylus	pos	-	posterior cell(s) of wing (first through
BDC	_	basal spermathecal duct			fourth)
BLL	_	bullae of occiput	PRO	_	proboscis
bsc	_	basal cell(s) of wing (first and second)	PRS	_	prosternum
BSE	_	basal extension of basistylus	PTP		pteropleuron
BSV	_	basal valve of ejection apparatus	PUL	_	pulvilli
BUL	_	bulb of aedeagus (= sperm pump of	R		radial vein(s) of wing $(1, 2+3, 4, 5)$
		authors)	rm	_	rm crossvein of wing
С	-	costal vein of wing	SAC	-	basal sac of spermathecal reservoir
CER	_	cercus	sbm	_	submarginal cell(s) of wing (first and
CDC	_	common spermathecal duct			second)
COX	_	coxa	SC	_	subcostal cell of wing
CuA	_	cubital-anal vein (1)	Sc	_	subcostal vein of wing
DIS	_	dististvlus	SCU	-	scutellum
DOR	_	dorsal prong of antennal sulcus	SPM	_	spermathecal reservoir of female genitalia
dsc	-	discal cell	STP	_	sternopleuron
EJC	_	ejection apparatus of female genitalia	SUL		apical or subapical sulcus of third antennal
EPA	_	epandrium			segment
EPB	_	epiphallic bridge	TAR	_	tarsi (first through fifth)
EPI	_	epiphallus, epiphallic complex	TER		abdominal tergite
FRO	-	front	TIB	_	tibia
GEN	_	gena	UPS	_	upper epiphallic spines
HAL	_	halter	VAG	_	vaginal apodeme (= furca of authors)
HUM	_	humeral callus	VAN	_	lateral vane of basal apodeme
HYP	_	hypopleuron	VEN	_	ventral prong of sulcus of third antennal
LAR	_	lateral ramus			segment
LAT	_	lateral epiphallic process	WNB	_	wing base
LOW	_	lower epiphallic spines			

.0

Phylogenetic Analyses

Cladistic analyses were made to infer phylogenetic relationships in (1) the genera of the Usiinae and (2) the genera of the Phthiriinae. An unpublished subfamilial analysis by me was done to test the presumably close phylogenetic relationship between the Usiinae and the Phthiriinae.

The rationale for the cladistic methodology is that if two or more taxa share the derived (apomorphic) state of a character, then that apomorphic trait is presumed to have arisen in a recent ancestor common to those taxa (Hennig, 1950). By contrast, primitive (plesiomorphic) states do not show evolutionary progression but rather evolutionary stasis, because taxa have inherited the plesiomorphic state from a common ancestor without any change in that character. Therefore, monophyly cannot be justified in groups possessing shared plesiomorphies.

Parsimony was implemented in these analyses following Farris (1983). Parsimony minimizes the total amount of homoplasy occurring in all characters, weights characters evenly, and allows a graphic representation (cladogram) of the simplest genealogy of the taxa being analyzed.

Character states were coded in binary form ex-



cept for the shape of the spermathecal reservoir in the Usiinae analysis and the pattern of bisected compound eyes in the Phthiriinae analysis. For these polymorphic characters, Transformation Series Analysis (Mickevich, 1982) was used to estimate character evolution and aid in coding states of these characters in the data matrix. Plesiomorphic states for characters in the list below and in the data matrices (Tables III-IV) are indicated by a zero (0); apomorphic states are indicated by a one (1), two (2), three (3), or four (4). Rationale and justification for the polarities chosen for character states in the analyses of the Usiinae and Phthiriinae are discussed after each character concerned. Because of the poorly understood phylogenetic relationships of the subfamilies of the Homoeophthalmae, no sister group could be found for either the Usiinae or Phthiriinae to be used as an outgroup in this study. Bombylius Linnaeus was used to determine polarities for most of the characters used in the Usiinae and Phthiriinae analyses; exceptions are discussed in the annotations of characters for the Usiinae and Phthiriinae.



Fig. 2. Cladogram of the genera of the subfamily Usiinae. Solid boxes represent apomophies; open boxes represent homoplasies.

Fig. 3. Cladogram of the genera of the subfamily Phthiriinae. Solid boxes represent apomophies; open boxes represent homoplasies.

Characters used in the phylogenetic analyses

The following characters were used in each of the two phylogenetic analyses. Data concerning some of these characters may be incidental to the needs of this study but are given here because of their potential usefulness in future phylogenetic studies of this family. Characters marked with an asterisk (*) were deleted from the final analysis. Reasons for their deletion are annotated under each character concerned.

Usiinae analysis

Head:

1. Male compound eyes (A): 0 = holoptic; 1 = dichoptic.

Males of taxa considered primitive within the Bombyliidae (sensu Hull, 1973) (e.g., Bombyliinae, Toxophorinae), as well as males of taxa of the Asiloidea and other brachycerous families related to the Bombyliidae, have holoptic eyes. Males of subfamilies of the bombyliid section Tomophthalmae characteristically have dichoptic eyes, with some exceptions (e.g., Cythereinae).

- 2. Male compound eyes (B): 0 = both large andsmall facets present; 1 = facets one size. This character is apparently correlated with the condition of holopticism versus dichopticism. The plesiomorphic state is found in males of those taxa in which courtship display or swarming takes place. Species of Usia Latreille s. lat. do not have holoptic males, nor do they engage in courtship displays or swarming. Mating in Usia takes place within flowers (DuMerle, 1971). Some South African species of Apolysis Loew [e.g., maherniaphila Hesse, hirtella Hesse, seminitens Hesse, anomalus (Hesse), elegans (Hesse)] have dichoptic males, but nothing is known of their courtship or mating habitats.
- 3. Posteroventral portion of occiput: 0 = normal in size (Fig. 11c); 1 = inflated posteriorly (Fig. 11d).

The apomorphic state is apparently a special-

ized condition found only infrequently outside of *Apolysis* (e.g., *Geron inflatus* Evenhuis from Australia).

- 4. Gena (A): 0 = broad (Fig. 18b); 1 = narrow or absent (Fig. 23b).
 The apomorphic condition is found in very few taxa of the Bombyliidae. Within the Usiinae it is only found in the genus Usia s. lat.
- 5. Gena (B): 0 = tumid; 1 = flat to concave.
- Maxillary palpus: 0 = short, clavate (Fig. 25); 1 = long, thin (Fig. 13b). The plesiomorphic condition is found in many primitive Bombyliidae (sensu Hull, 1973). Most taxa have maxillary palpi that rarely extend beyond the oral margin. The apomorphic state is considered an exaggerated condition and may possibly be correlated with visitation and/or pollination of specific flowers.
- 7. Third antennal segment (A): 0 = articulating arista present (Fig. 12); 1 = articulating arista absent (Figs. 19, 24).

 Third antennal segment (B): 0 = rounded apically (Fig. 20a); 1 = pointed apically (Fig. 19(20b), Fig. 19 b)c

- Third antennal segment (C): 0 = not clavate apically (Fig. 20a); 1 = clavate apically (Fig. 24a).
- Third antennal segment (D): 0 = not inflated medioventrally; 1 = inflated medioventrally. The apomorphic states in characters 8-10 are autapomorphies for certain genera and species groups within the tribe Usiini.
- 11. Third antennal segment (E): 0 = subapical sulcus absent; 1 = subapical sulcus present. The apomorphic state is the condition shared by the genera of the Usiinae. The plesiomorphic state is found in Bombylius, but some dischistine genera of the Bombylinae (e.g., Brychosoma Hull) have an analogous subapical sulcus of different form.

Thorax:

- 12. Integument: 0 = not scrobiculate; 1 = scrobiculate.
 - The apomorphic state for this character is found only in Usia (Micrusia), new subgenus. Other taxa within the Bombyliidae have integumental textures that are usually characterized by outgrowths (mucrones, tubercles, etc.) rather than indentations.

Wing:

- 13. Discal cell: 0 = present; 1 = absent. The plesiomorphic state of this character is found in Bombylius and most other genera of Bombyliidae. The apomorphic condition (i.e., the absence of a crossvein closing the apex of the discal cell) is here considered a reduction of the plesiomorphic state and is found in few taxa within the family. In the Usiinae, Apolysis humilis Loew possesses the apomorphic state. Other species within this highly variable genus, however, possess the plesiomorphic state. Because of other overlapping character states exhibited in various species groups of Apolysis, the presence or absence of the discal cell cannot be used as a diagnostic character (see Results of Analyses for further discussion).
- 14.*Inflation at base of medial vein: 0 = absent; 1 = present.

This character exhibits polymorphism within the Usiinae. *Parageron* Paramonov has the apomorphic state, but some species of *Usia* and *Apolysis* possess each state.

Male genitalia:

- 15. Genital capsule (A): 0 = rotated 180°; 1 = rotated 45-90°.
 Species of the genus Bombylius Linnaeus have genitalia rotated 90°, as do genera of the more derived (sensu Mühlenberg, 1971) bombyliid subfamily Anthracinae. Primitive genera of the Asiloidea and most other lower brachycerous taxa have genitalia rotated 180°, hence the condition found in Bombylius is interpreted to be apomorphic for this analysis.
- 16.* Genital capsule (B): 0 = small, length about equal to last two abdominal segments combined; 1 = large, length about one-half length of abdomen.

The plesiomorphic condition is common among most Bombyliidae, including Bombylius, Phthiriinae, and others. The apomorphic condition is characteristic for Usia (Micrusia); however, some species within Usia s. str. possess the plesiomorphic state.

- 17. Position of dististylus on basistylus: 0 = apical; 1 = subapical.
- 18. Length of aedeagus: 0 = longer than basistylus; 1 = shorter than basistylus.

Female genitalia:

- 19. Sclerotized plate of vaginal orifice: 0 = absent; 1 = present (Fig. 9). The apomorphic state is apparently a specialized condition found only in the Usiini. An analogous plate-like structure is found in other bombyliid genera such as Mythicomyia Riley (see Hall & Evenhuis, 1986).
- 20. Apical spermathecal duct: 0 = less than 3 times length of ejection apparatus; 1 = more than 7 times length of ejection apparatus. Bombylius possesses the plesiomorphic state of this character, but other genera currently treated within the Bombylinae (viz., Conophorus Meigen and Sparnopolius Loew) have the apomorphic state. The placement of these last two genera within the Bombylinae is most likely in error (they appear closer to therevoid taxa); the phylogenetic relationships of these genra are in need of reevaluation.
- 21. Spermathecal reservoir: 0 = large, ellipsoid to obpyrifirm (Fig. 9); 1 = small, bulbous (Fig. 17c); 2 = straight (Figs. 17a, d); 3 = tortuous (Fig. 17e); 4 = coiled (Fig. 17b).
- 22. Lateral papillae of ejection apparatus: 0 = absent (Fig. 42); 1 = present (Figs. 9, 17). The plesiomorphic state of this character is not exhibited in *Bombylius*, but since more primitive outgroups within the Asiloidea have that condition, the condition exhibited in *Bombylius* is interpreted here as apomorphic. Other taxa of Bombyliidae possess the apomorphic condition at the generic level, but not consistently within subfamilies. These genera include Acrophthalmyda Bigot, Anastoechus Osten Sacken, and Aphoebantus Loew.

Phthiriinae Analysis

Head:

- 1. Face: 0 = narrow in frontal view; 1 = broad in frontal view.
- 2. Third antennal segment (A): 0 = with hairs on dorsal surface; 1 = dorsal surface bare.
- Third antennal segment (B): 0 = apical sulcus absent; 1 = apical sulcus present. The derived state of this character is one of the apomorphies of the Phthiriinae. This apomorphic condition is not to be confused with



Fig. 4. Heads of *Neacreotrichus aztec* (Painter) showing general morphological features. a) male, dorsal view; b) male, lateral view; c) female, lateral view.

the subapical placement of this sulcus in the Usiinae.

- 4.* Third antennal segment (C): 0 = bare or with short hairs; 1 = with long hairs dorsally. Most of the phthiriine genera analyzed have either the plesiomorphic or the apomorphic state for this character. Some Neacreotrichus species, however, have the plesiomorphic state [e.g., olmeca (Painter)] and others the apomorphic state [e.g., cingulatus (Loew) (see Fig. 40)].
- 5.* Third antennal segment (D): 0 = ventral prong absent; 1 = ventral prong present. This character is fairly consistent within most genera in the Phthiriinae; however, some African species of *Phthiria* Meigen s. str. have the plesiomorphic state (e.g., *lanigera* Bezzi) and others have the apomorphic state (e.g., *pulla* Bezzi).
- Basolateral spicules of proboscis: 0 = absent;
 1 = present.
- 7. Pattern of division of male compound eyes into areas of large and small ommatidia: 0 =

upper and lower; 1 = frontal and lateral/posterior; 2 = not bisected.

The plesiomorphic state is found in *Bombylius* and in many other genera with holoptic males. The transformation series presumes that the most derived state is that in which the bisection of the compound eyes into areas of large and small ommatidia is lost. The most derived state is presumably correlated with a modification of the usual type of phthiriine courtship or mating behavior which, to my knowledge, has not yet been recorded.

8.* Facial pilosity: 0 = absent to sparse; 1 = dense. Using the exemplar approach, this character was discrete for the taxa examined. When other species in each genus were examined, this character was shown to be highly variable within the genera Phthiria, Acreotrichus Macquart, Acreophthiria Evenhuis, Neacreotrichus, and Pygocona Hull. Some species (both described and undescribed) in these genera possess each state of the transformation series.

Thorax:

- 9. *Metapleuron:* 0 = bare; 1 = with micropubescence.
- 10. Male and female mesonotal pattern and coloration: 0 = dimorphic; 1 = monomorphic. This character is plesiomorphic in the genera of the Phthiriini, which typically have male bodies black and female bodies varicolored. Genera of the Poecilognathini possess the apomorphic state, with the bodies of males and females similarly colored and patterned.
- 11. Pteropleuron: 0 = bare; 1 = pilose.
- 12.* Pile of sternopleuron: 1 = present; 0 = absent.

This character is discrete for all the genera of the Phthiriinae except *Euryphthiria* Evenhuis. In that genus, *E. grandis* Evenhuis has specimens possessing both states.

Legs:

13. Fore tarsal pollen hairs: 0 = present; 1 = absent.

These are elongate hairs found on the mesal surface of the tarsi in many genera of Bombyliidae including *Bombylius;* they have spoonshaped or bulbous apices. Their presence is presumably evidence of an evolutionary adaptation to flower visitation by these flies in which they gather pollen with the forelegs and transfer this pollen to the proboscis (J.L. Neff, in litt.). These hairs are found in all genera of Phthiriinae except for *Euryphthiria*.



Fig. 5. Thorax of Usia aenea (Rossi) showing general morphological features.

Wing:

14. Costal vein: 0 = complete or ending at anal vein (Fig. 41); 1 = incomplete, ending before anal vein (Figs. 46, 52).
The apomorphic state of this character is homoplastic in this analysis but is autapomorphic for Pygocona in the Phthiriini and Tmemophlebia Evenhuis in the Poecilognathini.



Fig. 6. Wing of Apolysis cincturus (Melander) showing venation and cell terminology.









Abdomen:

15. Female abdomen: 0 = ovate; 1 = apical segments laterally compressed. The apomorphic state is found only in Australiphthiria Evenhuis and appears to be a modification of abdominal structure to accommodate a specialized form of oviposition as yet unobserved (see also Evenhuis, 1986).

Male genitalia:

- 16. Epiphallic penial guide: 0 = absent; 1 = present.
- 17. Epiphallic spines: 0 = absent; 1 = present.
- 18. Basal extension of basistylus: 0 = present; 1 = absent.
 The derived states for characters 16-18 are

apomorphies defining the Poecilognathini.

19. Genital capsule: 0 = rotated 180°; 1 = not rotated.

The apomorphic state for this character is found only in *Australiphthiria*. It is a modification of the usual rotated genital capsule and apparently allows for copulation with females of this genus, which have the terminal abdominal segments modified as if for piercing (see character 15).

- 20. Basistylus: 0 = bilobed; 1 = lobes fused, conical.
- 21. Dististylus: 0 =thin; 1 =broad, thick.
- 22. Sclerotized villi at apex of epandrium: 0 = absent; 1 = present.

The apomorphic state is found only in the genera *Tmemophlebia* and *Relictiphthiria* Evenhuis. Detailed examination through scanning electron microscopy may show these villi to be sensory structures, which could be used in copulatory behavior.

- 23. *Epandrium*: 0 = notched, flat, or concave apicomedially; 1 = pointed apicomedially.
- 24. Mesally directed lobe of basistylus: 0 = not bearing denticles; 1 = bearing denticles.

Female genitalia:

- 25. Vaginal apodeme: 0 = absent or consisting of paired parallel bars; 1 = consisting of paired L-shaped sclerites.
- 26. Apical portion of spermathecal reservoir (A):
 0 = conical to ellipsoid (Fig. 50a-e); 1 = dactylethroid (thimble-shaped), apex blunt (Fig. 42d).



Fig. 9. Female genitalia of *Parageron lutescens* (Bezzi) showing general morphological features.

- 27. Apical portion of spermathecal reservoir (B):
 0 = small, conical to blunt apically, length shorter than ejection apparatus (Fig. 42d);
 1 = large, ellipsoid, length greater than ejection apparatus (Fig. 50e).
- 28.* Apical portion of spermathecal reservoir (C):
 0 = curved; 1 = straight.
 There are no outgroups that could be used to determine polarities for characters 26-28, which are unique to the Phthiriinae. The genus Phthiria was used as the presumed most ancestral taxon within the Phthiriinae, and the polarities were determined as such. Poecilognathus Jaennicke has species possessing the plesiomorphic state of character 28 (e.g., sulphureus Loew) and others having the apomorphic state (e.g., loewi Painter).
- 29. Basal sac of spermathecal reservoir: 0 = absent; 1 = present.

Results of Analyses

Analysis of the genera of the Uŝiinae

Three genera (Apolysis, Parageron, and Usia) were studied. Because of the distinctiveness of the *lutescens* and *incisus* groups within the genus Parageron, representatives of each group were selected for analysis. Due to the variability of many of the taxa in the genus Apolysis, representatives of numerous species groups exhibiting a full array of variation were studied. Also included in the taxa representing Apolysis are A. mus (Bigot) and A. mitis (Cresson), the type species of the nominal genera of Rhabdopselaphus Bigot and Pseudoge-ron Cresson, respectively.

A single most-parsimonious tree with a length of 30 steps and a Consistency Index of 0.800 resulted from the analyzed data set of 22 characters (Table III) and is shown in Fig. 2.

Monophyly of the Usiinae is based on two apomorphies: the presence of lateral papillate projections on the ejection apparatus of the female genitalia, and the presence of a subapical dorsal sulcus on the third antennal segment. Two tribes are recognized in the Usiinae. The cladogram shows the monogeneric tribe Apolysini to be monophyletic, defined by the following apomorphies: the presence of long, thin maxillary palpi; the rotation of the male genital capsule 45-90°; the apical spermathecal duct of the female genitalia being more than seven times the length of the ejection apparatus; and a non-obpyriform spermathecal reservoir in the female. The tribe Usiini is monophyletic and possesses two apomorphies: lack of an articulating arista on the apex of the third antennal segment, and the vaginal orifice armed with a vaginal plate. In addition to being an apomorphy for the genus Apolysis, the apomorphic state of a long, thin maxillary palpus is also a parallelism in this analysis because it is an autapomorphy for Parageron lutescens Bezzi.

The genus Usia is a monophyletic group based on three apomorphies: the dichoptic eyes of the male; the male compound eyes not being divided into areas of large and small ommatidia; and the gena being very narrow or absent. No synapomorphies were found to resolve the trichotomy of the Usia-Parageron group.

Groupings within the monophyletic genus *Apolysis* were based primarily on shape of the spermathecal reservoir. *Apolysis mus, A. mitis,* and *A. sedophila* (Brunetti) all have a small, bulb-shaped spermathecal reservoir (Fig. 17c), *A. flavi-femoris* (Hesse) has a long, straight reservoir, while *A. cinereus* Evenhuis, *A. sp. B* from Greece, and *A. humilis* all have variations of a coiled spermathecal reservoir. *Apolysis mus* and *A. mitis* form a monophyletic group based on the apomorphic subapical placement of the dististylus on the basistylus of the male genitalia.

The present analysis shows that the presence or absence of a discal cell is not uniquely derived. The cladogram shows that *A. humilis* and *A. cinereus* form a monophyletic group with *A.* sp. B (Greece) based on the shared apomorphic state of the variously coiled spermathecal reservoir [i.e., either tortuous (Fig. 17e) or strictly coiled (Fig. 17b)]. Apolysis humilis and A. cinereus lack a discal cell, but A. sp. B (Greece) has a discal cell. Melander (1946a) noted the inconsistent presence of a discal cell in some of his species [especially A. instabilis (Melander)], which he placed in Oligodranes Loew. The series of specimens upon which the original description of A. instabilis was based included many that lacked a discal cell in one or both wings. The median field is subject to variability in the loss of certain medial veins and associated crossveins throughout the families of brachycerous Diptera, Hardy (1955) mentions this reduction of venation in brachycerous Diptera as an evolutionary step toward the extreme reduction of venation in Empidoidea.

Parallelisms in the Usiinae analysis are exemplified by the presence of dichoptic eyes, the absence of a division of the eyes into areas of large and small ommatidia (shared by Usia s. lat. and Apolvsis flavifemoris), the long, thin maxillary palpus (shared by Parageron lutescens and Apolysis), the subapical placement of the dististylus on the basistylus [shared by Apolysis sp. B (Greece), and A. mus, and A. mitis], and the length of the aedeagus being shorter than the basistylus (shared by the African species Apolysis flavifemoris and A. humilis). No reversals are apparent in this analysis; however, some reconstructions of the cladogram would present reversals (primarily with regard to character 6 if that character were treated as apomorphic at the base of the cladogram).

More work needs to be done on the African species of Apolysis having dichoptic males. Hesse (1975) described many new species of Apolysis, including those that have dichoptic males, and pointed out certain leg characters that need further analysis. Only a few specimens of A. flavifemoris and A. maherniaphila were available for the present study. Also, further analysis is needed at the species level for species constituting the lutescens and incisus groups of Parageron. This phylogenetic analysis did not reveal synapomorphies to resolve the trichotomy of those two species groups and Usia s. lat. More detailed analysis of long series of specimens of the two species groups may show that they are subgenerically distinct within Apolysis.

Analysis of the genera of Phthiriinae

All ten genera of the subfamily Phthiriinae were analyzed in this study. The data set containing 29 characters (Table IV) resulted in one most-parsimonious tree (Fig. 3) with unresolved trichotomies, a length of 26 steps, and a Consistency Index of 0.962.

The Phthiriinae appear monophyletic based on two apomorphies: the presence of an apical sulcus on the third antennal segment, and the presence of a basal sac of the spermathecal reservoir of the female genitalia.

Of the two tribes recognized within the Phthiriinae, the Poecilognathini is shown to be monophyletic based on the following apomorphies: the monomorphic thoracic pattern in males and females; the presence of an epiphallic penial guide and epiphallic spines; and the absence of a basal extension of the basistylus in the male genitalia; and the vaginal apodeme in the female genitalia consisting of paired, L-shaped sclerites. The tribe Phthiriini is monophyletic based on the apomorphic condition of the presence of micropubescence on the metapleuron.

Within the four genera of the Poecilognathini, *Tmemophlebia* and *Relictiphthiria* are a monophyletic group and share the following two synapomorphies: sclerotized villi on the mesoapical portion of the epandrium, and broad, thick dististyli in the male genitalia. *Euryphthiria* and *Poecilognathus* constitute the other monophyletic grouping and possess the synapomorphy of the large, ellipsoid apical portion of the spermathecal reservoir. In this apomorphic state, the length of the reservoir is greater than the length of the ejection apparatus.

Within the six genera of the Phthiriini, the genera *Pygocona*, *Acreotrichus*, and *Australiphthiria* are monophyletic defined by the synapomorphy of the polymorphic pattern of bisection of the compound eyes. (In the case of *Pygocona* and *Australiphthiria*, the division of large and small ommatidia is vertical, so that large ommatidia are in the front and small ommatidia are more lateral and posterior.) The secondarily derived state of this character is found in the genus *Acreotrichus*, which has lost the bisection of the compound eyes into large and small ommatidia. No synapomorphies could be found to resolve the trichotomy of *Pygocona*, *Australiphthiria*, and *Acreotrichus*.

The Old World genera of Phthiriini (*Phthiria*, Acreotrichus, Australiphthiria, and Pygocona) form another monophyletic group based on the synapomorphy of the presence of pile on the pteropleuron. The Nearctic genera Acreophthiria and Neacreotrichus form a monophyletic group separate from the Old World Phthiriini based on the synapomorphy of a small, blunt apical portion of the spermathecal reservoir complex in the female genitalia.

Homoplasy was found in only one character in the analysis. This parallelism exists in the apomorphic state of an incomplete costal vein in the wing. Both *Pygocona* and *Tmemophlebia* share this trait; however, *Pygocona* belongs to the Phthiriini and *Tmemophlebia* belongs to the Poecilognathini. This apparent apomorphic character state is also found in a few other genera of Bombyliidae (e.g., some *Apolysis* species) and is usually correlated with small, pale-colored species.

A detailed analysis of the southern African species of *Phthiria* is needed. These species exhibit differences in the shape of the third antennal segment and of the apical portion of the spermathecal reservoir; both characters must be reanalyzed from longer series of specimens than were available in this study. Further analysis of these African species may show them to be subgenerically distinct from *Phthiria* s. str.

Systematic History of the Subfamilies Usiinae and Phthiriinae

Though various taxonomic works on Bombyliidae before 1900 treated a few genera and placed them in broadly defined subfamilies, no real subfamilial classification existed for the family as a whole until Becker (1913). Within his classification scheme, the genera Usia, Legnotomyia Bezzi, and Psiatholasius Becker constituted his new subfamily Usiinae, and the genera Phthiria, Geron, Oligodranes, Apolysis, Rhabdopselaphus, Crocidium Loew, Semiramis Becker, Apatomyza Wiedemann, and Acreotrichus constituted his new subfamily Phthiriinae. The key in Becker (1913) separates Usiinae from Phthiriinae on purely artificial characters: 'Breit gebaute Arten mit kurzen Hinterleib' for Usiinae, versus'...nicht breite gebaute buckelige Arten' for Phthiriinae. Size has never been a good character for separation of taxa at any level (species, genera, or subfamilies) in the Bombyliidae because of the extreme interspecific and intergeneric variation exhibited in that character throughout the family. Becker also separates Phthiriinae from Usiinae by the lack of leg bristles. However, examination of specimens during the present study shows that leg bristles are absent not only in *Phthiria*, but also in *Usia* and other genera within the Usiinae (sensu Becker).

Since Becker (1913), various classificatory schemes have been proposed in the family (Table I). The composition of genera in the subfamilies Usiinae and Phthiriinae has varied considerably, with some genera being placed in the Usiinae in one classification, and in the Phthiriinae in another (Table II).

Despite the various classifications that have been proposed, Becker's (1913) characterization and generic composition of the Usiinae and Phthiriine has been followed by many contemporary workers, due primarily to traditional bombyliid taxonomic concepts and ideology. There has been no thorough phylogenetic study of the genera comprising these two subfamilies. Regional workers have treated a few of the genera in one or both subfamilies taxonomically but, for the most part, have retained the framework of the original generic composition laid out by Becker (1913).

Bezzi (1924) was the next worker after Becker (1913) to propose a system of classification for the Bombyliidae. Though Bezzi (1924) studied only the genera of Bombyliidae in the Ethiopian (= Afrotropical) Region, he presented in his introduction a list of all the bombyliid genera known at that time and placed them in the subfamilies listed by Becker (1913). Bezzi's major contribution to bombyliid classification was the splitting of the family into two 'sections': (1) the Homoeophthalmae, comprised of genera having the hind margin of the eye entire and not bisected posteriorly, and having the occiput not hollowed; and (2) the Tomophthalmae, consisting of genera having the hind margin of the eye bisected and indented pos-

TA	B	LI	E.	I.	Sub	famil	ial	com	position	of	the	Bomb	vliidae	Homoeo	phthalmae
	_		-	_						~,			,		

Subfamily	Works*														
	A	В	С	D	E	F	G	Н	I	J	К	L	This study		
Bombyliinae	×**	×	×	×	×	×	×	×	×	×	×	×	×		
Cythereinae	×	×	×	×	×	×	1	×	×	×	9***	×	9		
Mariobezziinae	×	×	-+	×		×	1	×	1	-	4	11	11		
Heterotropinae	×	×	×	×	×	×	×	×	×	×	×	×	×		
Usiinae	×	×	7	×	7	×	×	×	×	7	×	×	×		
Cyrtosiinae	×	×	×	×	3	×	3	×	6	6	6	×	6		
Phthiriinae	×	×	×	×	×	×	×	×	×	×	×	×	×		
Systropodinae	×	×	×	×	×	×	×	×	5	12	×	×	12		
Toxophorinae	×	×	×	×	×	×	×	×	×	×	×	×	×		
Cylleniinae	×	×	×	×	×	×	9	×	×	×	9	×	9		
Xenoprosopinae	—	-	×		-	-	×	×	×	-	-	-	×		
Mythicomyiinae	10	10	10	10	×	10	×	×	×	×	×	×	×		
Gerontinae	7	7	×	7	7	×	×	×	5	×	×	×	×		
Ecliminae	-	-	_	2	2	2	1	×	—	×	×	×	×		
Henicinae	-		2	2	-	-	2	×	2	-	-	_	2		
Oniromyiinae	-	-	11	-	-	—	1	×	×	_	-	—	9		
Platypyginae	10	10	10	10	×	10	×	6	6	6	6	×	6		
Corsomyzinae	-	-	1	8	-	-	1	8	11	-	×	_	11		

* Works in which the classification schemes, presented in the table above, are proposed are indicated by letters as follows: A, Becker (1913); B, Bezzi (1924); C, Hesse (1938); D, Paramonov (1938); E, Painter & Painter (1965); F, Zaitzev (1966); G, Hull (1973);; H, Hall (1975); I, Bowden (1980); J, Hall & Evenhuis (1980); K, Theodor (1983); L, Zaitzev (1989).

** Works in which the subfamily is treated.

*** Subfamilies under which the subfamily listed in the table was treated synonymously or the section to which that subfamily was removed in a particular work are indicated as follows: 1, Bombyliinae; 2, Cylleniinae; 3, Platypyginae; 4, Corsomyzinae; 5, Toxophorinae; 6, Mythicomyiinae; 7, Phthiriinae; 8, Usiinae; 9, removed to section Tomophthalmae; 10, Cyrtosiinae; 11, Cythereinae; 12, treated as a family.

⁺ Subfamilies not treated in a particular work are indicated by a dash (-). This lack of treatment is due often to the regional limits of that particular work.

teriorly, and having the occiput hollowed and strongly bilobed. These two sections correspond roughly to pre-1820 concepts of the families Bombyliidae (with Bombylius-like genera) and Anthracidae (with Anthrax-like genera), respectively, which were united by Meigen (1820) into the Bombyliidae. The genera of the subfamilies Usiinae and Phthiriinae are found in the section Homoeophthalmae. Bezzi's (1924) Usiinae included the fossil genus Lithocosmus Cockerell, and the extant genera Corsomyza Wiedemann, Callynthrophora Schiner, Megapalpus Macquart, Psiatholasius, Legnotomyia, and Usia. His Phthiriinae contained the fossil genera Acreotrichites Cockerell and Geronites Cockerell, and the extant genera Phthiria, Crocidium, Semiramis, Apatomyza, Acreotrichus, Neacreotrichus, Desmatomyia Williston, Apolysis, Oligodranes, Geron, and Rhabdopselaphus. Male and female genitalic characters had still not been used widely in bombyliid systematics in Bezzi's time and his key (1924) separates the Usiinae and Phthiriinae on just a single wing character (viz., whether the cubital fork is widely open or not). Had Bezzi examined the male and female genitalia, as well as other characters, he might have discovered that a number of genera in his Phthiriinae did not belong there, and that some of the genera allied to and including Corsomyza did not belong in the Usiinae.

Bezzi's (1924) listing of genera was updated by Paramonov (1938) who maintained Becker's subfamilies and developed no new classificatory scheme.

Hesse (1938) produced one of the most prodigious tomes on bombyliid taxonomy. His work on the South African bombyliid fauna [which comprises three parts (1938, 1956a, 1956b)] is still a paradigm of bombyliid systematics. Hesse was one of the first bombyliid workers to recognize the value of male genitalic characters, and he augmented his species descriptions with detailed illustrations of male genitalia as well as antennae and other salient characters. Working on the Bombyliidae of a region that included over 1,000 specific forms and more than 100 genera (see Bowden, 1980), Hesse was able to determine the amount of variation that existed for certain characters within and among genera in that area. Although Hesse described new genera to accommodate the many new forms he discovered, he did not describe any new genera for the Phthiriinae (he did not recognize the Usiinae as occurring in the region and continued to place Apolysis and Oligodranes in the Phthiriinae). However, through detailed study of characters overlooked by previous workers, Hesse was able to justify the removal of *Geron* and allies to a separate subfamily, the Geroninae [sic], and recognized the placement of *Crocidium*, *Adelogenys* Hesse, and *Apatomyza* in the Bombyliinae rather than in the Phthiriinae. He also removed *Gonarthrus* Bezzi from the Phthiriinae and *Corsomyza*, *Callynthrophora*, *Megapalpus*, and *Hyperusia* Bezzi from the Usiinae and placed them all in the Bombyliinae, recognizing that the *Corsomyza*-group of genera constituted a separate and distinct assemblage.

It was not until nearly 30 years after Hesse (1938) that another classification scheme was developed (Zaitzev, 1966). During that 30-year interval, none of the limited regional catalogs or restricted taxonomic studies (e.g., Melander, 1946a; Painter & Painter, 1965), presented any new ideas concerning subfamilial classification.

The work by Zaitzev (1966) is very useful, as it brings together much of the previous, and sometimes obscure, Russian taxonomic bombyliid literature and presents it in the context of his monographic systematic study of the Bombyliidae of Transcaucasia. Zaitzev was one of the first workers to recognize the taxonomic potential of female genitalia in bee flies. He illustrated primarily spermathecal reservoirs, but also the vaginal apodeme and associated sclerites. His classification included only Palearctic genera, but he added genera described by Paramonov subsequent to Bezzi (1924) to the Usiinae and Phthiriinae. Usia, Parageron, and Dagestania Paramonov constituted Zaitzev's Usiinae; he placed Phthiria, Oligodranes, Semiramis, Tamerlania Paramonov, and Apolysis in the Phthiriinae.

A major problem with all of the classification schemes listed thus far was the lack of a proper broad-spectrum phylogenetic perspective that could be used to determine synapomorphies among the taxa previously considered as belonging to either the Usiinae or Phthiriinae. The only worker to attempt such an analysis was Mühlenberg (1971), who attempted to determine phylogenetic relationships among all of the bombyliid subfamilies. The results of his analysis were rather icarian for several reasons, the most important of which was that he restricted his analysis by using a limited group of characters (primarily associated with and including the female genitalia). Also, his analysis did not have an outgroup, thereby leaving his character-state polarities unjustified and open to debate, though most seem reasonable. Of the dozen or so genera known in the Usiinae and Phthiriinae at that time, Mühlenberg studied only Usia, Oligodranes, and Phthiria. His limited results, therefore, leave considerable room for further analysis in the present study with the goal of determining possible natural relationships among the taxa of these two subfamilies.

Hull (1973) brought together for the first time all the bombyliid systematic literature (up to 1965) and presented a monographic review of all the genera of the family. The work is marred by egregious errors, omissions, and considerable neglect with regard to the rules of nomenclature; however, its usefulness as a reference for the systematics of the genera of the Bombyliidae cannot be overstated. Despite Hull's shortcomings with respect to thoroughness and accuracy, he apparently had an aptitude for discerning generic and, to a lesser degree, suprageneric relationships. His classification introduced a number of new tribes, which consisted of groups of genera that had previously lacked infrasubfamilial treatment. Some of Hull's tribes have been used in subsequent works (i.e., Bowden, 1980), but others have been reduced to junior synonymy as a result of more detailed morphological study (e.g., Bowden, 1985). Hull's (1973) concept of the genera comprising the Usiinae (viz., Apolysis, Oligodranes, Dagestania, and Usia) prompted Hesse (1975) to revise his subfamilial concept of the Phthiriinae in the South African fauna by removing Oligodranes and Apolysis to the Usiinae. Bowden (1980), however, did not agree with Hesse's revised composition of the Usiinae and returned Oligodranes and Apolysis to the Phthiriinae. Hull's Phthiriinae included only the genera Acreotrichus and Phthiria (1973: 62), but on p. 195 he added his new subgenera of Phthiria (Agenosia and Pygocona) to the group. Except for the placement of Oligodranes in the Usiinae, Hull's (1973) classification of the Usiinae and Phthiriinae forms the foundation of the classification presented in the present study.

Hall (1975) dealt primarily with the Bombyliidae of Chile; however, in an appendix he lists the bombyliid genera of the world and their subfamilial arrangement. This classification essentially follows that of Bezzi (1924) and differs considerably from that presented in Hull (1973). (Hall's work was submitted for publication before Hull's monograph was published.) In the work by Hall (1975) the subfamily Usiinae is rather large and comprises the genera Callynthrophora, Corsomyza, Dagestania, Eusurbus Roberts, Gnumyia Bezzi, Hyperusia, Isocnemus Bezzi, Legnotomyia, Megapalpus, Psiatholasius, Pusilla Paramonov, Usia, and Zyxmyia Bowden. A number of these genera had been removed by Hull (1973) to the Bombyliinae (e.g., the *Corsomyza*-group of genera). Hall's (1975) Phthiriinae included the genera *Acreotrichus, Apolysis, Desmatomyia, Gonarthrus, Oligodranes, Parageron, Phthiria, Semiramis,* and *Tamerlania.* Of these, *Gonarthrus* had been justifiably removed to the Bombyliinae by Hesse (1938) and others (viz., *Apolysis, Oligodranes*) were placed in the Usiinae by Hull (1973). Hall's placement of *Eusurbus* in the Usiinae evidently follows Roberts (1929), who decided on this subfamilial placement following Bezzi's (1924) key to subfamilies. Hull (1973) and subsequent authors (Theodor, 1983; Bowden, 1985) place *Eusurbus* in the Bombyliinae.

In his catalog of Afrotropical Bombyliidae, Bowden (1980) presents a major change in bombyliid classification. In his classification, Usia is the only Afrotropical representative of the Usiinae, the Bombyliinae and Heterotropinae are listed between the Usiinae and Phthiriinae, and the Phthiriinae consists of Apolysis, Oligodranes, and Phthiria. This classification and generic composition of subfamilies is a highly conservative approach to the taxonomy and phylogeny of the Usiinae and Phthiriinae. Though no explanation of this classification or of why the Usiinae and Phthiriinae were so widely separated was published in the catalog, subsequent works (e.g., Bowden, 1985) mention that some of the classification published in the catalog follows Greathead (1980a). There is no explanation of the classification used in Greathead (1980a); however, another work by Greathead (1980b) stated that a new system of classification was being developed by him and Bowden, based on fewer subfamilies and more tribes. Except for the portion of this new classification pertaining the Afrotropical fauna (Bowden, 1980), this scheme has yet to be published.

Theodor (1983) is a valuable reference work on the male and female genitalic characters in the Bombyliidae. Unfortunately, Theodor based his classificatory decisions on examination of only a few representative specimens, much as Hull (1973) had done previously. Moreover, Theodor apparently was unacquainted with bombyliid taxa outside of the Mediterranean area and with recent bombyliid taxonomic literature. Theodor's illustrations are useful for basic reference, but the improper procedure of slide-mounting the specimens used for these illustrations rather than placing them in a spot plate with glycerine resulted in distortions of shapes of genitalic structures that are critical in distinguishing genera. Because of

Subfamily	Works*												
	1	2	3	4	5	6	7	8	9	10	11	This study	
Acreophthiria	_**	_	-	_	-		-	_		P***	_	Р	
Acreotrichites+	-	Р	-	_		Р	-	_	_	_	—	D	
Acreotrichus	Р	Р	-	Р		Р	Р	—	Р	Р	—	Р	
Agenosia	-	—	—	_	_	Р	-	-	_	Р	—	Р	
Apatomyza	Р	Ρ	В	Р	-	В	-	В		_	—	в	
Apolysis	Р	Р	Р	Р	Ρ	U	Р	Р	U	_	U	U	
Australiphthiria	-	_	_	-	-	_	_	_	_	Р	_	Ρ	
Callynthrophora	_	U	В	U	_	В	U	СТ	-		_	СТ	
Corsomyza	_	Ū	В	Ū	-	В	Ū	CT	CZ		_	CT	
Crocidium	Р	P	B	P	В	B	B	B	U	-	Р	B	
Dagestania	_	-	_	P	Ũ	Ũ	ũ	_	_	-	Ũ	ũ	
Desmatomvia	_	Р	_	P	-	B	P	_	_	-	-	Ď	
Euryphthiria	_	_	_	_	_	_	_	_		Р	-	P	
Eusurbus	_	_	_	_	_	В	IJ	_	в	_	_	B	
Geron	Р	Р	G	Р	G	Ĝ	Ğ	G	Ğ	_	G	Ğ	
Geronites ⁺	-	P	-	_	_	Ğ	_	_	_	_	_	P	
Gnumvia	_	-	в	IJ	_	B	II	CT	C7	_	_	ĊT	
Gonarthrus	_	P	B	P	_	B	P	B	B	_	B	B	
Hyperusia	_	-	B	II.		B	Î	СТ	-	_	_	CT CT	
Isocramus	_	_	D _	U	_	B	U U	B	_	_	_	B	
Lacrotomuia	TI	TI	_	U	B	B	U U	B	TI	_	_	B	
Mallonhthiria	0	U		P	Б	D	D	Б	U	_	_	D	
Maaanalnus	_	- -	D	I I		D	D U	CT	C7	_	_	D CT	
Megapaipus	_	U	D	0	_	D	D	CI	CL	D D	_	P	
Megaphiniria	-	- D	-	_	_	-	r	_	_	D	_	D	
Neacreotrichus	-	P		- -	- -		- D	- D		r		P	
Oligoaranes	r	P	P	P	P	U	r	P	U	_	U	U U	
Parageron	-	-	-	-	U	U	P	-	D	-	U	U	
Phthina	P	P	Р	P	P	P	P	P	P	Р	P	P	
Poecilognathus	-	P	_	_	-	P	Р		P	-	_	P	
Protophthiria	-	Р	-	_	-	P	_	_	_	-	-	CY	
Pseudempis	-	_	-	P	-	G	G	G	G	_	-	G	
Pseudoammictus	-	_	G	P	_	G	G	G	G	-	-	G	
Pseudogeron	-	Р	-	-	_	U	-	_	_	-	_	U	
Psiatholasius	U	U	_	U	В	В	U	В	U	_	_	В	
Pygocona	_	-	_	-	-	Р	_	-	Р	Р	-	Р	
Relictiphthiria	-	_	-	_	-		-		-	Р	-	Р	
Rhabdopselaphus	Р	Р	_	Р	-	U	Р	Р	U	-	_	U	
Semiramis	Р	Ρ	_	Р	Р	В	Р	_	_	-	Р	B	
Timiomyia ⁺⁺	_	-	-	Р	Р	В	Р	_	-	-	P	?	
Tmemophlebia+++	_	Ρ	-	_	_	Р	Р	_	_	Р	—	Ρ.	
Zarzia	-	_	_	_	_	_	-	_	_	_	_	RH	
Zyxmyia	-	-	-	-	-	В	U	СТ	CZ		-	СТ	

TABLE II. Subfamilial allocation of genera treated in the Usiinae or Phthiriinae at one time or another (includes taxa previously or now considered junior synonyms).

Works are indicated by number as follows: 1, Becker (1913); 2, Bezzi (1924); 3, Hesse (1938); 4, Paramonov (1938);
 5, Zaitzev (1966); 6, Hull (1973); 7, Hall (1975); 8, Bowden (1980); 9, Theodor (1983); 10, Evenhuis (1986); 11, Zaitzev (1989).

** Taxa not treated in a particular work are indicated by a dash (-).

*** Subfamilies are indicated as follows: B = Bombyliinae; CT = Cythereinae; CY = Cylleniinae; CZ = Corsomyzi₁ nae; D = Desmatomyiinae; G = Gerontinae; O = Oligodraninae; P = Phthiriinae; RH = Rhagionidae; U = Usiinae.

+ fossil genus.

++ new name for Tamerlania Paramonov (1931) (preoccupied by Skrjabin, 1924).

+++ new name for Cyclorhynchus Macquart (1840) (preoccupied by Sundevall, 1835).

these problems, statements by Theodor (1983) regarding some of the male genitalic characters should be viewed with caution. Despite such problems, Theodor corroborated Hull's (1973) placement of *Apolysis* and *Usia* in the Usiinae and of the *Phthiria*-group of genera in the Phthiriinae. He also presented an interesting proposal of infrafamilial grouping (alternate to the traditional sections Homoeophthalmae and Tomophthalmae) based on the shape of the occipital foramen, the merits of which must still be determined by further study.

I reviewed the genera of the Phthiriinae of Australia and the New World (Evenhuis, 1986) in order to make available generic names to accommodate disparate species groups that were to appear in upcoming monographs and catalogs of Nearctic and Australasian Diptera. In my review of the Phthiriinae, I recognized two groups of genera, the Phthiria group and the Poecilognathus group (since given tribal status in Hall & Evenhuis, 1987), based on male and female genitalic and pleural sclerite characters; described the new genera Acreophthiria, Australiphthiria, Euryphthiria, and Relictiphthiria; and found Macquart's Cyclorhynchus to be a good genus, proposing the replacement name Tmemophlebia, noting that Cyclorhynchus was preoccupied. Additionally, I removed Megaphthiria Hall to the Crocidiini of the Bombyliinae and erected a new genus in the Bombyliinae for the aberrant South American Phthiria luridus Walker (a non-phthiriine).

Zaitzev (1986) recently described an amber fossil genus, Zarzia, and added it to the Phthiriinae. Examination of the description and accompanying photograph reveal characters that preclude its placement not only in the Phthiriinae, but probably in the Bombyliidae. In the present work it is tentatively placed in the Rhagionidae pending further study. For a more detailed discussion see under Genera Removed from the Usiinae and Phthiriinae.

Zaitzev (1989) provided the most recent catalog of Palearctic Bombyliidae. In his classification, he follows Hull (1973) in placing Apolysis, Usia, Dagestania, Parageron, and Oligodranes in Usiinae; however, for some unexplained reason he places Crocidium in the Phthiriinae. His concept of Phthiriinae also includes Phthiria, Semiramis, and Timiomyia. Zaitzev's concept of Oligodranes is much the same as proposed here except that he includes hyalipennis Séguy, langemarki François, and modestus Loew, which are transferred to other genera in this study. Zaitzev also includes Usia ornatus and U. tomentosus Engel under Oligodranes. I have not been able to examine material of either of these two species to verify their generic placement within the Usiinae.

In all, 44 genus-group names have at one time been associated with either the Usiinae or Phthiriinae. Some have been justifiably placed in other subfamilies previous to the present study or are removed herein, leaving the genera Phthiria, Poecilognathus, Acreotrichus, Neacreotrichus, Apolysis, Oligodranes, Rhabdopselaphus, Usia, Dagestania, Parageron, Pygocona, Agenosia Hull, Acreophthiria, Australiphthiria, Euryphthiria, Relictiphthiria, and Tmemophlebia.

Key to the Subfamilies of Bombyliidae Homoeophthalmae (excluding the Systropodinae)

- 1. Clypeus attached to antennal bases; face absent between oral margin and antennae 2
- 2. Wing with four posterior cells; antennal sulcus apical, bordered by dorsal and/or ventral prongs of varying lengths Phthiriinae
- Wing with three posterior cells; antennal sulcus subapical and without dorsal and/or ventral prongs
- 3. Wing vein R_{4+5} not forked . Mythicomylinae

- 4. First antennal segment with bulbous ventral protrusion; mouthparts vestigial (may be Cythereinae) Xenoprosopinae

- Wing with four posterior cells 7
- 6. Prothorax well developed, it and mesonotum with strong bristles; second posterior cell length one-half its width Toxophorinae
- Prothorax normal, not strongly developed, dorsum of thorax without strong bristles (ex-

cluding prealar macrochaetae); second posterior cell length $2 \times$ width Gerontinae

- 7. Anterior tentorial pits present; apex of maxillary palpi small Bombyliinae
- Anterior tentorial pits absent; apex of maxillary palpi variable in size and shape 8
- 8. Maxillary palpus two-segmented . Ecliminae
- Antennal arista long, as long as first antennal segment; arista with a subapical sulcus containing a sensillum; mentum concave; female acanthophorites without spines . Desmatomylinae
- Antennal arista not as long as above; arista without sulcus; mentum convex; female acanthophorites with spines Heterotropinae

Taxonomic Treatment of the Genera of Usiinae and Phthiriinae

The subfamilial status of the Usiinae and Phthiriinae has been open to question since the publication of the paper by Rohdendorf (1964). In that work and subsequently (1977), it was proposed that the family Bombyliidae be split into four families, the Bombyliidae, Cyrtosiidae, Usiidae, and Systropodidae. The treatment of the Systropodidae as a separate family was followed by Hall & Evenhuis (1980) and Evenhuis (1982), but recent phylogenetic evidence indicates that this may have been premature. The systropodids are left here as a separate family until further study is undertaken to ascertain their phylogenetic placement within the Bombylioidea. The Cyrtosiidae (= Mythicomyiinae in the present sense; see Bowden, 1975b) may well warrant separate familial status. I am in the process of analyzing phylogenetic information on the genera of this monophyletic subfamily. Results obtained thus far show good evidence for following Rohdendorf (1964) in treating this group as a separate family and will be published elsewhere. Rohdendorf's Bombyliidae refers to all the remaining subfamilies of the section Homoeophthalmae except the Usiinae plus all the subfamilies of the Tomophthalmae (i.e., Antoniinae, Anthracinae, and Cylleniinae). The generic composition of Rohdendorf's Usiidae is not defined in his work, but it is assumed here that he intended the family to comprise only the subfamily Usiinae (i.e., Usia and allies).

No rationale or explanation is given by Rohdendorf (1964) for this proposed splitting of the family. He states only that more work must be done to corroborate his proposal. The present study presents no evidence to support the raising of the Usiinae to familial status. Even when the Usiinae and Phthiriinae are grouped together by virtue of their both lacking a sand chamber in the female abdomen (a structure used by the female to gather sand for coating eggs during oviposition), no strong evidence exists for raising them to family level because many other disparate elements within the Bombyliidae s. lat. also lack a sand chamber [e.g., Gerontinae, Toxophorinae, Antoniinae, Aphoebantus and Petrorossia Bezzi (Anthracinae), and Lordotus Loew (Bombyliinae)]. Based on results obtained during this study. I feel the Usiinae and Phthiriinae should remain in the family Bombyliidae as separate subfamilies.

Discussed below are those genera that, based on this study, belong to the Usiinae and Phthiriinae. A synonymical history, generic diagnosis and description, distribution, and brief systematic history of each genus is presented. In the list of specimens examined for each genus below, type specimens of species that were examined during this study are indicated by an asterisk (*) and original genus (for new combinations) is listed in parentheses.

The Genera of the Usiinae

The Usiinae as defined herein comprises the genera Apolysis, Usia, and Parageron. Characters that separate the Usiinae from the Phthiriinae include the following: there are three posterior cells in the wing, the bases of the fore coxae are attenuate (Fig. 10b), the third antennal segment possesses a subapical sulcus containing a transparent sensillum, and the ejection apparatus of the female genitalia possesses numerous lateral papillae (Figs. 9, 27, 30). In contrast, the Phthiriinae have four posterior cells (though vein M2 may be secondarily lost or rudimentary in some aberrant species, thus leaving three posterior cells), the fore coxae are separated at their bases (Fig. 10a), the third antennal segment has an apical sulcus bordered by ventral and/or dorsal prongs, and the female ejection apparatus lacks laterally projecting papillae. Additionally, genera in the Phthiriinae are characterized by the membranous to semimembranous basal sac of the female spermathecal reservoir (Figs. 42, 54).

Two new tribes of Usiinae are proposed in the present study: (1) Usiini, comprising the genera Usia and Parageron, and (2) Apolysini, consisting solely of the highly variable and widespread genus Apolysis. The Apolysini are characterized by the sulcus of the third antennal segment possessing an articulating pubescent arista in addition to the transparent sensillum, the male genitalia being rotated 45°–90°, and the female genitalia lacking a sclerotized plate at or near the vaginal opening at the base of the common spermathecal duct. The Usiini lack an articulating antennal arista (a structure similar to an arista may be present but is fused to the dorsal surface of the third segment and does not articulate), the male genitalia are rotated 180°, and the female genitalia typically possess a sclerotized plate or crescent-shaped structure surrounding the vaginal opening between the bursa copulatrix and the common spermathecal duct.

Key to the genera of the Usiinae



Fig. 10. Insertion of fore coxae onto thorax, anterior view. a) *Poecilognathus sulphureus* (Loew); b) *Apolysis humilis* Loew.

- 2. Integument of thorax and abdomen scrobiculate, usually shining to subshining

..... subgenus Usia Latreille s. str.

 Integument of thorax and abdomen not scrobiculate, usually shining to subshining (pollinose in males of some species)

..... subgenus Micrusia, subg. nov.

3. Antennal segment III with an articulating, spine-like arista and with sensillum placed in a subapical sulcus; male genitalia rotated 45–90°; female spermathecal reservoir long, coiled, curved, or straight; wing veins thin; ambient vein complete or stopping at or before anal vein

Antennal segment III with subapical sulcus

Tribe Apolysini, new tribe

Genus Apolysis Loew

- Apolysis Loew, 1860a: 86 [1860b: 269]. Type species: Apolysis humilis Loew, 1860, by monotypy.
- Rhabdopselaphus Bigot, 1886a: ciii [1886b: ciii]. Type species: Rhabdopselaphus mus Bigot, 1886, by monotypy. New synonymy.
- Pseudogeron Cresson, 1915: 201. Type species: Pseudogeron mitis Cresson, 1915, by original designation. New synonymy.
- Dagestania Paramonov, 1929: 133. Type species: Dagestania pusilla Paramonov, 1929, by monotypy. New synonymy.
- Oligodranes, authors, not Loew, 1844, misidentification.

Apolysis is a virtually cosmopolitan genus (absent only in the Australian and eastern Oriental regions) and comprises small, usually black, individuals characterized by the subapical sulcus of the third antennal segmnt containing an articulating, spine-like, pubescent arista and a transparent sensillum, and by the three posterior cells of the wing (discal cell may be present or absent).

Lengths. Body: 1.0–6.5 mm; wing: 1.5–7.0 mm. Head (Fig. 11). Width equal to or narrower than width of thorax; in lateral view as high as or slightly higher than long; oral margin extending to base of antennae; gena narrow or broad, often gray pollinose; antennae placed at upper tip of oral margin; face not present below antennae; occiput normally flattened, swollen posteroventrally in some species; occipital bullae sometimes present lateral to occipital foramen; ocellar tubercle prominent in male, less so in female; eyes holoptic or dichoptic in male, dichoptic in female; vestiture variable, often sparse (if present, densest on gena and occiput); antenna with segment I small, subcylindrical; segment II subequal in length to or shorter than segment I; segment III (Fig. 12) variable in length and shape, with dorsal subapical sulcus containing apically placed pubescent arista and small posteriorly or medially placed transparent sensillum; dorsal surface of segment III without hairs (pubescence may be evident); proboscis variable in length, commonly longer than head height, labellum about 1/4 length of proboscis; maxillary palpus (Fig. 13) one-segmented, varying in length from 1/10 to 1/2 length of proboscis.

Thorax. Usually concolorous with head, often pollinose, sparse to dense pilose; pronotal collar strongly produced or narrow in lateral view;



Fig. 11. Heads of Apolysis, lateral view. a) A. mitis (Cresson), male; b) A. mus (Bigot), male; c) A. mitis (Cresson), female; d) A. mus (Bigot), female.

mesopleuron pilose, sternopleuron bare, rarely with pile; metapleuron and hypopleuron bare or with pile. Legs thin, without spines or spicules on femora or tibia; fore coxae attenuate at prosternum in frontal view; claws large; pulvilli slightly longer than claws.

Wing (Fig. 14). Hyaline to subhyaline, infrequently infumate; veins brown to pale yellow; ambient vein incomplete, stopping at vein M_1 , CuA₁, or anal vein, or complete; anal cell closed before wing margin by stalk of variable length; with three posterior cells and two submarginal cells; discal cell present or absent; vein R_{2+3} straight to wing margin and parallel with R_{4+5} or curving slightly upward at extreme tip; rm crossvein variable in position, proximal or distal to middle of discal cell; vein closing apex of discal cell straight or sinuous; anal lobe large, subtriangular; axillary lobe well developed.

Abdomen. Width subequal to or narrower than width of thorax, attaining greatest width at segment II, tapering thereafter to apex; seven segments visible in both sexes; vestiture and patterning variable; ground color often dull gray to black, with pollinosity.

Male genitalia (Figs. 15, 16). Basistylus usually shorter than epandrium, with apicomesal lobe long or short; dististylus placed apically or sub-



Fig. 12. Apolysis third antennal segments. a) A. retrorsus (Melander); b) A. humilis Loew; c) A. cinereus Evenhuis; d) A. mus (Bigot); e) A. flavifemoris (Hesse); f) A. sp. A (Chile); g) A. longirostris (Paramonov); h) A. sp. B (Greece).

apically on basistylus, broad basally, tapering to apex, with or without lateral or mesal lobes; epiphallus usually conical in lateral view, tapering sharply to aedeagal tip, as large as or larger than basistylus, broad or narrow in ventral view; aedeagal bulb small or large; basal aedeagal apodeme variable in size and shape, rounded or elliptical, reduced or well developed; epandrium triangular to rectangular; cerci small, apical in position, slightly exserted or not exserted.

Female genitalia (Fig. 17) with vaginal apodeme U-, H-, or V-shaped, thinly sclerotized, medially sclerotized, or membranous; spermathecal reservoir long and coiled, twisted, or straight, or short and bulbous; apical spermathecal duct long, thin (length sometimes $2 \times$ that of abdomen, necessitating a boustrophedonic recurving resulting in spermathecal reservoirs facing posteriorly or anteriorly), slightly sclerotized apically, membranous basally near apex of ejection apparatus; apical valve present or absent, cylindrical or discshaped; basal valve present, cylindrical or discshaped; ejection apparatus with laterally projecting sclerotized papillae; basal spermathecal duct short or long, membranous, as wide as ejection apparatus or slightly thinner; common duct short or absent; vaginal opening membranous, without sclerotization or associated sclerotized plates.

Remarks. Loew (1860a, b) described the genus Apolysis for his single South African species A. humilis. In his generic diagnosis, Loew (1860b: 269) placed Apolysis in a group of genera including Phthiria, Geron and Oligodranes, noting that Apolysis was closest to the last two genera. Loew (1860b) implied, and Hesse (1938) stated explicitly, that the maxillary palpus of Apolysis comprised two segments. Examination in the present study of a long series of A. humilis plus additional specimens from South Africa and other parts of the world show that this interpretation is incorrect; the maxillary palpus is only one-segmented (Figs. 13a, b). One of the primary characters Loew (1860b) gave in distinguishing this genus from other genera with three posterior cells in the wing was the absence of a discal cell. This character has been used by all subsequent workers in separating



Fig. 13. Apolysis maxillary palpi. a) A. cinereus Evenhuis; b) A. humilis Loew.



Fig. 14. Apolysis wings. a) A. maherniaphila Hesse; b) A. quebradae Hall.

Apolysis from its apparent closest relative, Oligodranes, which possesses a discal cell. The presence or absence of the crossvein closing the distal portion of the discal cell is shown here to be a variable character in the genus Apolysis as defined herein (much the same as in Empidideicus Becker in the Mythicomyiinae, which resulted in the sinking of Anomaloptilus Hesse as a junior synonym).

Loew (1873) described a second species of *Apolysis* from Turkestan, and in the next 60 years just a few other species were described, all from the Palearctic fauna. The first major revisionary work of the genus (Hesse, 1938) showed that the majority of the species of *Apolysis* were to be found in the Afrotropical Region, especially in

southern Africa. Hesse's work gave detailed information on characters defining the genus and revealed variation in palpal length, wing venation, antennal shape, and the presence of both holoptic and dichoptic eyes in males.

Paramonov (1929) described a new genus, Dagestania, based on his single included species D. pusilla. Almost 20 years later, Paramonov (1947) added a second species, D. longirostris, to the genus. The unique female type specimens of both species were destroyed (Liepa, 1969), and the only record of additional collecting of the genus is found in Zaitzev (1966). Through the courtesy of Dr. V.F. Zaitzev, I have been allowed to examine one of the two known existing female specimens of Dagestania longirostris Paramonov. It exhibits characters found in Apolysis as defined herein. The wing has a discal cell and the palpi are onesegmented. The sparseness of hair on the thorax and abdomen, used by Paramonov (1929) in distinguishing the genus, can hardly be considered a diagnostic character. Vestiture is highly variable throughout the genera of the Usiinae. The shape of the third antennal segment (Fig. 12g) and female spermatheca (Fig. 17d) falls within the range of variation exhibited in Apolysis. Based on study of all the salient characters in the genus, I here place Dagestania as a junior synonym of Apolysis.

Melander (1946a) revised the Nearctic species of *Apolysis* and described eight new species, all from California. In his work, Melander noted that all Nearctic species possess one-segmented maxillary palpi, in contrast to Hesse's (1938) statement that Old World species had two segments. Melander refrained from giving his Nearctic species separate generic status, noting that Hesse (1938) has



Fig. 15. Male genitalia of *Apolysis cinereus* Evenhuis. a) lateral view; b) detail of dististylus; c) ventral view of basistylus and epiphallic complex.

Figure 15 is reprinted from 'Studies in Nearctic Bombyliidae (Diptera). II. Notes on the genus *Apolysis* with descriptions of two new species, 'by Neal L. Evenhuis, in *International Journal of Entomology*, Vol. 25, copyright by Bishop Museum Press, used by permission.



Fig. 16. Male genitalia of *Apolysis leberi* Evenhuis. a) lateral view; b) ventral view of basistylus and epiphallic complex.

Figure 16 is reprinted from 'Studies in Nearctic Bombyliidae (Diptera). II. Notes on the genus *Apolysis* with descriptions of two new species, 'by Neal L. Evenhuis, in *International Journal of Entomology*, Vol. 25, copyright by Bishop Museum Press, used by permission. shown that this palpal character was variable within other genera such as *Gonarthrus*. In the same work, Melander (1946a) also revised the Nearctic species of what he considered to be *Oligodranes*. Melander's generic identification of these species, however, was incorrect. Had he examined the syntype series of *Oligodranes obscuripennis* Loew and noticed the differences in palpal characters and head shape characteristic of true *Oligodranes*, Melander would have had to place his Nearctic species in the next available genus, *Rhabdopselaphus*.

Melander (1946b) described a fossil species, Apolysis magister, from the Oligocene Florissant shale of Colorado. I have not been able to examine the type specimen of A. magister to verify its generic placement, though the illustration (if correct) agrees with the characters of Apolysis as defined herein.

Hesse (1975) described new species of Apolysis



Fig. 17. Female spermathecal reservoirs of *Apolysis*. a) *A. quebradae* Hall; b)*A. analis* (Melander); c) *A. mus* (Bigot); d) *A. longirostris* (Paramonov); e) *A.* sp. A (Chile).

(as Apolysis and misidentified as Oligodranes) from southern Africa. That paper by Hesse is important for a number of reasons; among them, the fact that he follows Hull (1973) in placing Apolysis and Oligodranes in the Usiinae, and he shows, for the first time, the dichoptic condition of males of some species of his 'Oligodranes'.

Hall (1975) described 2 new species of Apolysis from Chile, thereby increasing the distribution of the genus from the Old World and Nearctic Region to include the southern Neotropical. The Chilean A. quebradae Hall differs from typical Apolysis (represented by the southern African A. humilis) in its dense pilosity and straight spermathecae (most species of Apolysis are rather bare and have coiled spermathecae). These characters, however, are shown herein to be subject to variability exhibited throughout the genus and as such have no value as being generically diagnostic.

Owing to characters of the face, palpi, and antennae, I have concluded from the present study that *Oligodranes* does not belong to either the Phthiriinae or Usiinae, and the genus is here transferred to the new subfamily Oligodraninae (see Genera Removed from Usiinae and Phthiriinae for detailed discussion). Of the species previously allocated to this genus, only the Palearctic species *flavus* Paramonov, *fumipennis* Loew, *gobiensis* Zaitzev, *obscuripennis*, and *superbus* Engel are retained in *Oligodranes*. The genus is thus autochthonous to the middle and southwestern Palearctic Region.

Two names are available for the remaining species from the Nearctic, Palearctic, and Afrotropical regions previously allocated to Oligodranes of previous authors (i.e., species possessing a discal cell): Rhabdopselaphus and Pseudogeron. Each represents a distinct group of species. Species fitting the description of Rhabdopselaphus characteristically have an oblong head, conspicuously so in females (Figs. 11b, d), and long maxillary palpi. Species fitting Pseudogeron, conversely, have a much shorter head and short maxillary palpi (Fig. 11a, c). Examples of each type of head shape and palpal length described above are found in species in regions of the world other than the southwestern Nearctic (the locality of the type species of Rhabdopselaphus and Pseudogeron). At first glance, one might be tempted to treat the two groups as distinct genera. However, the examination of representatives of each of the two nominal genera above plus additional individuals representing other species groups of Apolysis s. lat. throughout the world shows that Rhabdopselaphus and Pseudogeron are congeneric because of the large amount of variation in the characters examined. Moreover, further examination in this study of representatives of *Rhabdopselaphus*, *Pseudogeron*, and a number of taxa unplaceable in the above genera (as defined previous to this study) shows that *Rhabdopselaphus* and *Pseudogeron* comprise species that possess characters of male and female genitalia, wing venation, and antennae that fall within the range of variation exhibited in *Apolysis*. The genera *Rhabdopselaphus* and *Pseudogeron* are thus synonymized here with *Apolysis*.

A result of the treatment here of Rhabdopselaphus and Pseudogeron as junior synonyms of Apolysis, based on the aforementioned characters of antennae, palpi, and male and female genitalia, is the fact that the presence or absence of a discal cell has no taxonomic significance with regard to generic characterizations in this taxon. Apolysis humilis (the type of Apolysis) consists of specimens that lack a discal cell and possess coiled spermathecal reservoirs. Specimens of Rhabdopselaphus mus and Pseudogeron mitis (the types of their respective genera) possess a discal cell and have straight, or small and bulb-like, spermathecal reservoirs. If one compares specimens of only the type species of Rhabdopselaphus and/or Pseudogeron with Apolysis, a separation of specimens into Rhabdopselaphus and/or Pseudogeron and Apolysis seems straightforward. But both groups possess specimens in which these characters overlap. For example, specimens of the Chilean A. quebradae lack a discal cell and have straight, not coiled, spermatheca (Fig. 17a). Specimens of the Nearctic Oligodranes analis Melander (a Pseudogeron-like species) and an undescribed species from Greece possess a discal cell but have coiled spermathecae (Fig. 17b). An intermediate form exists in an undescribed species from Chile (Fig. 17e), which possesses a tortuous spermatheca.

Additionally, most South African *Apolysis* species have male genitalia with a triangular or conical epandrium, a basistylus smaller than the epandrium, and dististyli that are placed apically on the basistylus. Typical Nearctic *Rhabdopselaphus* species have male genitalia with a rectangular epandrium, a basistylus that is subequal in size to the epandrium, and dististyli that are placed subapically on the basistylus. Examination of representative specimens of numerous species groups of both genera show that the epandrium grades from conical to rectangular, the basistylus varies in size, and the dististyli vary in their placement on the basistylus.

Generic limits have always been a matter of

subjective preference. Given the differences in the species groups examined, one could separate the species fitting the description of Apolysis (as defined herein) into Apolysis s. str. (those species lacking a discal cell and having holoptic males), Rhabdopselaphus (those species with an oblong head, a discal cell, and long palpi), and Pseudogeron (those species with a short head, a discal cell, and short palpi) either at the generic or subgeneric level. New genus groups would be needed for those species lacking a discal cell and having dichoptic males, and for those species possessing a discal cell and having dichoptic males. After taking this course of action, the question remains of what to do with the residue of species that exist in the borderline areas (i.e., those species that possess combinations of characters of two or more of the groups above and that cannot be defined solely by those characters). Because of the variation exhibited among the species of these groups worldwide, grouping all these disparate elements of Rhabdopselaphus, Pseudogeron, Dagestania, and Apolysis into Apolysis is the more pragmatic solution.

The synonymy of Rhabdopselaphus, Pseudogeron, and Dagestania with Apolysis and the transferrence to Apolysis of species previously misidentified as Oligodranes results in a total of about 100 species currently known in the genus and four junior secondary species-group homonymies for which new replacement names are proposed herein. Based on studies of the types, the Afrotropical Oligodranes fumatus Greathead is here transferred to Phthiria, and the northern African Oligodranes hyalipennis Séguy is transferred to Parageron. Though examination of the type of Oligodranes modestus Loew was not possible during this study, the original description and subsequent descriptions by Engel (1932) and Paramonov (1947) confirm that it also should be transferred to Parageron.

During this study, examination of specimens of *Apolysis stuckenbergi* Hesse showed that it is conspecific with *A. humilis*. Characters given by Hesse (1975) in separating the two are variable among the specimens examined. Further study at the species level is likely to show that other species of Hesse (1975) are synonymous with older names.

Distribution. Nearctic, Palearctic, southern Neotropical, western Oriental, and south and western Afrotropical regions.

Species examined: AFROTROPICAL: Apolysis brachycera Hesse, A. brevirostris Hesse, A. capicola Hesse, A. corollae Greathead*, A. ele-

gans (Hesse)* (Oligodranes), new combination, A. flavipleura (Bowden)* (Oligodranes), new combination, A. fumalis Hesse, A. hirtella Hesse, A. humilis Loew, A. lactearia Hesse, A. maherniaphila Hesse, A. maskali Greathead*, A. minuscula Hesse, A. monticola Hesse, A. namaensis Hesse, 1975 [preoccupied by namaensis (Hesse), 1938; = hesseana Evenhuis, new replacement name], A. namaensis (Hesse), 1938 (Oligodranes), new combination, A. oreophila Hesse, A. a puberulas (Hesse) (Oligodranes), new combination, A. stuckenbergi Hesse (= humilis), new synonymy, A. semiflava Hesse, A. seminitens Hesse, A. thornei Hesse. NEARCTIC: Apolysis analis (Melander) (Oligodranes), new combination, A. anthonoma (Melander)* (Oligodranes), new combination, A. ater (Cresson) (Pseudogeron), new combination, A. bicolor (Melander) (Oligodranes), new combination, A. bifaria (Melander) (Oligodranes), new combination, A. bilineata (Melander)* (Oligodranes), new combination, A. bivittata (Cresson) (Pseudogeron), new combination, A. cinctura (Melander)* (Oligodranes), new combination, A. cinerea Evenhuis, 1983* [preoccupied by cinerea (Stguy, 1926); = crisis Evenhuis, new replacement name], A. colei (Melander)* (Oligodranes), new combination, A. comosa (Melander) (Oligodranes), new combination, A. disjuncta Melander, A. distincta (Melander)* (Oligodranes), new combination, A. divisa (Melander)* (Oligodranes), new combination, A. druias Melander*, A. eremitis (Melander) (Oligodranes), new combination, A. fasciola (Melander) (Oligodranes), new combination, A. formosa (Melander) (Oligodranes), new combination, A. glauca Melander, A. humbug (Evenhuis)* (Oligodranes), new combination, A. knabi (Cresson)* (Pseudogeron), new combination, A. leberi Evenhuis*, A. loricata (Melander)* (Oligodranes), new combination, A. lugens (Melander)* (Oligodranes), new combination, A. marginalis (Cresson) (Pseudogeron), new combination, A. matutina (Melander) (Oligodranes), new combination, A. mitis (Cresson) (Pseudogeron), new combination, A. montana (Melander) (Oligodranes), new combination, A. mus (Bigot)* (Rhabdopselaphus), new combination, A. neuter (Melander)* (Oligodranes), new combination, A. obscura (Cresson) (Pseudogeron), new combination. A. palpalis (Melander)* (Oligodranes), new combination, A. panneus (Melander) (Oligodranes), new combination, A. parkeri (Melander)* (Oligodranes), new combination, A. polius (Melander)* (Oligodranes), new combination, A. pulcher (Melander) (Oligodranes), new combination, A. pullata (Melander)* (Oligodranes), new combination, A. retrorsa (Melander) (Oligodranes), new combination, A. scapularis (Melander)* (Oligodranes), new combination, A. setosa (Melander) (Oligodranes), new combination, A. sigma (Melander) (Oligodranes), new combination, A. sipho (Melander)* (Oligodranes), new combination, A. speculifer (Melander)* (Oligodranes), new combination, A. timberlakei Melander*, A. togata (Melander)* (Oligodranes), new combination, A. trifida (Melander)* (Oligodranes), new combination, A. trochila (Coquillett) (Oligodranes), new combination, A. zzyzxensis (Evenhuis)* (Oligodranes), new combination. NEOTROPICAL: Apolysis quebradae Hall, A. sp. (Chile). ORIEN-TAL: Apolysis sedophila (Brunetti)* (Usia), new combination. PALEARCTIC: Apolysis cinerea Séguy*, A. eremophila Loew, A. longirostris (Paramonov) (Dagestania), new combination.

OTHER NEW REPLACEMENT NAMES: Apolysis melanderella Evenhuis, for A. cinerea (Melander), 1946 (Oligodranes); preoccupied by A. cinerea Séguy, 1926. Apolysis zaitzevi Evenhuis, for A. montana Zaitzev, 1972; preoccupied by A. montana (Melander), 1946 (Oligodranes).

Tribe Usiini, new tribe

Genus Parageron Paramonov

Parageron Paramonov, 1929: 127. Type species: Parageron orientalis Paramonov, 1929 [= Usia lutescens Bezzi, 1925], by monotypy.

Parageron includes gray to yellow species similar in size and shape to some Apolysis and as large as or larger than some Usia species. The genus is apparently common in the Mediterranean and extends eastward into the Middle East, Mongolia, and southern USSR. The shape of the third antennal segment with a subapical sulcus containing a sensillum and without an arista will distinguish it from *Apolysis*. The holoptic or nearly holoptic eyes in the male, which are divided into an upper half with large-faceted and a lower half with smallfaceted ommatidia, and the broad gena lateral to the oral margin will easily separate this genus from species of Usia.

Lengths. Body: 2.0–12.0 mm; wing: 2.0–11.0 mm.

Head (Fig. 18). Narrower than thorax; ground color yellow (lutescens group) or dull gray to blackish pollinose; eves in male touching from just anterior to ocellar tubercle to frontal triangle or eyes separated, at most by width of single ommatidium; eves separated in female at vertex by almost $3 \times$ width of ocellar tubercle; ocellar tubercle small, pronounced in male, less pronounced and wider in female; occiput flat or nearly so in male, slightly inflated posteriorly in female, with or without occipital bullae lateral to occipital foramen; in frontal view with gena prominent, width at least 1/4 width of oral margin, often greater, with or without vestiture of varying lengths and density; antenna placed at upper tip of oral margin; antennal segment I short, cylindrical; segment II equal to or shorter than segment I: both segments bearing short pile and pubescence; segment III of two types (Fig. 19), either blunt apically, or anteroventral portion projecting forward, pointed, with subapical sulcus containing single transparent sensillum; anterior articulating arista absent (sometimes small projecting structure similar to arista present, fused to dorsal portion of segment III, not articulating), with pubescence and short, sparse dorsal hairs near sulcus; proboscis 2-6× length of head; labellum about 1/8length of proboscis; maxillary palpus (Fig. 20) one-segmented, usually shorter than antennae, often slightly inflated apically.



Fig. 19. Parageron third antennal segments. a) P. lutescens (Bezzi); b) P. ignorata (Becker); c) P. sp. (Gambia).

Thorax. Concolorous with head, sparse to densely pilose; pteropleuron bare; hypopleuron bare or with small tuft of tomentose hairs posterior to posterior thoracic spiracle; halter usually pale with knob yellow to whitish; legs devoid of definite spines, small, thin, spicules sometimes present on tibiae, tarsi, and apices of femora; legs usually densely pilose; claws 1/2 length of last tarsal segment; pulvilli as long as claws.

Wing (Fig. 21). Hyaline to subhyaline, without spots or infumate areas (except in Parageron punctipennis Loew); veins dark brown to brown; ambient vein ending at anal cell, infrequently continuing around anal lobe faintly; anal lobe well developed; with three posterior and two submarginal cells; rm crossvein at or before middle of discal cell; R_4 originating at or beyond base of second posterior cell; anal cell closed before wing margin by stalk, stalk length shorter than rm crossvein; vein closing apex of discal cell straight or



Fig. 18. Head of *Parageron ignoratus* (Becker). a) lateral view; b) frontal view.



Fig. 20. Parageron maxillary palpi. a) P. ignorata (Becker); b) P. lutescens (Bezzi).

slightly sinuous; squama usually whitish.

Abdomen. Ovate to ovate-linear, wider than, equal to, or narrower than thorax, widest at second segment, concolorous with rest of body, usually pollinose; posterior margins of segments often with pale-colored fascia.

Male genitalia (Fig. 22). Basistylus in lateral view as high as wide, subtriangular to subquadrate, usually equal in size to epandrium; dististylus short or long, often with laterally or dorsally directed lobes near apex; epiphallus with ventral process longer than aedeagus (*lutescens* group) or without ventral process; tip of epiphallus variable in size and shape, often membranous and/or with small spicules; aedeagus slightly sinuous to tip; basal aedeagal apodeme small, 1/2–1/4 length of epiphallus, slightly rounded; lateral ramus small, foliate; epandrium variable in size and shape, often subrectangular; cercus small, apical in position, slightly exserted.

Female genitalia (Fig. 9). Vaginal apodeme Ushaped, consisting of paired thin or thick, semicircular lateral sclerites connected medially by sclerotized or membranous medial sclerite (termed herein 'vaginal plate'); vaginal plate fairly large, of specific form, usually with broad, medial projection directed caudally; spermathecal reservoir obpyriform, sclerotized, with or without papillae apically and/or mucrones basally, without minute glands; apical spermathecal duct thin, membranous to slightly sclerotized apically at base of spermathecal reservoir, length about 1- $1.5 \times$ length of ejection apparatus; ejection apparatus cylindrical with lateral, darkly sclerotized, lacrymiform projections; apical and basal ducts wide, darkly sclerotized, disc-shaped; basal duct thin, subequal in length to ejection apparatus, membranous; common duct very short, vestigial, or absent.

Remarks. Parageron was described by Paramonov (1929) for his new species, P. orientalis, from Ashkabad, USSR. Parageron orientalis is one of a group of species that are yellow in color and have a characteristic shape of the third antennal segment



Fig. 21. Wing of Parageron ignoratus (Becker).

(cf. Fig. 19a). The other group of species in this genus are usually gray and have the third antennal segment as in Figs. 19b, c. The majority of *Parageron* species are found in the latter group.

After Paramonov's (1929) description, Engel (1932) reduced *Parageron* to subgeneric status under *Usia*. This arrangement was followed by Hull (1973), but Paramonov (1947), in his work on the *Usia* group of genera, retained *Parageron* as a separate genus.

Efflatoun (1945) was apparently either unaware of or ignored the existence of *Parageron* because many of his new species that fit the description of *Parageron*, including a new variety of Bezzi's *P. lutescens* (subsequently found to be synonymous with the type species of *Parageron*) were placed in *Usia*. No mention of *Parageron* is found in Efflatoun's work.

This confusion with respect to the generic status of *Parageron* apparently lies in the superficial resemblance of some species (especially in the *P. incisa* Wiedemann species group) to species of *Usia*. Male genitalia (to a lesser degree) and female genitalia (to a greater degree) show similarities in *Usia* and *Parageron* (cf. Figs. 22 and 26, 9 and 27). Moreover, the two genera share apomorphic characters that group them together phylogenetically (see Phylogenetic Analyses).

A number of new combinations in Parageron result from redefinition of the genus in this study, including many of Efflatoun's (1945) Egyptian Usia species. Unfortunately, not all of Efflatoun's species could be studied because the Efflatoun Collection is not allowed to leave Egypt and I was not able to travel to Cairo to examine types. Species of Usia sensu Efflatoun (1945) that are newly transferred here to Parageron include: deserticola, efflatouni Venturi (= bicolor Efflatoun), elbae, flavipes, griseus, minusculus, parvulus, and tewfiki. Other Usia species treated here as new combinations in Parageron include: Parageron aridus (Baez), P. glaucus (Evenhuis) (= griseus Paramonov), P. inornatus (Engel), P. martini (François), P. punctipennis (Loew), P. striatus (Baez), and P. vagans (Loew). Based on the original description and subsequent descriptions in Engel (1932) and Paramonov (1947), Oligodranes modestus is here transferred to Parageron.

Though the present study is limited to a revision of genera, it should be noted here that Paramonov's (1947) objection to Engel's (1932) synonymizing of *P. orientalis* Paramonov under *P. lutescens* Bezzi and Paramonov's (1961) argument with respect to Efflatoun (1945) decision to follow Engel's (1932) synonymy of these species are not



Fig. 22. Male genitalia of *Parageron lutescens* (Bezzi). a) lateral view; b) detail of dististylus; c) detail of epiphallic complex; d) ventral view of basistylus and epiphallic complex.

justified. The characters that Paramonov (1947) asserts are strong enough to separate the two species (viz., length and color of the proboscis, and amount of contrasting color in the thoracic pattern) are variable within species of the species group in question and are not diagnostic at the species level. Thus, the synonymy given by Engel (1932) is maintained here. I have examined specimens fitting the description of P. lutescens from Senegal, Cyprus, and the Sudan. Given that P. lutescens ranges from western Africa to the southern USSR, it is possible that the other species in this yellow-colored species group (viz., P. erythraea, P. minor, and possibly others) may be no more than color variations of P. lutescens. Further studies at the species level should be undertaken to confirm this.

Distribution. Throughout the Mediterranean area eastward to Mongolia and the Southern Palearctic Region.

Species examined: Parageron erythraeus (Greathead)* (Usia), new combination, P. gratus (Loew) (Usia), new combination, P. hyalipennis (Séguy)* (Oligodranes), new combination, P. ignoratus (Becker) (Usia), new combination, P. incisus (Wiedemann) (Usia), P. lutescens (Bezzi) (Usia), P. minor (Efflatoun) (Usia), new combination, P. punctipennis (Loew) (Usia), new combination, P. zimini Paramonov.

Genus Usia Latreille

Usia Latreille, 1802: 430. Type species: Voluccella florea Fabricius, 1794, by monotypy.

Volucella, authors, not Geoffroy, 1762, misidentification.

Voluccella, error for Volucella.

This genus is strictly Mediterranean and comprises primarily shining black species with wide abdomens. Most species are sparsely pilose, but Usia (Usia) vestita Macquart is densely pilose and superficially resembles large specimens of Parageron. Usia is easily distinguished from related genera by the dichoptic eyes in the males and an extremely reduced gena lateral to the oral margin (Fig. 23b). Two subgenera (one new) are recognized here: (1) those species with scrobiculate integument (Usia s. str.), and (2) those without scrobiculate integument (Micrusia, new subgenus).

Subgenus Usia Latreille

Usia Latreille, 1802: 430 (as genus). Type species: Voluccella florea Fabricius, 1794, by monotypy.

The nominate subgenus is easily distinguished by the scrobiculate integument, clavate apex of the third antennal segment, and the normally smaller male genitalia than in the subgenus *Micru*sia (a few species such as *U. vestita* have large male genitalia).

Lengths. Body: 3.0-10.0 mm; wing: 3.0-9.5 mm.

Head (Fig. 23). Compound eyes dichoptic in both sexes, eyes separated at vertex by width of ocellar tubercle, slightly more so in females than in males; front widest at level of antennae, this width remaining the same from level of antennae



Fig. 23. Head of Usia (Usia) bicolor Macquart male. a) lateral view; b) frontal view.

to mentum at closure of oral genal cup; eyes not bisected into areas of large and small faceted ommatidia; face absent below antenna; front predominantly shining black, pollinose to pruinose areas, if present, immediately lateral to and above antenna, vestiture consisting of short, sparse pile, small longitudinal depression sometimes present just anterior to ocellar tubercle; gena absent or greatly reduced to narrow strip; oral margin large with narrow lateral marginal lip, lip shining brown to black; occiput slightly rounded, most species with paired bullae lateral to occipital foramen; antenna with segments I and II cylindrical, almost subspherical, length of each subequal to width, with short sparse hairs on dorsal, lateral, and ventral surfaces; segment III (Fig. 24) inflated on basoventral one-third, apex subclavate, arista absent, short hairs dorsally along most its length, subapical sulcus with single sensillum; antennal ratio: 1:1:5; proboscis long, tubular, length about $3.5-4.0 \times$ head height; labellum short, pointed, length about one-sixth that of proboscis; maxillary palpus (Fig. 25) short, clavate apically with long hairs, length about one-half that of antenna.

Thorax. Dorsum of mesonotum relatively flattened, not as rounded as in Usia (Micrusia) or in Parageron; thorax in frontal view strongly triangular, more so than in other usiine genera; mesonotum and scutellum shining black, integument scrobiculate; pleura matte to pollinose; mesopleuron with pile; ptero-, sterno-, and hypopleura usually bare; halter normal with pale-colored knob. Legs with integument of femora scrobiculate; femora without spines, with long, fine hairs; tibiae and tarsi with small spicules on lateral and mesal surfaces; claws normal in size and shape; pulvilli broad, almost as long as claws.



Fig. 24. Usia (Usia) third antennal segments. a) U. (U.) aenea (Rossi); b) U. (U.) bicolor Macquart; Fig. 25. Usia (Usia) atrata (Fabricius) maxillary palpus.

Wing (cf. Fig. 21). Hyaline to subhyaline, without spots on crossveins; sometimes subcostal, marginal, and first basal cells infuscated brown to yellow; costal vein complete, ending beyond anal vein; veins thick, brownish; anal lobe reduced or well developed; three posterior cells; two submarginal cells; vein R_4 bifurcating at or slightly beyond end of discal cell; rm crossvein at or slightly beyond middle of discal cell; anal cell closed at wing margin by stalk, stalk length $0.2-2.5 \times$ length of rm crossvein; squama milky white with short, sparse fringe.

Abdomen. Broader than thorax, widest at second and third segments: ground color usually shining black, integument scrobiculate, vestiture usually consisting of sparse, short, stiff hairs; seven segments visible in both sexes.

Male genitalia (Fig. 26). Genitalia rotated 180°; genital capsule usually small (very large in U. vestita Macquart), usually placed subapically on sternum; basistylus subrectangular to subspherical in lateral view, membranous in some ventroapical and dorsomedial portions, with small mesoapical extension medial to insertion of dististylus, with narrow basal extension in some species connecting with medial bridge-like sclerite of epiphallus; dististylus placed apically on basistylus, of variable shape and size, usually with lobes and other projections of specific form; epiphallic complex consisting of a medial aedeagal sheath, paired broad lateral sclerites, and medial bridge-like sclerite (the last two connected to basal extension of basistylus); aedeagal sheath often of specific form apically, usually with membranous, winged keel apically; aedeagus enclosed within medial aedeagal sheath, sheath tubular below keel, fused with medial bridge basally (best seen in ventral view); aedeagal bulb small; basal apodeme as large as epiphallic complex, subtriangular, rounded dis-
tally; lateral rami broad in dorsal view, linearelliptical to foliate; epandrium larger than basistylus, subquadrate to rhomboid, curved inward dorsally, posterodorsal projections of varying sizes and shapes; cercus fairly large, well exserted.

Female genitalia (Fig. 27). Vaginal apodeme V-shaped, lateral sclerites thick or thin, connected medially by vaginal plate of variable size and shape, often of specific form; vaginal plate often with sclerotization reduced to lateral and apical rim and vaginal orifice or vaginal plate membranous; spermathecal reservoir ellipsoid, sclerotized, with or without minute glands basally; apical spermathecal duct thin, membranous, length about equal to ejection apparatus; ejection apparatus cylindrical, with numerous lateral papillate projections; apical and basal valves darkly sclerotized, disc-shaped; basal duct thin, membranous, length subequal to length of ejection apparatus; common duct small or vestigial.

Remarks. Usia is an old and well-known genus in the Bombyliidae and, as a result, is well represented in the bombyliid literature. Evenhuis (1983) records almost 150 articles dealing with *Usia.* Some of the pre-1850 literature (primarily Fabricius' articles) erroneously record species of *Usia* in the genus *Voluccella*. This was a misidentification (and misspelling) of Geoffroy's *Volucella* (a syrphid genus).



Fig. 26. Male genitalia of *Usia (Usia) bicolor* Macquart. a) lateral view; b) detail of epiphallic complex; c) isometric view of epandrium.



Fig. 27. Female genitalia of Usia (Usia) bicolor Macquart.

Becker (1906) was the first worker to revise the species of Usia s. lat. He placed the species into three groups, based on color of body pile (dark or pale) and whether or not the integument was shining or matte. He recognized 29 species in his study (some of which have been transferred in the present study to Parageron) and presented a key to all the species in the genus. Brunetti (1909) described two new species of Usia from India that, based on examination of types during this study, are transferred to Apolysis. Séguy (1926) gave a key to nine species of Usia occurring in France. His key follows Becker (1906) in separating the genus into groups based on dark or pale body pile. Engel (1933) reviewed 30 species of Usia from the Palearctic Region (treating Parageron as a subgenus of Usia). Efflatoun's (1945) work has already been discussed in detail under Parageron because most of the species of Usia he records from Egypt belong in Parageron and not Usia as defined in this study. Paramonov (1947, 1950) provided the next revisionary works on Usia. He placed his species in groups that are considered here either as genera (e.g., Parageron) or subgenera (Usia, subgenus Micrusia). Venturi (1948) presented an interesting ecological work on Usia in which he gave geographical and temporal distributions for eight species of Usia occurring in Italy. He also provided a table with the distributional ranges of 40 species of Usia throughout the Mediterranean. Zaitzev (1966) redescribed three species of Usia from Transcaucasia and provided the first illustrations of the male genitalia of Usia crinipes Becker and U. transcaspica Paramonov.

Greathead (1967) described Usia erythraea from Ethiopia and illustrated the male genitalia. Usia erythraea types were examined by me in the BMNH during the present study, the results of which show that the holotype male belongs in *Parageron* and is a member of the *lutescens* species group. The female paratypes are considerably different in antennal shape and in thoracic pattern and coloration, and though collected at the same time and place, they probably do not represent the same species as the holotype male. Species of *Parageron* as currently known do not show a dimorphic pattern in males and females nor do they have differently shaped antennae in males and females of the same species.

DuMerle (1971) provides a valuable reference to the biology and mating behavior of Usia atrata (Fabricius) and Usia sp. Bowden's (1980) catalog of the Bombylidae of the Afrotropical Region lists six species, all of which are transferred here to Parageron, thus leaving the genus Usia absent from the Afrotropical Region. Baez (1983) records two new species of Usia from the Canary Islands, but these are also transferred to Parageron in the present study (see Remarks section under Parageron for more details).

Distribution: Throughout the Mediterranean and Middle East and into western and central Europe.

Species examined: Usia (Usia) aenea (Rossi), U. (U.) atrata (Fabricius), U. (U.) bicolor Macquart, U. (U.) claripennis Macquart*, U. (U.) cuprea Macquart*, U. (U.) florea (Fabricius), U. (U.) vestita Macquart*.

Subgenus Micrusia, new subgenus

This subgenus is easily separated from the nominate subgenus by the non-scrobiculate integument and the non-clavate apex of the third antennal segment. The genitalic capsule of the males is very large, normally one-half the length of the abdomen.

Type species: Usia forcipata Brullé.

Lengths. Body: 2.5–4.5 mm; wing: 2.5–4.5 mm. Head. Males and females dichoptic; eyes of male not divided into large- and small-faceted ommatidia; eyes of male separated at vertex by width of ocellar tubercle, narrowing slightly anterior to ocellar tubercle, then widening at oral margin; eyes of female separated at vertex by $1.0-1.5 \times$ width of ocellar tubercle; ocellar tubercle not prominent in lateral view; gena extremely narrow to non-existent, usually only lateral marginal lip present; occiput bilobed, slightly inflated in both sexes; occipital bullae present or absent lateral to occipital foramen, not prominent; antenna placed at upper end of oral margin; antennal segments I and II short, cylindrical to globular, of equal lengths; segment III (Fig. 28) $4-6 \times$ length of segment II, with pubescence and small hairs dorsally; subapical sulcus with single transparent sensillum, without apical pubescent arista, proboscis length about $2 \times$ head height, usually with small hairs or spicules laterally on labrum or ventrally on labium; maxillary palpi one-segmented, short, clavate, similar to those in *Parageron* (Fig. 20a).

Thorax. Mesonotum slightly rounded, more so than in Usia s. str., integument non-scrobiculate, dorsum of mesonotum and scutellum subshining to shining, sometimes pollinose in males, vestiture consisting of short, sparse, stiff hairs (almost bristle-like); pleura subshining, ground color predominantly black; mesopleuron with pile; ptero-, sterno-, and hypopleura bare; halter normal in size and shape, knob pale-colored. Legs with femora slightly thinner than in Usia s. str., integument non-scrobiculate, with long, fairly stiff hairs ventrally; tibiae and tarsi with short, fine hairs and spicules, spicules becoming spine-like to scale-like mesoapically on tibiae and medially on tarsi; claws normal; pulvilli as long as claws.

Wing (cf. Fig. 21). As in Usia s. str. but anal lobe often more reduced.

Abdomen. Broader than thorax, ovate, widest at second and third segments, tapering to apex, ground color shining to subshining, males often pollinose; seven segments visible in both sexes; vestiture variable, often long, sparse pilose dorsally, sparser pilose ventrally.

Male genitalia (Fig. 29). Genital capsule large, often more than half of length of abdomen: genitalia rotated 180°; basistylus subspheroid in lateral view; dististylus at tip of apical basistylar lobe, mesoapical lobe of basistylus absent: dististylus of variable shape, usually onion-shaped with tapered or thin neck, lobes or other projection infrequent; epiphallus consisting of paired. thin sclerites, straight to aedeagal tip, hooked or curved apically, with terminal structure of specific form; aedeagus long, thin, slightly sclerotized, usually exposed outside epiphallic sclerites; basal apodeme of variable form, usually large, shorter than or subequal to aedeagal complex; lateral rami small, foliate; epandrium characteristically with large, prominent caudal projections of specific form; epandrium large, subhemispheroid in lateral view; cercus small, slightly exserted, at apex of epandrium.



Fig. 28. Third antennal segment of Usia (Micrusia) versicolor (Fabricius).

Female genitalia (Fig. 30). Vaginal apodeme V-shaped, thickened at apices of lateral arms; spermathecal reservoir subellipsoid to obpyriform, sclerotized; apical spermathecal duct membranous, thin, length slightly shorter than length of ejection apparatus; ejection apparatus cylindrical, with numerous papillate lateral projections; apical and basal valves darkly sclerotized, discoid; basal duct thin, membranous, length subequal to apical duct; common duct not evident.

Remarks. Becker (1906) was the first to recognize the distinctiveness of this group of species; however, he grouped them on the basis of the color of pile. Paramonov (1950) followed Becker and grouped the same species, and additional new species, together in his key to species in the genus Usia. Theodor (1983) also noted this assemblage of species and remarked upon the small size of species and disproportionately large male genitalia, stating that they 'may have to be considered as a subgenus'. The characters of the male and female genitalia examined in the present study, as well as the non-scrobiculate integument of the thorax and abdomen and the shape of the third antennal segment, corroborate Theodor's suggestion of subgeneric rank. Micrusia is proposed here for those species fitting the characters given in the key and described above.

Distribution. Southern Europe, northern Africa, and the Middle East.

Species examined: Usia (Micrusia) aurata (Fabricius), U. (M.) forcipata Brullé, U. (M.) hyalipennis Macquart^{*}, U. (M.) novakii Strobl, U. (M.) pusilla Meigen^{*}, U. (M.) sicula Egger, U. (M.) versicolor (Fabricius).



Fig. 29. Male genitalia of Usia (Micrusia) forcipata Brullé. a) lateral view; b) ventral view of basistylus and epiphallic complex; c) ventral view of epandrium; Fig. 30. Female genitalia of Usia (Micrusia) versicolor (Fabricius).

The Genera of Phthiriinae

Two tribes of the Phthiriinae were proposed in Hall & Evenhuis (1987). The Poecilognathini are characterized by the bare metapleuron, presence of an epiphallic penial guide fused to the basistylus, the presence of spines on the epiphallus, and the L-shape of the vaginal apodeme. The genera of the Poecilognathini are found only in the New World. The Phthiriini are characterized by the pubescent metapleuron, absence of spines on the epiphallus, lack of a penial guide, and the straight, bar-shape of the vaginal apodeme. The genera of the Phthiriini are found worldwide.

Key to the Genera of Phthiriinae

(modified from Evenhuis, 1986)

- Male genitalia not rotated 180°, basistylus ventral in position; apical segments of female abdomen compressed; last sternite of female abdomen pointed, possessing two spike-like bristles on apex Australiphthiria Evenhuis
- Costal vein incomplete, ending at vein M₂; basistylus not bilobed, consisting of a single conical sclerite Pygocona Hull
- 4. Basistylus with mesal lobe bearing spines or

denticles, apicomesal lobe reduced, small or inconspicuous; basistylus deeply emarginate, lobes fused medially by narrow, bridge-like sclerite; antennal segment III ovate or bulging at apical two-thirds; primarily gray-colored species; males and females similarly colored .. (Nearctic) Acreophthiria Evenhuis Basistylus without mesal lobe bearing spines, apicomesal lobe well developed; basistylus normal or deeply emarginate; antennal segment III shape variable; males and females usually dimorphic in pattern and coloration 5

- 5. Antennal segment III with conspicuous long hairs at dorsal bulge; face and body densely pilose in male; abdomen wider than thorax; basistylus deeply emarginate (Australia) Acreotrichus Macquart

- Female spermathecal reservoir curved apically (Old World, Chile) Phthiria Meigen
- Ambient vein incomplete, ending before anal vein; dististylus not broad in lateral view, length about 1/4 to 1/3 of basistylus .. (Nearctic, Neotropical) Tmemophlebia Evenhuis

- Large species (length 8–12 mm); proboscis flat, short, with spicules basolaterally; face broad, rounded in frontal view; oral margin small (Nearctic) Euryphthiria Evenhuis Usually smaller energies (length often 2.6 mm);
- Usually smaller species (length often 2–6 mm);

proboscis tubular, long, without spicules basolaterally; face narrow in frontal view; oral margin large, well developed (New World) Poecilognathus Jaennicke

Tribe Phthiriini

Genus Acreophthiria Evenhuis

Acreophthiria Evenhuis, 1986: 6. Type species: Acreotrichus americanus Coquillett, 1895, by original designation.

Members of this genus are superficially similar in appearance to those of the Australian genus Acreotrichus Macquart, but they differ primarily in male and female genitalic and antennal and abdominal characters and in having a bare pteropleuron. This genus is characterized in the male by the presence of a mesally directed basistylar process bearing spines (Fig. 33). The basistylus is often deeply emarginate, the lobes attached only by a narrow, bridge-like sclerite. The female spermathecal reservoir is not curved apically and the ejection apparatus has both apical and basal valves. The body coloration is normally uniform gray to dark brown, darker in the male, usually without pattern on the head, thorax, or abdomen. The Afrotropical species Phthiria lanigera is very similar in appearance but differs in male genitalic characters and shape of the third antennal segment.

Lengths. Body: 4.0-8.5 mm; wing 5.0-11.5 mm. Head (Fig. 31). Compound eyes in male touching for most of their length from anterior ocellus to frontal triangle, in female widely separated, width at vertex equal to about $3 \times$ width of ocellar tubercle; frontal area above antennae in male broad, predominantly bare, some hairs sometimes present medially directly above antennae, short pilose in female; facial area and gena broad in lateral view (in female produced above, receding below), rounded; oral margin without definite lateral marginal lip; antenna placed at upper tip of oral margin; face dense, long pilose; antennal segment I cylindrical, length $1.5-2.0 \times \text{length of sub-}$ spherical segment II; segment III in male long, thin, inflated at apical 2/3 or more, with apical sulcus bordered by dorsal and ventral prongs, long hairs dorsally near apical inflation; in female segment III shorter, more ovate, dorsal hairs shorter than in male; occiput flat in male, rounded in female, pilosity variable; proboscis $2.0-3.0 \times$ head height, labellum about 1/5 length of proboscis; palpus thin, 1/3-1/2 length of proboscis.

Thorax. Mesonotum fairly flat dorsally, sparse long pilose in male, sparser in female; pleura with meso- and sternopleura long pilose; small tuft of hair on posterior portion of hypopleuron; metapleuron with micropubescence; halter normal in shape, knob pale yellow to brown. Legs concolorous with pleura, slender, without definite spines, long hairs sometimes present, especially on coxae and femora, rarely on tibiae; claws normal; pulvilli as long as claws.

Wing (Fig. 32). Hyaline, or opaque and mottled; yellowish stigmatal area between end of veins Sc and R₁ faint in male, pronounced in female; veins dark brown to brown, ambient vein ending at anal vein, sometimes continuing faintly around anal lobe; vein R₁ ending at wing margin slightly closer to end of R₂₊₃ than to end of Sc; origin of R₄ at or before base of second posterior cell; rm crossvein near middle of discal cell (hyaline-winged species) or at apical 3/4 of discal cell (mottled-winged species); anal cell closed before wing margin by stalk, stalk length longer than rm crossvein; squama whitish.

Abdomen. Long, slender, equal to or narrower than width of thorax, tapering gradually to apex; color in male uniform gray to dark brown; color in female normally grayish, with paler colored fascia sometimes on tergites; vestiture of long, dense pile in male, shorter, sparser in female.

Male genitalia (Fig. 33). Basistylus consisting of two deeply emarginate lobes attached medially by narrow, bridge-like sclerite; in lateral view basistylus ovate-elliptical, with large basal extension, in dorsal view with mesally directed basistylar projection bearing spines or large denticles, apicomesal lobe short, without stout spines; dististylus short, stubby, with blunt apex; epiphallus smooth, gradually tapering toward thin apical neck, anterodorsal extension (ramus) short or long; aedeagus narrow, enclosed within epiphallus for most of its length; basal aedeagal apodeme elliptical or subcircular; lateral rami thin, foliate in ventral view; epandrium subhemispherical in ventral view



Fig. 31. Heads of Acreophthiria egerminans (Loew). a) female, dorsal view; b) male, lateral view; c) female, lateral view.

(i.e., rounded laterally) with small apicomesal notch, subtriangular in lateral view; cercus small, rounded, subapical, partially exserted.

Female genitalia (Fig. 42a). Vaginal apodeme consisting of two straight sclerotized lateral bars; spermathecal reservoir complex with apical portion ellipsoid-conical, not curved apically, darkly sclerotized; basal sac membranous, outer wall thick; apical spermathecal duct subequal in length to ejection apparatus, slightly sclerotized, sclerotization darkening apically near basal sac; ejection apparatus with apical and basal valves present, sclerotized, discoid; basal duct slightly longer than ejection apparatus, membranous; common duct short or absent.



Fig. 32. Wing of Acreophthiria egerminans (Loew).



Fig. 33. Male genitalia of *Acreophthiria similis* (Coquillett). a) lateral view; b) ventral view of basistylus and epiphallic complex; c) ventral view of epandrium; d) dorsal view of basistylus.

Remarks. Species in this genus have been previously treated in either *Acreotrichus* or *Phthiria* s. lat. Species of *Acreophthiria* superficially resemble those of *Acreophthiria* superficially resemble those of *Acreotrichus*, due primarily to the similar shape of the third antennal segment, which is conspicuously inflated at the apical 2/3 and has long hairs. In species of *Acreotrichus* these hairs are much longer and the shape of the third antennal segment is different (cf. Figs. 31, 35). Both genera are treated here within the Phthiriini. Despite their superficial similarities, the differences in male and female genitalic characters are such that the two should be kept as separate genera.

Distribution. Western Nearctic Region.

Species examined. Acreophthiria americanus (Coquillett)* (Acreotrichus), A. egerminans (Loew)* (Phthiria), A. maculipennis (Cole)* (Acreotrichus), A. similis (Coquillett)* (Phthiria).

Genus Acreotrichus Macquart

- Aceotrichus. Incorrect original spelling of Acreotrichus (Macquart, 1850: 315). Determined by First Revisor Principle in Evenhuis (1986).
- Acreotrichus Macquart, 1850: 425. Type species: Acreotrichus gibbicornis Macquart, 1850 [= Bombylius antecedens Walker, 1849], by original designation.

Members of this endemic Australian genus are distinguished by the conspicuous long hairs on the dorsal bulge and the prominant ventral prong on the third antennal segment (Fig. 35). The head (Fig. 34) and body are long, dense pilose, and the abdomen is wider than the thorax (in contrast to the more normal slender or conical abdomen in other phthiriine genera). Most species have hyaline wings; however, some undescribed species have spotted wings.

Lengths. Body: 2.5-8.0 mm; wing: 2.5-7.5 mm.

Head (Fig. 34). Width of head greater (in small specimens) or less than or equal to (in larger specimens) width of thorax; compound eyes in male holoptic, touching for entire length from ocellar tubercle to front, eyes separated at vertex in female by 1.5× width of ocellar tubercle, widening to venter of oral margin; front in male fairly broad, densely pilose; front in female broad, with transverse groove halfway between ocellar tubercle and antenna, sparse, short pilose, with a few short, stiff hairs along inner eye orbits; face broad in both sexes, visible in dorsal view as well as lateral view, densely pilose, ground color gravish, sometimes paler in female; occiput flattened (male) or slightly rounded (female), long pile concentrated and densest posterolaterally, sparse pilose in female, female often with pale stripe along posterior margin of eyes; antenna length equal to head height; segment I cylindrical, segment II subspheroid, both densely pilose dorsally and ventrally: segment III (Fig. 35) widest at or slightly beyond middle, apical sulcus with thickened, long, ventral prong rounded apically, dorsal prong small, papillate; antennal ratio: 2:1:5; proboscis long, tubular, with small hairs ventrally on labrum, length about 2-3× head height; labellum about one-fourth length of proboscis; maxillary palpus long, thin, length subequal to that of antenna.

Thorax. Mesonotum only slightly rounded in



Fig. 34. Heads of Acreotrichus antecedens (Walker). a) male, lateral view; b) female, lateral view.



Fig. 35. Antenna of Acreotrichus antecedens (Walker); Fig. 36. Wing of Acreotrichus antecedens (Walker).

lateral view, flatter than in other phthiriines; ground color dark grayish, often with pale postalar calli, scutellum, and notopleural suture in female; dorsum densely pilose in male, less so in female; pleura grayish; meso-, sterno-, and pteropleura and posterior portion of hypopleuron with long pile, denser in male; metapleuron with micropubescence, otherwise devoid of hairs; halter stem long, thin, knob of variable coloration. Legs thin; femora without spines; femora and bases of tibiae with long hairs and appressed tomentum; tibiae with a few short spines laterally and apically; tarsi with spicules laterally; claws normal; pulvilli almost as long as claws.

Wing (Fig. 36). Hyaline, subhyaline, or with spots on crossveins (the last in undescribed species); veins brown; costal vein ending at anal vein; base of vein R_4 often with proximally directed stump of a vein; anal cell closed in wing margin by stalk, stalk length about $1/_2$ length of rm crossvein; rm crossvein at $3/_5-7/_8$ distance along discal cell; anal lobe and alula well developed; squama subhyaline with brown rim and pale fringe of hairs.

Abdomen. As wide as or slightly wider than thorax (male), broadly ovate, wider than thorax (female), seven segments visible dorsally in both sexes, long dense pilose and tomentose in male, less so in female, ground color uniformly dark in most specimens, pale fascia present on posterior margins of tergites in some female.

Male genitalia (Fig. 37). Basistylus dorsal in position, deeply emarginate, lobes widely separated above; in lateral view with basistylus ovate, with basal extension; apicomesal lobe of basistylus well developed, with stiff hairs; dististylus long, broad, squared apically, with small hook at apex; epiphallus smooth, broad basally, sharply tapering to thin upper neck; anterodorsal exten-

sion (ramus) short; aedeagus sclerotized, bifurcate on upper half, pointed apically; basal aedeagal apodeme subtriangular to rounded, darkly sclerotized; lateral rami foliate in ventral view; epandrium subtriangular in ventral view, with deep apical notch above anterodorsal process; cercus small, apical in position, exserted.

Female genitalia (Fig. 42b). Vaginal apodeme lost; spermathecal reservoir darkly sclerotized, curved in a long U-shape; basal sac membranous, outer wall thick; apical spermathecal duct membranous, sclerotized only at apex near basal sac of reservoir, duct slightly longer than ejection apparatus; ejection apparatus as in Acreophthiria; basal duct long, membranous, about $2 \times$ length of ejection apparatus; common duct absent.

Remarks. Bowden (1971) redescribed the male of *Acreotrichus antecedens* (Walker) and first described and illustrated the male genitalia. Evenhuis (1986) augmented Bowden's description with a description of the female genitalia.

I was able to examine types of all the species currently treated in this genus. Additionally, the type of *Phthiria lineifera* Walker was examined in the BMNH and found to be congeneric with *Acreotrichus*. The new combination is listed below.

Distribution. Restricted to the Australian continent.

Species examined: Acreotrichus antecedens (Walker)*, A. fusicornis Macquart*, A. gibbicornis Macquart*, A. inappendiculatus Bigot*, A. lineifer (Walker)* (Phthiria), new combination.

Genus Australiphthiria Evenhuis

Australiphthiria Evenhuis, 1986: 8. Type species: Phthiria hilaris Walker, 1852, by original designation.

Members of this genus are easily separated from other genera in the Phthiriinae by the ventral position of the basistylus in the male genitalia and the laterally compressed apical segments of the female abdomen, the apex of which appears to be modified for a piercing type of oviposition. The genus is endemic to Australia.

Lengths. Body: 3.0-8.0 mm; wing: 3.5-7.5 mm.

Head (Fig. 38). Compound eyes in male touching for almost their entire length from anterior ocellus to frontal triangle, eyes in female separated at vertex by slightly more than width of ocellar tubercle; front widest in female at level of antenna, width $3\times$ width of ocellar tubercle, bare along inner eye orbits; front in male broad, triangular, with small patch of hairs above bases of antennae, bare laterally; face below antenna absent; oral



Fig. 37. Male genitalia of Acreotrichus antecedens (Walker). a) lateral view; b) ventral view of epandrium; c) ventral view of basistylus and epiphallic complex; d) dorsal view of basistylus.

margin rounded; in lateral view female gena produced or not produced at level of antenna; mentum produced ventrally, more so in female than in male; occiput flat in male, rounded in female; vestiture of head normally sparse; antennal segment I $1.5 \times$ length of segment II; segment II subspherical; segment III (Fig. 38) with widest point at or before middle, apex acute, with apical sulcus containing single sensillum, bordered by short but definite dorsal and ventral prongs; proboscis $2 \times$ head height; labellum about $\frac{1}{4}$ length of probiscis; maxillary palpus long, thin, about one-half length of proboscis.

Thorax. Mesonotum dark gray, brown, or black in male, paler shades of these colors in female, rounded more than in Acreophthiria, moderately fine pilose dorsally in male, sparser and shorter pilose in female; pleura normally grayish; meso-, sterno-, pteropleura, and posterior portion of hypopleura long pilose; metapleuron with micropu-



Fig. 38. Heads of Australiphthiria hilaris (Walker). a) male, lateral view; b) female, lateral view.

bescence, usually with longitudinal striation; halter stem pale, knob pale yellow to brown; legs long, slender, devoid of spines, small spicules present on tarsal segments; male usually sparse, long pilose on coxae and femora, shorter, more tomentose in female; claws normal; pulvilli as long as claws.

Wing. Hyaline; veins brown to dark brown; costal vein ending at anal vein, sometimes continuing faintly around anal lobe; yellow stigmatal area in cell Sc prominent in both sexes; R_1 ending in wing margin closer to end of R_{2+3} than to end of Sc; R_4 originating at or slightly before end of discal cell; anal cell closed before wing margin by stalk, stalk length subequal to rm crossvein; squama smoky brown to white.

Abdomen. Long, slender, equal to width of thorax, tapering to conical apex in male; abdomen shorter, compressed laterally on segments VI-IX in female, forming a pointed abdominal apex; eight segments visible in male, nine in female; vestiture consisting of fine, long pile in male, shorter pile and more tomentum in female.

Male genitalia (Fig. 39). Not rotated, basistylus ventral, bilobed, deeply emarginate, lobes widely separated at apex; basistylus ovate-elliptical in lateral view, with large basal extension; dististylus fairly broad, rounded apically, with small beak- or hook-like process at apex, with small denticles and short, stiff hairs; epiphallus in dorsal view broad basally, tapering sharply at apical $\frac{2}{3}$ to straight, narrow neck, small flap-like process medially (not to be confused with spine-like structures in genera of Poecilognathini); anterodorsal extension (ramus) normal in size and shape; aedeagus long, thin, tapering gradually to apex; basal apodeme subtriangular, vaned basally; lateral ramus thin, linear-foliate in dorsal view; epandrium subtriangular in ventral view, with small apicomedial notch or indentation (appearing bilobed in situ because of incomplete apical invagination), in lateral view long, subtriangular, with deep basal notch above anteroventral process; cercus small, subapical in position, barely exserted.



Fig. 39. Male genitalia of *Australiphthiria hilaris* (Walker). a) dorsal view of basistylus and epiphallic complex; b) lateral view; c) dorsal view of epandrium; d) ventral view of basistylus.

Female genitalia (Fig. 42c). Contained entirely within sternite IX (ovipositor); vaginal apodeme absent; spermathecal reservoir darkly sclerotized, curved strongly apically; basal sac membranous, outer wall thin, with numerous minute glands; apical spermathecal duct membranous, length subequal to length of ejection apparatus; ejection apparatus cylindrical, outer wall torulose; apical and basal valves present, sclerotized, discoid; basal spermathecal duct long, membranous, about $2 \times$ length of ejection apparatus; common duct short, semi-sclerotized.

Distribution. Endemic to the Australian continent.

Species examined. Australiphthiria hilaris (Walker)*, A. pallipes (Bigot)*.

Genus Neacreotrichus Cockerell

Neacreotrichus Cockerell, 1917: 377. Type species: Acreotrichus atratus Coquillett, 1904 [= Phthiria cingulata Loew, 1846], by monotypy. This genus is restricted to the New World and can be distinguished from other phthiriines by the long third antennal segment with a prominent ventral prong, and by the straight spermathecal reservoir of the female genitalia.

Lengths. Body: 2.0-5.5 mm; wing: 2.5-7.5 mm. Head (Fig. 4). As wide as or slightly less than width of thorax; compound eyes of male holoptic, touching for entire length from ocellar tubercle to front; eyes of female separated at vertex by almost 2× width of ocellar tubercle, widening to venter of oral margin; front well developed in both sexes or somewhat reduced; front in female with transverse depression almost halfway between ocellar tubercle and antenna, front strongly angled upward from depression to level of antenna; face absent below antenna; gena narrow or broad in lateral view, receding from antenna to mentum; front and gena short or long pilose in male (less so than in Acreotrichus), sparse pilose in female; occiput slightly rounded in both sexes, dense, long pilose laterally in male, less so in female; mentum normal in size and shape in male, inflated basally in some females [this space taken up by coiled proboscis much the same as in Apolysis corollae Greathead shown in Greathead (1966b)]; antennal length about three-fourths head height; segment I cylindrical, segment II globular, both with short hairs dorsally and laterally; segment III (Fig. 40) linear to linear-lanceolate, apical sulcus with thick ventral prong rounded apically, dorsal prong small, papillate, dorsal surface with a few short hairs, ventral surface of some females with mat of minute fine hairs hooked apically; antennal ratio: 1.5:1:6; proboscis long, tubular, length about $2.5-4 \times$ head height; labellum about one-fifth length of proboscis; maxillary palpus long, thin, non-clavate apically, subequal to three-fourths length of antenna.

Thorax. Black in male, paler, varicolored, and often patterned in female; mesonotum rounded in lateral view; thoracic pile sparse in both sexes, longer and denser in male; pleura with meso- and sternopleura pilose, pteropleuron and anterior portion of hypopleuron bare; halter normal, knob pale to black. Legs slender; femora without spines, with sparse hairs; tibiae and tarsi with small fine spicules; fore tarsi of some females with long hairs modified for collecting pollen (J.F. Neff, in litt.); claws normal; pulvilli almost as long as claws.

Wing (Fig. 41). Hyaline to subhyaline, rarely infuscated anteriorly; veins yellow to brown; costal vein ending at anal vein, continuing beyond faintly; second submarginal cell length $4-5\times$



Fig. 40. Third antennal segment of *Neacreotrichus cingulatus* (Loew); Fig. 41. Wing of *Neacreotrichus cingulatus* (Loew).

width; anal cell closed in wing margin by stalk, stalk slightly shorter than rm crossvein; rm crossvein at middle to ${}^{3}/{}_{5}$ of discal cell; anal lobe large, subtriangular in most species, rounded and slightly smaller in members of the *olmeca* group; squama subhyaline with brown to yellow rim, with sparse, short fringe of hairs.

Abdomen. Black in male, paler, often patterned in female, sparse to moderately pilose dorsally in male, less so in female, width narrower than thorax, tapered to apex, broadest in female; seven segments visible dorsally in both sexes.

Male genitalia (Fig. 7). Basistylus semilacrymoid in lateral view, with basal extension, apicomesal lobe prominent, with denticles, spicules, or other prominences; dististylus fairly short, slightly longer than wide, with lateral lobes or other protrusions; epiphallus without spines, broad basally, tapering to pointed, curved apex; aedeagus completely enclosed within epiphallus; basal apodeme large, rounded, often of specific form; lateral rami linear-lanceolate to elliptical in ventral view; epandrium subtriangular in ventral view, with mesoapical notch bordered by admedian papillae.

Female genitalia (Figs. 42d). Vaginal apodeme consisting of paired lateral sclerites connected medially by long, narrow membrane; spermathecal reservoir complex with apical portion dactylethroid with broad basal rim, darkly sclerotized; basal sac $2\times$ width of apical portion, outer wall thick to thin; apical spermathecal duct slightly



Fig. 42. Female spermathecal reservoirs. a) Acreophthiria similis (Coquillett); b) Acreotrichus antecedens (Walker); c) Australiphthiria hilaris (Walker); d) Neacreotrichus diversus (Coquillett).

shorter than ejection apparatus, smooth, semisclerotized on apical half, torulose, membranous on basal half; ejection apparatus cylindrical; apical and basal valves discoid, sclerotized or not; basal duct slightly longer than ejection apparatus, thin at basal valve, widening to slightly more than width of ejection apparatus; common duct membranous, torulose, as wide as widest portion of basal duct, length about 1/2 that of ejection apparatus.

Remarks. Male genitalia of the group of genera allied to Phthiria (i.e., Phthiria, Neacreotrichus, and Acreophthiria) are fairly similar among most of the species with the exception of species in Acreophthiria, which possess deeply emarginate basistyli. Because of this and the similarity of the body characters, species in each of these groups have been grouped at one time or another in a broadly defined concept of the genus Phthiria. A number of specimens from the Nearctic, Palearctic, Neotropical, and Afrotropical regions have been examined in this study to ascertain the status of certain generic names and unnamed species groups. Evenhuis (1986) declined to resurrect Neacreotrichus from synonymy with Phthiria until further study could be undertaken to find characters that might support its generic status. Examination of female genitalia and characters of the third antennal segment support the raising of Neacreotrichus in the present study to generic status.

Species examined. NEARCTIC: Neacreotrichus atrata (Coquillett)*, N. aztec (Painter)*, new combination, N. cingulata (Loew), new combination, N. consors (Osten Sacken)*, new combination, N. diversa (Coquillett)*, new combination, N. dolorosa (Williston)*, new combination, N. floralis (Coquillett)*, new combination, N. humilis (Osten Sacken)*, new combination, N. melanoscuta (Painter)*, new combination, N. mixteca (Painter)*, new combination, N. olmeca (Painter)*, new combination, N. picturata (Coquillett)*, new combination, N. toltec (Painter)*, new combination, N. vittiventris (Coquillett)*, new combination.

Genus Phthiria Meigen

Phthiria Meigen, 1803: 268. Type species: Bombylius pulicarius Mikan, 1796, by monotypy.

This genus is restricted primaily to the Old World, with a small representation in southern Chile and Argentina. The Nearctic species of *Phthiria* (sensu Evenhuis, 1986, and previous authors) are transferred in this study to *Neacreotrichus. Phthiria*, as considered here, can be distinguished by the characters given in the key. Males are normally black or dark colored with infrequent pale coloration. Females usually are paler with thoracic and/or abdominal vittae or other patterns.

Lengths. Body: 1.5-8.0 m; wing: 2.0-8.0 mm.

Head: Eyes in male holoptic, touching for entire length from ocellar tubercle to front; eyes in female separated at vertex by approximately 2× width of ocellar tubercle; front in male of varying widths, in lateral view either inflated dorsally or not, sparse to densely pilose; front in female nearly parallel-sided for entire length, with transverse groove halfway between ocellar tubercle and bases of antennae, portion below groove often sharply angled upward toward antennal bases, sparse to densely pilose; occiput flat to slightly rounded, density of pile variable; face absent below antenna; gena of variable shape and size, often dull colored and tumid, shining, well produced in other species (as in some Poecilognathus species); mentum convex, inflated [as in Apolysis corollae (Greathead, 1966b)] or normal; antennal segment I cylindrical, length 1.0-1.5× length of segment II; segment II subspheroid; segments I and II often with long pile in male, shorter, sparser in female; segment III (Fig. 43) linear-lanceolate, inflated near middle in some species (much like Acreotrichus), apical sulcus with long dorsal prong, ventral prong small and inconspicuous (in African species of the pulla group the ventral prong is the same length as or longer than the dorsal prong; this group needs more study and may warrant subgeneric status); antennal ratio: 1.5:1:5; proboscis tubular, length $2-5 \times$ head height; labellum about $\frac{1}{5}$ length of proboscis; maxillary palpus long, thin, of variable length but always projecting beyond oral margin.

Thorax. Black in male, varicolored, often patterned in female, integument shining or dull; mesonotum rounded; pleura with meso- and sometimes sternopleura pilose; metapleuron with micropubescence; hypo- and pteropleura bare; halter normal with knob pale to dark. Legs slender; femora without spines, long hairs and/or tomentum present in some species; tibiae and tarsi with or without small spicules; claws normal; pulvilli almost as long as claws.

Wing (cf. Fig. 41). Hyaline to slightly infumate; veins yellow to brown, thin or thick; costal vein ending at anal vein or complete to alula; second submarginal cell long, length $4 \times$ width; anal cell closed in wing margin by stalk, stalk length about equal to rm crossvein; rm crossvein at or near middle of discal cell; squama translucent whitish with brown rim and sparse fringe of pale hairs.

Abdomen. Black in male, black or varicolored and/or patterned in femal, equal to or narrower than width of thorax, vestiture variable, usually denser pilose in male than female.



Fig. 43. Third antennal segment of *Phthiria gaedei* Wiedemann; Fig. 44. Male genitalia of *Phthiria pulicaria* (Mikan). a) lateral view; b) ventral view of basistylus and epiphallic complex; c) ventral view of epandrium.

Male genitalia (Fig. 44). Genital capsule rotated 180°, basistylus dorsal in position, subovate to crescent-shaped in lateral view, with basal extension; apicomesal lobe well developed (reduced in some species of the pulla group); dististylus hooked to curved, often with spines on dorsal surface; epiphallus usually broad basally, tapering to recurved tip, parallel-sided in some species (tip pointed, not recurved in some pulla-group species); aedeagus completely enclosed within epiphallus; basal apodeme long or short, ovate to subcircular, with basolateral vanes; lateral rami of varying sizes, foliate to elliptical in ventral view; epandrium subtriangular in ventral view, with apicomesal notch; cercus small, slightly exserted or not at all.

Female genitalia (Fig. 50a). Vaginal apodeme consisting of paired parallel bars, these bars short or long, close together in most species, widely separated in others: spermathecal reservoir complex with apical portion darkly sclerotized, conical, curved apically; basal sac large to small, outer wall thin; basal portion of reservoir cup-shaped in some species, sclerotized; apical spermathecal reservoir subequal in length to ejection apparatus, with or without sclerotization on apical portion near basal sac, membranous on basal half at least, sometimes basal half torulose near apical valve; ejection apparatus of varying sizes, with or without dark sclerotization; apical and basal valves present, small to large, discoid; basal duct thin, membranous, subequal in length to ejection apparatus; common duct often present, membranous, of variable length.

Remarks. Engel (1933) noticed that Palearctic species could be placed into two groups: (1) those with a long dorsal prong at the apex of the third antennal segment and (2) those with a short dorsal prong. DuMerle (1972) further corroborated this delineation in the Palearctic species with supportive behavioral evidence: species with a long dorsal prong (Phthiria gaedei Wiedemann, P. umbripennis Loew, etc.) are sciophilic (active only in the early morning and/or late afternoon) whereas species with a short dorsal prong [Phthiria pulicaria (Mikan), P. vagans Loew, P. grisea Zaitsev and others] are heliophilic (active during the middle of the day). Unfortunately, basing species groups on antennal and behavioral character breaks down when species of Phthiria from other regions are taken into account. Afrotropical species such as Phthiria lanigera, P. pulla, and other southern African species bear certain resemblances to some species of Nearctic Acreophthiria and Poecilognathus. The shape and size of the dorsal prong of the third antennal segment in these species varies considerably, and some species have the dorsal prong reduced and papillate.

Until all the Old World species of *Phthiria* can be studied, especially Afrotropical species, no assumptions can be made here as to infrageneric classification.

Distribution. Throughout the Palearctic, Afrotropical, and Oriental regions, with a small population in Chile and Argentina.

Species examined. AFROTROPICAL: Phthiria crocogramma Hesse, P. cognata Hesse, P. flavigenualis Hesse, P. flaviscuta Hesse, P. fumata Greathead* (Oligodranes), new combination, P. laeta Bezzi*, P. lanigera Bezzi*, P. namaquensis Hesse, P. nigribarba Hesse, P. nitidigena Hesse, P. pilirostris Hesse, P. pulla Bezzi*, P. tinctipennis Hesse. NEOTROPICAL: Phthiria austrandina Edwards*, P. cana Philippi, P. chilena Rondani, P. exilis Philippi, P. homochroma Hall*, P. philippiana Rondani, P. tristis Bigot. ORIEN-TAL: Phthiria gracilis Walker. PALEARCTIC: Phthiria asiatica Zaitzev, P. gaedei Wiedemann, P. grisea Zaitzev, P. minuta (Fabricius), P. mongolica Zaitzev, P. pulicaria (Mikan), P. vagans Loew, P. sp. (Korea).

Genus Pygocona Hull

Pygocona Hull, 1973: 195 (key) (as subgenus of *Phthiria*). Type species: *Phthiria flavicincta* Hull, 1973, by original designation.

Pygocona is an endemic Australian genus comprising three known species and is characterized by the conical basistylus in the male and the incomplete costal vein, which ends at M_2 or CuA₁ and never extends to the anal vein. Evenhuis (1986) examined both described and undescribed species of Pygocona and raised Hull's subgenus to generic status, the concept of which is followed here.

Lengths. Body: 1.6–6.0 mm; wing: 1.5–6.0 mm. Head (Fig. 45). Compound eyes in male touching for entire length from anterior ocellus to frontal triangle; eyes in female separated at vertex by slightly more than width of ocellar tubercle; front in male small, triangular, densely pilose; front in female widest at level of antenna, width about $4\times$ that of ocellar tubercle, with transverse depression just above antenna, densely pilose; face narrow in frontal and lateral views, with or without hairs on gena; occiput slightly rounded in both sexes, sparse pilose; antennal segments I and II subequal in length, segment III linear-ovate, with slight dorsal bulge near middle, apical sulcus angled upward slightly, bordered by small dorsal and ventral prongs, dorsal hairs short and few in number; antennal ratio: 1:1:4; proboscis $1.5-2.5 \times$ head height, tubular, labellum about one-fourth length of proboscis; palpus very thin, length about one-third that of proboscis.

Thorax. Mesonotum not conspicuously rounded, generally gray to dark gray in both sexes; scutellum and pleura contrastingly pale, with fine pile; meso-, sterno-, and pteropleura with long pile; metapleuron with micropubescence; halter stem and knob pale colored. Legs slender, generally pale colored, devoid of definite spines, small stout spicules present on apical portion of mesal surface of mid tibia; claws normal; pulvilli as long as claws.

Wing (Fig. 46). Similar to that in *Tmemophle*bia; hyaline; veins brown; costal vein incomplete, ending at M_2 or CuA₁, not extending to anal vein; stigmatal area in cell Sc pale yellowish; vein R₄ originating just before end of discal cell; rm crossvein slightly beyond middle of discal cell; anal cell closed before wing margin by short stalk, stalk length $\frac{1}{2}$ that of rm crossvein; squama translucent whitish.



Fig. 45. Heads of *Pygocona flava* (Hardy). a) male, lateral view; b) female, lateral view; Fig. 46. Wing of *Pygocona flava* (Hardy).



Fig. 47. Male genitalia of *Pygocona flava* (Hardy). a) lateral view; b) ventral view of basistylus and epiphallic complex; c) ventral view of epandrium; d) dorsal view of basistylus.

Abdomen. Slender, conical, tapering to apex; equal in width to thorax in male, slightly wider than thorax in female; vestiture of sparse, fine pile.

Male genitalia (Fig. 47). Basistylus dorsal, con-

ical, not bilobed, with apical notch; basistylus subcrescent-shaped in lateral view, with basal extension; dististylus thin, curved dorsally to pointed apex, thorn-like in shape; epiphallus broad basally, tapering sharply at middle, continuing straight to thin upper neck, anterodorsal extension (ramus) short, broad; aedeagus enclosed within epiphallus; basal apodeme of moderate size, rounded apically, with basodorsal appendages; lateral rami thin, linear; epandrium shorter than basistylus, deeply emarginate basally, slightly notched apically, with sclerotized claw-like process apically; cercus large, rounded, internal (not exserted).

Female genitalia (Fig. 50b). Vaginal apodeme not evident (similar to condition found in Australiphthiria); spermathecal reservoir complex with apical portion curved (almost coiled), darkly sclerotized; basal sac membranous, outer wall thick with numerous minute glands; apical spermathecal duct $2\times$ length of ejection apparatus, membranous, not sclerotized at apex near basal sac; ejection apparatus cylindrical; apical and basal valves small, disc-shaped, sclerotized; basal duct thick, membranous, subequal in length to ejection apparatus; common duct not present.

Remarks. The reason for the conical basistylus (which is not present in other phthiriines) is not clear; however, it is probably related to either courtship or mating behavior. It is likely no coincidence that the epandrium has evolved to look like the basistylus and the basistylus has taken on a shape that is much more like the epandrium. Field work on the behavior and other aspects of the biology of these flies should produce some interesting results.

Species examined: Pygocona flava (Hardy), P. sp. (Australia).

Tribe Poecilognathini

Genus Euryphthiria Evenhuis

Euryphthiria Evenhuis, 1986: 9. Type species: *Euryphthiria grandis* Evenhuis, 1986, by original designation.

Members of this genus include some of the largest species in the subfamily (length excluding proboscis up to 12 mm). They are easily distinguished by their large size, flattened proboscis with spicules basolaterally, the presence of a spine or bump mesally on the first antennal segment,

and the broad face with a narrow oral margin. The genus is endemic to the Nearctic Region from Arizona and New Mexico south into Guerrero in Mexico. The genus has been recently revised in Hall & Evenhuis (1987).

Lengths. Body: 7.0-12.0 mm; wing: 6.5-11.5 mm.

Head. Compound eyes in male touching for four-fifths their length from anterior ocellus to

frontal triangle; eyes in female separated at vertex by $3 \times$ width of ocellar tubercle, front widest just above antenna (width about 6× that of ocellar tubercle); front small, triangular in male, not bare; front broad with bulge above antenna in female; face narrow in lateral view, very broad, rounded in frontal view; oral margin small, lateral marginal lip vestigial on lower portion; occiput flat in male, slightly rounded in female; pilosity of head consisting of stiff, short hairs; antennal segment I wider than segment II, with mesal spine or bump; segment II subspherical; segment III linear, with apical sulcus angled slightly upward, bordered by strong ventral and less pronounced dorsal prongs; antennal ratio: 1.5:1:5; proboscis flat, with spicules basolaterally, length about $1.0-1.5 \times$ head height, labellum about one-fourth length of proboscis, labium flat, extending almost full length of proboscis, pointed apically; maxillary palpus about one-third length of proboscis.

Thorax. Mesonotum moderately to strongly rounded dorsally, without definite pattern in male, vittate in female, short, sparse, erect pilose; pleura varicolored, meso- and sternopleura with short, stiff hairs, pteropleuron with a few hairs anteroventrally in some specimens; hypopleuron with small tuft of hairs on posterior portion; metapleuron bare; halter normal, knob pale yellow to brown or black. Legs with femora stouter than other phthiriines but legs still slender, devoid of spines; small spicules on tarsal segments; short, stiff hairs on all leg segments; claws normal; pulvilli almost as long as claws.

Wing. Subhyaline to hyaline, with or without spots on crossveins; veins dark brown; costal vein ending at anal vein, continuing faintly around anal lobe; yellowish stigmatal area in cell Sc prominent in both sexes; vein R_1 ending in wing margin $3 \times$ closer to end of R_{2+3} than to end of Sc; vein R_4 originating at or slightly beyond middle of discal cell; anal cell closed at or before wing margin by a stalk, stalk length never more than one-third length of rm crossvein; squama smoky brown, translucent.

Abdomen. Equal to width of thorax in male, stout, wider than thorax in female, fasciate in both sexes; vestiture consisting of short, stiff hairs.

Male genitalia. Basistylus dorsal, bilobed, not deeply emarginate apically in dorsal view, basal extension absent; dististylus slightly L-shaped in lateral view, apex with dentations, spines dorsally; epiphallus with long, paired spines on lower portion, penial guide present on upper portion, anterodorsal extension (ramus) large, broad; aedeagus long, thin, enclosed within epiphallus; bas-

al apodeme large, rounded; lateral rami broad, foliate; epandrium in dorsal view concave apically, in lateral view large, rounded apically; cercus small, not exserted.

Female genitalia (Fig. 50c). Vaginal apodeme thick, L-shaped, lateral sclerites slightly connected medially; spermathecal reservoir complex with apical portion ellipsoid-linear, sclerotized, not curved apically; basal sac membranous, outer wall thick; apical spermathecal duct tapering from basal sac to ejection apparatus, sclerotized near basal sac, fading basally; ejection apparatus short, cylindrical; apical and basal valves large, sclerotized, discoid; basal duct thick, broadening basally toward common duct; common duct vestigial.

Species examined: Euryphthiria alternans (Williston)*, E. grandis Evenhuis*.

Genus Poecilognathus Jaennicke

- Poecilognathus Jaennicke, 1867: 350. Type species: Poecilognathus thlipsomyzoides Jaennicke, 1867, by monotypy.
- Geronites Cockerell, 1914b: 230. Type species: Geronites stigmalis Cockerell, 1914, by monotypy. New synonymy.
- Agenosia Hull, 1973: 195 (as subgenus of Phthiria). Type species: Phthiria vittata Hull, 1973, by original designation.

Poecilognathus was proposed as a genus by Jaennicke (1867) for the central Mexican species *thlipsomyzoides* Jaennicke. It has been treated as a subgenus of *Phthiria* by most workers but was returned to generic status by Evenhuis (1986) based on differences in male and female genitalia and the bare metapleuron. *Poecilognathus* is endemic to the New World and is easily distinguished from other genera in the Poecilognathini by the shape and vestiture of the third antennal segment and the concave caudal margin of the epandrium in the male genitalia. Males and females are frequently similarly patterned.

Lengths. Body: 2.0-9.0 mm; wing: 2.5-10.0 mm.

Head (Fig. 48). Eyes holoptic in male, touching for entire length from ocellar tabercle to frontal triangle; eyes separated in female by about $2\times$ width of ocellar tubercle; front small to large, usually shining, vestiture of stiff hairs and/or pile of variable length and density; face absent below antenna; gena in lateral view well developed anteriorly (Fig. 48b) in most species or small, narrow (cf. Fig. 4b) in minute species; oral margin with or without well developed lateral marginal lip; occiput flat to slightly rounded, pile variable; mentum



Fig. 48. Heads of *Poecilognathus sulphureus* (Loew). a) male, lateral view; b) female, lateral view; c) female, dorsal view. Fig. 49. Wing of *Poecilognathus sulphureus* (Loew).

convex, inflated in female of some species; antennal segment I cylindrical, subequal in length to segment II; segment II subspheroid; segment III long, linear, to short, ovate, apical sulcus with well developed, thick ventral prong and shorter dorsal prong, dorsal surface with hairs; antennal ratio: 1:1:4–7; proboscis long, tubular, retracted length about $3-5\times$ head height (proboscis can be extended, hence the length can be more than the above figure); labellum short, about $\frac{1}{6}$ length of proboscis; maxillary palpus long, thin, extending beyond oral margin, length variable though shorter than antenna.

Thorax. Male and female similarly patterned though male often darker; mesonotum rounded, vestiture consisting of sparse pile, some species with stiff hairs, or mesonotum relatively bare; pleura with meso- and sternopleura with pile or patches of hairs; hypo-, ptero-, and metapleura bare, shining; pleura often with pattern; halter normal with knob dark to pale colored. Legs slender; femora bare or with short, stiff or fine hairs; tibiae and tarsi with minute hairs or spicules; claws normal; pulvilli almost as long as claws.

Wing (Fig. 49). Hyaline (loewi group) or spotted (punctipennis group); veins brown to yellow; costal vein complete, ending at or beyond anal vein; stump veins present (in some species) at midpoint of vein R_1 , at junction of veins R_4 and R_5 , and on crossvein closing apex of discal cell; anal vein closed in wing margin by stalk, stalk equal to or slightly less than length of rm crossvein; rm crossvein at apical ${}^{3}_{5}-{}^{2}_{13}$ of discal cell; length of second submarginal cell ${}^{3}_{4}$ that of first posterior cell; squama subhyaline with brownish rim and sparse fringe of pale hairs.

Abdomen. Equal to or thinner than width of thorax, tapering slowly to apex in male, broader and more ovate in female; seven segments visible in both sexes; second tergite about $2 \times$ length of third tergite; vestiture variable, often consisting of short, sparse, stiff hairs and/or fine pile dorsally, to a lesser extent ventrally.

Male genitalia (Fig. 8). Genital capsule rotated 180°, basistylus dorsal in position, bilobed, emarginate apically and basally, without basal extension, without apicomesal lobe, subquadrate in shape in lateral view; dististylus long, thin, with spines on dorsal surface; epiphallus with spines on lower and upper portions; penial guide present (interpreted here as the apicalmost portion of the epiphallus, which is fused to the mesal portion of the basistylus); anterodorsal extension (ramus) large, rounded; aedeagus thin, sinuous, bordered laterally by epiphallus; basal apodeme large, rounded; lateral rami foliate, narrow to broad; epandrium in ventral view with apical margin concave or flat, in lateral view subtriangular to subquadrate; cercus small, exserted or not.

Female genitalia (Figs. 50d, e). Vaginal apodeme consisting of two lateral L- to V-shaped sclerites, fused, separate, or connected by membrane medially; spermathecal reservoir complex with apical portion darkly sclerotized, fairly long, ellipsoid, rounded apically, usually straight [curved only in *P. sulphureus* (Loew)]; basal sac hyaline or semi-sclerotized, fused to apical portion of apical spermathecal duct; apical duct mem-



Fig. 50. Female spermathecal reservoirs. a) Phthiria homochroma Hall; b) Pygocona flavicincta (Hull); c) Euryphthiria grandis Evenhuis; d) Poecilognathus sp. (Brazil); e) Poecilognathus loewi (Painter).

branous, longer than ejection apparatus; ejection apparatus of two types: (1) with large, flat apical and basal valves (Fig. 50e) and (2) with small, discoid apical and basal valves (Fig. 50d); basal duct membranous, longer than ejection apparatus; common duct subequal in length to ejection apparatus, shorter, or absent altogether, with or without small sclerite at junction of basal ducts.

Remarks. Since the review of this genus in Evenhuis (1986), I have seen the type of the fossil *Geronites stigmalis* Melander in the University of Colorado at Boulder Florissant Collection. It is a typical *Poecilognathus* much like *sulphureus*, with a well-produced genal area lateral to the oral margin. The new synonymy is given above.

Species examined: NEARCTIC: Poecilognathus badia (Coquillett)*, P. bicolor (Coquillett)*, P. inornatus (Coquillett)*, P. loewi (Painter)*, P. marginatus (Coquillett)*, P. punctipennis (Walker)*, P. pulchellus (Williston)*, P. relativitae (Evenhuis)*, P. scolopax (Osten Sacken)*, P. stigmalis (Cockerell)*, (Geronites) new combination, P. sulphureus (Loew)*, P. thlipsomyzoides Jaennicke, P. unimaculatus (Coquillett)*. NEO-TROPICAL: Poecilognathus fasciventris (Curran)*, P. stictopennis (Hall)*, P. xanthogaster (Hall)*, P. sp. (Brazil).

Genus Relictiphthiria Evenhuis

Relictiphthiria Evenhuis, 1986: 17. Type species: Phthiria psi Cresson, 1919, by original designation. Relictiphthiria is an apparent relict genus of four known species confined to putative Ice Age refugia of the southwestern United States and the northern and western states of Mexico. One species (R. insularis Hall & Evenhuis) is known only from Tres Marias Islands, an island group south of the Baja California peninsula near the coast of Nayarit, Mexico, and represents an allochthonous population of the genus. Species of this genus are distinguished from other poecilognathines by the absence of hairs on the third antennal segment, the convex or pointed caudal margin of the epandrium and the lack of lower epiphallic spines in the male genitalia, and the absence of a basal valve on the ejection apparatus in the female genitalia.

The genus was recently revised by Hall & Evenhuis (1987). The description in Evenhuis (1986) covers all the salient characters and is repeated here with a few modifications based on findings in the present study and Hall & Evenhuis (1987).

Lengths. Body: 2.0-4.0 mm; wing: 2.0-4.5 mm. Head. Compound eyes in male touching for almost entire length from anterior ocellus to frontal triangle; eyes in female separated at vertex by $2\times$ distance between lateral ocelli; frontal triangle in male small, pollinose and/or pilose; front in female widest at level of antenna, width about $4\times$ that of ocellar tubercle, with transverse depression halfway between ocellar tubercle and antenna; face narrow in lateral view, rounded; oral margin with small lateral marginal lip; occiput slightly rounded in both sexes; antennal segments I and II small, subspherical; segment III bare, widest point before middle, apical sulcus small, bordered by small dorsal and ventral prongs or ventral prong not evident; proboscis tubular, length about $2.5-3.0 \times$ head height, labellum about one-fifth length of proboscis; palpus thin, slightly clavate apically, length about one-sixth to one-fourth length of proboscis.

Thorax. Mesonotum rounded, with pattern dorsally, sparse or dense pilose; pleura varicolored; meso- and sternopleura with hairs; ptero-, meta-, and hypopleura bare; halter normal in shape, pale colored. Legs similar to those in *Pygocona*; mid tibia with sparse small spicules on mesoapical surface; claws normal; pulvilli as long as claws.

Wing. Hyaline or spotted; veins yellow to brown; costal vein ending at anal vein; vein R_4 originating slightly before, at, or beyond end of discal cell; rm crossvein at apical one-fourth to two-thirds of discal cell; anal cell closed before wing margin by a short stalk, stalk 1.0–1.5× length of rm crossvein; squama hyaline to translucent whitish,

Abdomen. Slightly wider than thorax in both sexes, though male often more slender; seven segments visible in both sexes; length and density of pile variable.

Male genitalia. Basistylus dorsal, bilobed, notched apicomedially, basal extension absent; dististylus L-shaped, with dentations at apex. small denticles present or absent on lateral surface; epiphallus with paired long upper spines, penial guide absent, lower spines absent, anterodorsal extension (ramus) subovate to elliptical: aedeagus long, thin, sinuous, with apex of variable shape; basal apodeme subquadrate, vaned basally or laterally from base to apex (the latter case similar to some species of Empidideicus and Paraconsors Hall & Evenhuis); lateral rami fairly large, ovate-conical to subrectangular; epandrium in ventral view subrhomboid, convex (usually) and pointed apicomedially; cercus small, not exserted.

Female genitalia (Fig. 54a). Vaginal apodeme U-shaped, consisting of two fused lateral sclerites; spermathecal reservoir complex with apical portion darkly sclerotized, ellipsoid, not curved apically; basal sac hylaine, not expanded outward, outer wall thick; apical spermathecal duct sclerotized, darkest at apex near basal sac of reservoir, length slightly longer than ejection apparatus; ejection apparatus cylindrical; apical valve sclerotized, discoid; basal valve absent; basal duct membranous, width equal to ejection apparatus; length about $1.5 \times$ that of ejection apparatus; common duct membranous, subequal in length to ejection apparatus.

Remarks. Because of their small size and generally pale coloration, members of this genus may be confused with species of *Tmemophlebia* Evenhuis or small representatives of *Poecilognathus*. The bare third antennal segment and costal vein ending at the anal vein should separate species of *Relictiphthiria* from *Tmemophlebia*. The pointed and darkly sclerotized mesoapical margin of the epandrium in the male genitalia will further serve to identify males of *Relictiphthiria*.

Distribution. Apparently restricted to the southwestern United States and north and western states of Mexico.

Species examined: Relictiphthiria chihuahuaensis Hall & Evenhuis*, R. insularis Hall & Evenhuis*, R. primgenita Evenhuis*, R. psi (Cresson)*.

Genus Tmemophlebia Evenhuis

- Cyclorhynchus Macquart, 1840: 114. Type species: Cyclorhynchus testaceus Macquart, 1840, by original designation. [Preoccupied by Sundevall, 1835.]
- Cyclorynchus Macquart, 1840: 123. Incorrect original spelling of Cyclorhynchus Macquart. Determined by First Revisor Principle in Evenhuis (1986).
- *Tmemophlebia* Evenhuis, 1986: 19 (new replacement name for *Cyclorhynchus* Macquart). Type species: *Cyclorhynchus testaceus* Macquart, 1840, automatic.

Tmemophlebia is an endemic New World genus of about seven known species. Characters that distinguish this genus include the incomplete costal vein (ending at vein M2 or CuA1, never reaching the anal vein) and the darkly sclerotized apicomedial notch on the epandrium of the male genitalia (high magnification shows that this dark sclerotization is actually densely packed dark brown villi in a patch on the surface of the epandrium). Pygocona shares the character of the incomplete costal vein but because this character is homoplastic, no close phylogenetic relationship exists between Pygocona and Tmemophlebia. Tmemophlebia is easily separated from Pygocona by the absence of vestiture on the metapleuron as well as by the different male and female genitalic characters that separate the two tribes.

Lengths. Body: 2.0-6.0 mm; wing: 2.5-6.0 mm.

Head (Fig. 51). Usually pale colored, darker in male; eyes holoptic in male, touching for most their length from ocellar tubercle to small frontal

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Fig. 51. Heads of *Tmemophlebia coquilletti* (Johnson). a) male, lateral view; b) female, lateral view.

triangle; frontal triangle usually pale colored, covered by silvery pollen making triangle appear shining; eyes in female dichoptic, fairly widely separated: front in female with sunken transverse groove just above level of antennal sockets; female ocellar tubercle gray to black, contrasting in color with front and usually occiput; mentum in female sometimes with bulge behind oral margin [this bulge is probably associated with an internally coiled proboscis as has been observed in other species of this tribe and also in species of other genera such as Apolysis (Greathead, 1966b)]; antennal segment III of variable shape, usually slightly linear-lanceolate, apical sulcus with small dorsal prong, ventral prong non-existent, very small, or present as a second sensillum or hair; proboscis black, length about 2.5-4× head height; palpus thin, filamentous, very slightly clavate apically, extending beyond oral margin, with short sparse pubescence;

Thorax. Gray, black, and/or yellow on mesonotum and scutellum, usually pollinose and dull colored in most species, sparse, pale pilose and tomentose, longer hairs on dorsum of scutellum; metapleuron gray to brown, bare; other pleural sclerites usually gray in male, lighter colored in female; halter with stem white to yellow, knob white to yellow or with some brown to dark brown



Fig. 52. Wing of Tmemophlebia coquilletti (Johnson).

at base and/or dorsum. Legs slender, without spines; color variable, but most species with femora brown basally; mid tibiae with small spicules apically; tarsi darker than tibiae; claws normal; pulvilli broad, rounded, almost as long as claws.

Wing (Fig. 52). Hyaline to milky hyaline; veins usually yellowish, especially basally and anterobasally; discal cell large; rm crossvein at middle to distal third of discal cell; origin of vein R_4 at or beyond end of discal cell; anal cell closed before wing margin by short stalk of variable length; costal vein ending before anal vein, usually at or near veins M_2 or CuA₁ but sometimes at or near vein M_1 ; squama milky white with sparse, short fringe of hairs.

Abdomen. Slightly broader than thorax, more slender in male than in female; color and pattern of tergites and sternites variable, mostly pale colored to fasciate, pile short, sparse to dense in certain areas of abdomen, especially anterodorsally; male genitalic capsule exposed; epandrium easily viewed from the venter, notched apicomedially with dark sclerotized villi bordering notch, shape of notch of specific form.

Male genitalia (Fig. 53). Basistylus short, subtriangular, rounded apically in lateral view; dististylus broad basally, very thin in caudal view, shape variable; epiphallus, aedeagus, and basal apodeme similar in shape to that in *Relictiphthiria*; epandrium as described above.

Female genitalia (Fig. 54b). Vaginal apodeme consisting of paired, straight (but not parallel), lateral sclerites, lateral sclerites curved, semimembranous distally, connected medially by small, curved membranous bridge; vaginal orifice slightly anterior to medial sclerite, at level with distal curve of lateral sclerite; spermathecal reservoir complex with apical portion straight, conical, not curved, darkly sclerotized on conical apical portion; basal sac slightly sclerotized on distal half, sclerotization fading basally, outer wall thin; basal cup of reservoir slightly sclerotized; length of entire spermathecal reservoir complex about



Fig. 53. Male genitalia of *Tmemophlebia coquilletti* (Johnson). a) lateral view; b) ventral view of basistylus and epiphallic complex; c) ventral view of epandrium; d) dorsal view of basistylus.

 $1.5 \times$ length of ejection apparatus; apical spermathecal duct thin, membranous, slightly sclerotized apically at basal cup of reservoir, length subequal to that of ejection apparatus; ejection apparatus thin, cylindrical, membranous; apical and basal valves not evident; basal duct membranous, slightly longer than ejection apparatus, thin at ejection apparatus, becoming widest at common duct; common duct membranous, short, length about one-fourth that of ejection apparatus.

Remarks. Macquart (1840) originally described this genus for a single pale-colored species from Brazil that possessed a partially coiled proboscis, hence its original name *Cyclorhynchus.* The coiled condition of the proboscis is, however, not a generic nor even a specific character, but most likely is a manifestation of drying of a teneralcaught specimen (other specimens within the genera of Phthiriinae that were collected as tenerals show this coiling or partial coiling of the proboscis after drying). In Macquart's (1840) original description are two spellings of the genus. Using the First Revisor Principle, Evenhuis (1986) determined that *Cyclorhynchus*, the spelling for this



Fig. 54. Female spermathecal reservoirs. a) Relictiphthiria psi (Cresson); b) Tmemophlebia coquilletti (Johnson).

genus most commonly referred to by subsequent authors and the one that is preoccupied by Cyclorhynchus Sundevall, 1835, is the correct original spelling; and Cyclorhynchus must be considered an incorrect original spelling and has no availability with regard to nomenclature. As a result of examination of many specimens fitting the description of this genus from the Nearctic and Neotropical regions, Evenhuis (1986) concluded that the genus Cyclorhynchus Macquart was a valid genus separate from both Phthiria and Poecilognathus. Thus the replacement name, Tmemophlebia Evenhuis, was proposed.

Distribution. Throughout the Nearctic south to Brazil and Argentina in South America.

Species examined. NEARCTIC: Tmemophlebia aldrichi (Johnson)*, T. amplicella (Coquillett)*, T. borealis (Johnson)*, T. coquilletti (Johnson)*, T. cyanoceps (Johnson)*, NEOTROPI-CAL: Tmemophlebia albida (Wiedemann), T. testacea (Macquart)*, T. sp. (Brazil).

Genera removed from the Usiinae and Phthiriinae

Genera previously treated in the literature in either the Phthiriinae or Usiinae are listed here under the subfamilies and tribes into which they are placed in this study. Some of the genera have been removed previously from the subfamilies Phthiriinae and Usiinae; others are removed here based on morphological and phylogenetic evidence presented in this study. Detailed morphological study was not required for some of these genera, since other existing recent studies present strong support for their removal from the Usiinae or Phthiriinae.

An asterisk (*) next to a species name listed below indicates that the primary types have been examined during this study.

Subfamily Bombyliinae Tribe Conophorini

Genus Legnotomyia Bezzi

- Legnotus Loew, 1855: 41 (as subgenus of Bombylius). Type species: Bombylius trichorhoeus Loew, 1855, by original designation. [Preoccupied by Schiødte, 1848.]
- Legnotomyia Bezzi, 1902: 191 (new replacement name for Legnotus Loew).
- Psiatholasius Becker, 1906: 145. Type species: Psiatholasius bombyliiformis Becker, 1906, by original designation.

Legnotomyia is a peculiar genus of ten species apparently restricted to northern and eastern Africa and the Middle East. Though very similar in appearance to some large species of the Parageron incisa group (previously placed in Usia), the genus is easily distinguished from genera of the Usiinae and Phthiriinae by the open anal cell, prominent face below the antennae, and shape of the third antennal segment. Not only have some morphological characters of Legnotomyia run convergent with usiine genera, but behavioral characters also seem to have converged with those found in usiine genera. Greathead (1966a) mentions the sluggishness of *L. striata* (Bischof) in the arid bush country of Kenya. Such behavior is characteristic of all the genera of Usiinae (*Usia, Parageron,* and *Apolysis*) and is rare in genera outside this subfamily (non-usiine genera are typically very wary and alert at normal temperatures).

Based on examination of male and female genitalia, I follow Hull (1973) and Bowden (1980) in placing *Legnotomyia* in the Conophorini.

While visiting the MNHN in Paris in 1986, I examined the male holotype of *Bombylius singularis* Macquart and was able to confirm its placement in *Legnotomyia*. The new combination is given below.

Species examined: Legnotomyia bombyliiformis (Becker)*, L. cineracea Austen*, L. singularis (Macquart)* (Bombylius), new combination, L. striata (Bischof), L. trichorhoea (Loew).

Tribe Crocidiini

Becker (1913), Bezzi (1924), and Paramonov (1938) all placed *Crocidium, Apatomyza*, and *Semiramis* in the Phthiriinae, probably because these genera all have wing venation superficially similar to that of species in *Phthiria* s. lat. That placement of those genera in Phthiriinae has been

shown to be incorrect based on antennal and male genital characters (Hesse, 1938). Hull (1973: 61) placed Crocidium, Adelogenys, Apatomyza, Semiramis, Mallophthiria Edwards, Tamerlania (= Timiomyia Evenhuis), and Desmatomyia in his new tribe Crocidiini. Bowden (1980) followed this treatment in placing the Afrotropical genera Crocidium, Apatomyza, and Adelogenys in the Crocidiini. I agree with Hull's (1973) placement of these three Afrotropical genera and also of Semiramis and Mallophthiria (see discussions below). Because its unique type specimen is presumed destroyed, however, Timiomyia is here placed in tribus inquirendus pending study of further material. Desmatomyia has been recently removed from the Phthiriinae to its own subfamily (Hall & Evenhuis, 1987), which is followed here.

Genus Adelogenys Hesse

- Adelogenys Hesse, 1938: 811. Type species: Adelogenys culicoides Hesse, 1938, by original designation.
- Adelogenys is a southern African genus containing three known species.

Species examined: Adelogenys culicoides Hesse.

Genus Apatomyza Wiedemann

- Apatomyza Wiedemann, 1820: 11. Type species: Apatomyza punctipennis Wiedemann, 1820, by original designation (on plate).
- Apatomyza Henning, 1832: 326. Type species: Apatomyza punctipennis Henning, 1832 [= Apatomyza punctipennis Wiedemann, 1820], by monotypy. [Preoccupied by Wiedemann, 1820.] New synonymy.

Apatomyza is a monobasic genus restricted to the southern Afrotropical Region.

Species examined: None.

Genus Crocidium Loew

Crocidium Loew, 1860a: 85. Type species: Crocodium poecilopterum Loew, 1860, by monotypy.

Crocidium is a southern Palearctic (Egypt) and Afrotropical genus consisting of 22 known species, most of which occur in southern Africa.

Species examined: Crocidium poecilopterum Loew.

Genus Mallophthiria Edwards

Mallophthiria Edwards, 1930: 169. Type species: Mallophthiria lanata Edwards, 1930, by original designation.

This endemic Chilean genus is represented only by the unique male holotype, which is deposited in the BMNH. Hull (1973) placed the genus in the Bombyliinae, noting its similarity to *Crocidium*. Hall (1975) examined the type and concurred with Hull's (1973) placement. Bowden, however, returned it to the Phthiriinae with the brief statement that '*Mallophthiria* Edwards, considered by Hall (1975) to belong in the Bombyliinae, is a Phthiriine, as originally placed by Edwards' without justifying this action.

The confusion of subfamilial placement of this genus is most likely due to the similarity of many of its features with other phthiriine genera, notably wing venation and the shape of the third antennal segment (which also has a sulcus).

Examination during this study of the unique holotype shows that Hull's (1973) placement of this genus near Crocidium is correct. The presence of a face below the antennae (Fig. 55) precludes Mallophthiria from being a member of the Usiinae or Phthiriinae. Though the face does not protrude forward as in other crocidiine genera, the characters of the male genitalia and wing venation show a close relationship to genera of the Crocidiini. The third antennal segment does possess a sulcus, but one unlike that in any other phthiriine genus. Phthiriine genera always have a apically placed sulcus bordered by a dorsal prong of variable size. No dorsal prong is present on the apex of the third antennal segment in Mallophthiria. Dissection of the male genitalia shows many similarities in the characters exhibited in Megaphthiria and Crocidium.

Based on the examination of the type during the present study, I follow Hull (1973) in placing Mallophthiria in the Crocidiini.

Species examined: Mallophthiria lanata Ed-wards*.



Fig. 55. Head of Mallophthiria lanata Edwards.

Genus Megaphthiria Hall

Megaphthiria Hall, 1975: 105 (as subgenus of *Phthiria*). Type species: *Phthiria pirioni* Edwards, 1930, by original designation.

Megaphthiria was originally proposed as a subgenus of Phthiria by Hall (1975) for Chilean species possessing a long maxillary palpus (more than one-half the length of the proboscis) and in which the epandrium of the male genitalia lacks an apical notch. Evenhuis (1986) examined type specimens of the four known Chilean species as well as a long series of specimens in addition to those that were recorded in Hall (1975) and made dissections of male and female genitalia. Those dissections revealed similarities to the genitalia of the Afrotropical genera Adelogenys, Apatomyza, and Crocidium.

The presence of spines on the female acanthophorites, the absence of a basomedial sac of the spermathecal reservoir, the 90° rotation of the male genitalia, and the presence of a face below the antennae preclude the placement of this genus in the Phthiriinae. The characters exhibited by *Megaphthiria* are typical for the tribe Crocidiini, to which this genus was transferred by Evenhuis (1986).

Species examined: Megaphthiria capnopennis (Hall)*, M. macrostoma (Hall)*, M. pirioni (Edwards)*, M. poliodes (Hall)*.

Genus Semiramis Becker

Semiramis Becker, 1913: 486. Type species: Semiramis punctipennis Becker, 1913, by original designation. Becker (1913) erected this genus for his single new species, S. punctipennis, from Iran. As Hull (1973) points out, the wing venation and head shape show it to be related to Crocidium. This close relationship with Crocidium and allies was apparently noticed by Bezzi (1924), who listed Semiramis between Crocidium and Apatomyza in his concept of the composition of the Phthiriinae. Since there is no asterisk next to the name Semiramis in that list (Bezzi placed an asterisk next to taxa he did not see), Bezzi presumably saw specimens of this genus when making judgements as to its placement within the Bombyliidae.

If Semiramis is congeneric with Crocidium, the records from Iran and southern Turkmenia could well represent a disjunct distribution of the more southern Afrotropical Crocidium. This type of distribution, labeled Afro-Iranian by Bowden (1975a), is exhibited by other genera of Bombyliidae and has been discussed by Bowden (1973, 1975a, 1980).

I was not able to examine specimens of this rare genus during the present study. The only collection record of *Semiramis* subsequent to Becker's (1913) original description is by Charkuliev (1972), who lists it among species collected in southern Turkmenia in the USSR. Because of the unavailability of material of this genus, its generic and tribal status could not be verified during the present study. The descriptions and illustrations in Hull (1973) show it is closely related to genera constituting the Crocidiini. I provisionally place it in the Crocidiini until further study clarifies its taxonomic status.

Species examined: None.

Tribe Dischistini

Genus Eusurbus Roberts

Eusurbus Roberts, 1929: 580. Type species: Bombylius crassilabris Macquart, 1855, by original designation.

The only reason *Eusurbus* is treated in this study is its placement in the Usiinae by Hall (1975). Hull (1973) and Theodor (1983) place the genus in the Bombyliinae. The shape of the head and the third antennal segment, presence of four posterior cells in the wing, and characters of the male genitalia preclude its placement in the Usiinae. Bowden (1985) placed it in the Dischistini of the Bombyliinae, which is followed here. Currently, four species are known in this endemic Australian genus.

Species examined: Eusurbus altus (Walker)*, E. crassilabris (Macquart)*.

Genus Gonarthrus Bezzi

Gonarthrus Bezzi, 1921: 88. Type species: Dischistus cylindricus Bezzi, 1921, by original designation. Bezzi (1924), Paramonov (1938), and Hall (1975) placed this Afrotropical genus in the Phthiriinae. Hesse (1938) showed that the characters Bezzi (1924) gave for the genus ally it with the 'Dischistus-group' of the Bombyliinae rather than with the Phthiriinae. After examination of the type species of the genus, I follow Bowden (1980) in placing *Gonarthrus* in the Dischistini. Twentynine species are known in the genus.

Species examined: Gonarthrus cycnus (Bigot)*, G. cylindricus (Bezzi)*.

Genus Isocnemus Bezzi

Isocnemus Bezzi, 1924: 101. Type species: Isocnemus nemestrinus Bezzi, 1924, by original designation.

Isocnemus has been placed in the Usiinae by Paramonov (1938) and Hall (1975). Hull (1973) redescribed the unique holotype deposited in the BMNH and gave characters that preclude its placement in either the Usiinae or the Phthiriinae. I have examined the holotype and agree with Bowden (1980, 1985) in placing this genus in the bombyliine tribe Dischistini.

Species examined: Isocnemus nemestrinus Bezzi*.

Tribus inquirendus

Genus Timiomyia Evenhuis

- Tamerlania Paramonov, 1931: 203. Type species: Tamerlania grisea Paramonov, 1931, by original designation. [Preoccupied by Skrjabin, 1924.]
- Timiomyia Evenhuis, 1978: 247 (new replacement name for Tamerlania Paramonov). Type species: Tamerlania grisea Paramonov, 1931, automatic.

Hull (1973: 61) places this genus in the tribe Crocidiini but gives no justification for this classification. Later (p. 192) he gives an English translation of Paramonov's (1931) original description and the genus is compared with *Conophorus*. The unique type specimen of *Timiomyia grisea* (Paramonov) is presumed destroyed (Liepa, 1969) and no further material has been seen since the original description. Based on the characters given in the original description, the placement of this genus in the Bombyliinae seems correct, but no definitive tribal placement or generic determinations are possible until further material is located and examined. *Timiomyia* is therefore here placed in tribus inquirendus.

Species examined: None.

Subfamily Cylleniinae

Genus Lithocosmus Cockerell

- Lithocosmus Cockerell, 1909: 72. Type species: Lithocosmus coquilletti Cockerell, 1909, by original designation.
- Protophthiria Cockerell, 1914a: 720. Type species: Protophthiria palpalis Cockerell, 1914, by original designation.

Hull (1973) treated the Florissant fossil genus Protophthiria in the Phthiriinae. Evenhuis (1984) examined the type species of the genus Protophthiria palpalis, showed it to belong to Lithocosmus, and gave characters that placed it in the subfamily Cylleniinae rather than the Phthiriinae. The other known fossil species of *Protophthiria* (*P. atra* Melander) was also examined during that study and found to belong in a new genus, *Tithonomyia* Evenhuis, which was tentatively placed in the Bombyliinae. Two species, both fossil, are currently known in *Lithocosmus*.

Species examined: Lithocosmus palpalis (Cockerell)*.

Subfamily Cythereinae Tribe Mariobezziini, **new status**

A family-group name derived from *Corsomyza* (Corsomyzini) was first proposed by Hull (1973) for the *Corsomyza*-group of genera listed below. *Mariobezzia*, currently recognized as a member of this genus group, is the root of the family group name Mariobezziinae, which was proposed by Becker (1913). Mariobezziinae is the older of these two family-group names and has priority according to the *International Code of Zoological Nomenclature* (Ride et al., 1985). Following current classification for this genus group, it should be given tribal, not subfamilial, status, hence a new tribal name is needed for it. The tribe to which all of these genera belong should be named Mariobezziini.

Hull (1973) placed his tribe Corsomyzini (which contained the genera here grouped in Mariobezziini) in the Bombyliinae. This differs from Bowden's (1980) placement of this tribe within the Cythereinae. The correct subfamilial placement of this group (i.e., either in the Cythereinae or Bombyliinae) is beyond the scope of the present study, but preliminary morphological comparison of the genera of the Corsomyza-group, which include Callynthrophora, Corsomyza, Gnumyia, Hyperusia, Mariobezzia Becker, Pusilla, and Zyxmyia, corroborates Theodor's (1983) evidence supporting a closer relationship with the Cythereinae than with the Bombyliinae. I tentatively follow Bowden (1980) in placing this group of genera in the Cythereinae pending further study.

Genus Callynthrophora Schiner

Callynthrophora Schiner, 1867: 313 [1868: 139]. Type species: Callynthrophora capensis Schiner, 1867, by original designation.

The first worker to place *Callynthrophora* into a subfamily was Bezzi (1924), who placed it in his broad concept of Usiinae. Paramonov (1938) and Hall (1975) followed Bezzi's classification. Hull (1973) erected the tribe Corsomyzini in the Bombyliinae and included *Callynthrophora* among the genera constituting that tribe. Hull's (1973) concept of generic composition of that tribe was corroborated by Bowden (1975) and in Bowden's

later catalog treatment of the Afrotropical component of the Corsomyzini (Bowden, 1980).

I agree with Hull (1973) and Bowden (1980) in that *Callynthrophora* should be placed in the *Corsomyza*-group of genera, here termed the Mariobezziini. *Callynthrophora* comprises three species, which are restricted to the Afrotropical Region.

Species examined: Callynthrophora marginalis Bezzi*.

Genus Corsomyza Wiedemann

- Corsomyza Wiedemann, 1819: 13 [1820: 13]. Type species: Corsomyza simplex Wiedemann, 1819, by subsequent designation of Wiedemann, 1820: pl. 1, fig. V.
- Corsomyza Henning, 1832: 329. Type species: Corsomyza simplex Henning, 1832 [= Corsomyza simplex Wiedemann, 1819], by present designation. [Preoccupied by Corsomyza Wiedemann, 1819.] New synonymy.
- Lasioprosopa Macquart, 1855: 82. Type species: Lasioprosopa bigotii Macquart, 1855 [= Corsomyza nigripes Wiedemann, 1819], by monotypy.
- Denamyza Hull, 1973: 165 (as subgenus of Corsomyza). Type species: Corsomyza ochrostoma Hesse, 1938, by original designation.

Corsomyza was first placed in a subfamily by Bezzi (1924), who treated it, along with the associated genera *Megapalpus* and *Callynthrophora*, in the Usiinae. This treatment was followed by Paramonov (1938) and Hall (1975) but differed from Hull's (1973) classification.

Examination of homotypic specimens of Corsomyza simplex show the relationship of this genus to Callynthrophora, Gnumyia, Hyperusia, Mariobezzia, Megapalpus, Pusilla, and Zyxmyia. I follow Bowden (1980) in this grouping of genera and place Corsomyza in the tribe Mariobezziini. Thirty-two species of Corsomyza are presently known.

Species examined: Corsomyza bigotii (Macquart)*, C. fuscipennis Macquart*, C. hirtipes Macquart*, C. simplex Wiedemann.

Genus Gnumyia Bezzi

Gnumyia Bezzi, 1921: 82. Type species: Gnumyia brevirostris Bezzi, 1921, by original designation. Gnuymia, known from only two Afrotropical species, has been transferred from subfamily to subfamilial placement has differed from author to author, the genus has always been kept within the Corsomyza-group of genera. Examination during this study of homotypic specimens of the type species of the genus confirms its association with the Corsomyza-group of genera. It is placed here in the tribe Mariobezziini.

Species examined: Gnumyia brevirostris Bezzi.

Genus Hyperusia Bezzi

Hyperusia Bezzi, 1921: 4, 84. Type species: Hyperusia minor Bezzi, 1921, by monotypy.

Hyperusia, an Afrotropical genus consisting of six species, was placed in the Usiinae by Paramonov (1938) and Hall (1975) and was treated with usiine genera by Bezzi (1924) though not listed as such in his subfamilial classification (Bezzi, 1924: 13). Hull (1973) placed Hyperusia in his new tribe Corsomyzini, and that placement was followed by Bowden (1975a, 1980). The association of this genus with the Corsomyza-group of genera by Hull (1973) is shown to be correct by Bowden (1975a). It is placed here in the tribe Mariobezziini.

Species examined: Hyperusia luteifacies Bezzi*, H. minor Bezzi*.

Genus Megapalpus Macquart

- Megapalpus Macquart, 1834: 394. Type species: Phthiria capensis Wiedemann, 1828, by monotypy.
- Dasypalpus Macquart, 1840: 112. Type species: Dasypalpus capensis Macquart, 1840, by monotypy.
- Dasypalpoides Evenhuis, 1978: 247 (new replacement name for Dasypalpus Macquart). Type species: Dasypalpus capensis Macquart, 1840, automatic.

The genus *Megapalpus*, consisting of three known species, has been considered a member of the Usiinae by Bezzi (1924), Paramonov (1938), and Hall (1975). Though Hesse (1938) was the first to recognize its distinctness from other usiine genera, Hull (1973) was the first to place *Megapalpus* in another subfamily (Bombyliinae, tribe Corsomyzini). This tribal placement is corroborated by

Bowden (1975a, 1980). Examination of specimens of *Megapalpus* during the present study shows the genus-group placement of Hull (1973) and Bowden (1980) to be correct. *Megapalpus* is here placed in the Mariobezziini.

The name Dasypalpus, treated as a junior objective synonym of Megapalpus by most authors, may need resurrection from synonymy. Its type species, long considered to be Phthiria capensis Wiedemann, is actually a different species labeled by Macquart as 'Dasypalpus capensis Nob.' ('Nob.' indicates that this was a new species and not a new combination; other new combinations listed by Macquart do not have 'Nob.' after the species name.) Though there is no species description, the name is validated by reference to a plate and figure number. The specimen shown in the illustration by Macquart is not a typical Megapalpus and is not Megapalpus capensis Wiedemann). In 1986 I visited the MNHN in Paris to search for some of Macquart's bombyliid types. All that remains of the type of Dasypalpus capensis is the name label. Until more research is done to ascertain the true status of Macquart's Dasypalpus, it is here provisionally placed as a junior synonym of Megapalpus.

Species examined: Megapalpus capensis (Wiedemann), M. nitidus Macquart*.

Genus Pusilla Paramonov

Pusilla Paramonov, 1954: 27. Type species: Pusilla longirostris Paramonov, 1954, by original designation.

Pusilla, a monobasic genus confined to the Afrotropical Region, was considered by Hull (1973) to be a junior synonym of *Corsomyza*. That it is actually a good genus is evidenced by Bowden (1975), who examined the type and paratype in the BMNH. Based on characters given by Paramonov (1954) and my examination of the type in the BMNH, it is apparent that *Pusilla* belongs to the Mariobezziini comprising the *Corsomyza*-group of genera.

Species examined: Pusilla longirostris Paramonov*.

Genus Zyxmyia Bowden

- Zyxmyia Bowden, 1960: 213. Type species: Zyxmyia megachile Bowden, 1960, by original designation.
 - Zyxmyia, known only from its type species, is a

recent addition to the *Corsomyza*-group of genera. It has been placed in the Corsomyzini of the Bombyliinae by Hull (1973) and in the Usiinae by Hall (1975). Bowden (1975a, 1980) follows Hull in placing it among the *Corsomyza*-group of genera.

This placement is correct, as evidenced by head, antennal, wing, and male genitalic characters. It is placed here in the Mariobezziini.

Species examined: Zyxmyia megachile Bowden*.

Subfamily Gerontinae

The names Geron, Pseudoammictus Bigot, and Pseudempis Bezzi were treated in the early bombyliid literature in a broadened concept of Phthiriinae. Hesse (1938) removed Geron and related genera to his new subfamily Geroninae [sic]. Subsequent to Hesse (1938), Pseudoammictus was given subgeneric rank and Pseudempis was found to be synonymous with Pseudoammictus (Bowden, 1974). Bowden (1980) later reduced Gerontinae to tribal status within the Toxophorinae (a subfamily which, according to Bowden's classification, also includes the Systropodinae as a tribe). That action was done in a catalog, hence no explanation for that classification scheme was given. Based on my preliminary examination of Geron, Toxophora, and Systropus, Bowden's grouping of these three appears to based on symplesiomorphies (e.g., possession of a coiled spermathecal reservoir), and thus this subfamilial concept cannot be maintained. I here return Gerontinae to subfamilial status comprising Geron and allies.

Genus Geron Meigen

- Geron Meigen, 1820: 223. Type species: Geron gibbosus Meigen, 1820 [= Bombylius gibbosus Olivier, 1789], by subsequent designation of Duponchel in d'Orbigny (1845: 206).
- Amictogeron Hesse, 1956b: 918. Type species: Amictogeron meromelanus Hesse, 1938, by original designation.

Over 100 species are known in this genus worldwide.

Subgenus Geron Meigen

Species examined: AFROTROPICAL: Geron anomalus (Hesse), G. australis Hesse, 1938 [preoccupied by australis Macquart, 1840; replacement name needed], G. delicatus Hesse, G. nasutus Bezzi^{*}, G. semifuscus Séguy^{*}. AUSTRA-LIAN: Geron australis Macquart^{*}, G. mysticus Evenhuis^{*}, G. terminatus Evenhuis^{*}. NEARC-TIC: Geron arenicola Painter, G. holosericeus Walker^{*}, G. subauratus Loew. NEOTROPI-CAL: Geron albidus Walker, G. insularis (Bigot)^{*}, G. senilis (Fabricius). PALEARCTIC: Geron sp. PATRIA IGNOTA: Geron tenuis Walker^{*}.

Subgenus Pseudoammictus Bigot

- Pseudoammictus Bigot, 1892: 342 (as genus). Type species: Amictus heteropterus Wiedemann, 1821, by original designation.
- Pseudempis Bezzi, 1921, 24: Type species: Amictus heteropterus Wiedemann, 1821 [misidentification, = Pseudoamictus bezzii Paramonov, 1930], by original designation. Species examined: None.

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Subfamily Desmatomyiinae

Genus Desmatomyia Williston

- Desmatomyia Williston, 1895: 268. Type species: Desmatomyia anomala Williston, 1895, by original designation.
- Acreotrichites Cockerell, 1917: 376. Type species: Acreotrichites scopulicornis Cockerell, 1917, by

original designation. New synonymy.

This genus, currently known from four species (including two fossil species), has been treated previously in the Phthiriinae (Bezzi, 1924; Paramonov, 1938; Hall, 1975; Painter et al., 1978).



Fig. 56. Heads of *Oligodranes obscuripennis* Loew. a) male; b) female.

Desmatomyia is superficially similar to Phthiria and Poecilognathus in wing venation and general body shape; however, the characters of the face, the shape of the third antennal segment, and the characters of the male and female genitalia preclude its placement in either the Phthiriinae or Usiinae. Examination of male and female genitalia show similarities to some Therevidae, but the presence of just four posterior cells (rather than the characteristic five for therevids) apparently excludes it from that family as currently defined. Hall & Evenhuis (1987) erected a new subfamily for this genus and their new genus *Inyo* (the



Fig. 57. Third antennal segment of Oligodranes obscuripennis Loew; Fig. 58. Maxillary palpus of Oligodranes obscuripennis Loew.

latter incorporating the enigmatic Nearctic species *Heterotropus senex* Melander).

Examination of the type of the fossil Acreotrichites scopulicornis Cockerell deposited in the USNM shows that it is a junior synonym of Desmatomyia, under which it is placed in this study. This synonymy shows that Desmatomyia was extant as early as the Oligocene and associated with Phthiriinae at that time as it is today (fossil Phthiria s. lat. having been collected in shale from the same stratum as the fossil of A. scopulicornis). The type of the fossil Psilocephala scudderi Cockerell (formerly treated in Therevidae) was also examined in the USNM and found to belong to Desmatomyia. The resulting new combinations for both of these fossil taxa are given below.

Species examined: Desmatomyia anomala Williston*, D. jambalaia Hall & Evenhuis*, D. scopulicornis (Cockerell) (Acreotrichites)*, new combination, D. scudderi (Cockerell) (Psilocephala)*, new combination.

Subfamily Oligodraninae, new subfamily

Genus Oligodranes Loew

Oligodranes Loew, 1844: 160. Type species: Oligodranes obscuripennis Loew, 1844, by subsequent designation of Becker (1913: 484).

Previous to the present study, this genus had been placed in either the Phthiriinae or Usiinae by various authors (see Table II). The presence of three posterior cells, antennal characters, and general body shape and coloration resulted in the association of this genus with *Apolysis*. Examination of the type male and female of *O. obcuripennis* in the HMB revealed the presence of a face below the base of the antennae (Fig. 56a, b) and a two-segmented maxillary palpus (Fig. 58), characters that preclude it from being a member of either the Phthiriinae or Usiinae. Detailed examination of the third antennal segment (Fig 57) and male and female genitalic characters shows that it belongs in another subfamily.

The male genitalia are similar to those found in some genera in the Mariobezziini of the Cythereinae. The female genitalia, however, do not correspond with those of other genera of that tribe and are more similar to those found in genera of the Bombyliini and Conophorini of the Bombyliinae. The presence of only three posterior cells apparently precludes it from placement in either the Bombyliinae or Cythereinae in light of current knowledge of these subfamilies (both of which have taxa that possess four posterior cells in the wing). Evidently, no bombyliid subfamily exists in which *Oligodranes* can be placed. I therefore propose the new subfamily Oligodraninae to accommodate this unusual genus, which is phylogenetically close to Bombyliinae.

Species examined: Oligodranes flavus Paramonov, O. obscuripennis Loew*, O. sp. (Israel).

? Family Rhagionidae

Genus Zarzia Zaitzev

Zarzia was erected for the south-central Asian amber fossil species Z. zherichini by Zaitzev (1986) and placed by him in the Phthiriinae. This is apparently not only an incorrect subfamilial placement but also an incorrect family placement. Based on the description and figure provided in the original description, this species should probably be placed in the Rhagionidae near the genus Bolbomyia Loew. Characters that preclude it from being in the Phthiriinae as currently defined herein include the anal cell open in the wing margin, a multi-segmented arista, and a short, fleshy labellum. All of these characters are consistent with genera allied to *Bolbomyia* in the Rhagionidae (all of which possess four posterior cells in the wing as opposed to the normal five in other genera of Rhagionidae). Apparently, the presence of four posterior cells in the wing led Zaitzev to place this genus in the Bombyliidae, but the multi-segmented arista (a character of primitive orthorrhaphous Brachycera) should have led him to place *Zarzia* in one of the lower brachycerous families.

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Zarzia Zaitzev, 1981: 105. Nomen nudum.

Zarzia Zaitzev, 1986: 818 [1987: 152]. Type species: Zarzia zherichini Zaitzev, 1986, by original designation.

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Appendix Taxa Used in Phylogenetic Analyses

Usiinae Subfamily Analysis

Usia aenea (Rossi) Usia versicolor Macquart Parageron lutescens Bezzi Parageron incisus (Wiedemann) Apolysis humilis Loew Apolysis sedophila (Brunetti) Apolysis mus (Bigot) Apolysis mitis (Cresson) Apolysis flavifemoris (Hesse) Apolysis cinereus (Evenhuis) Apolysis sp. (Greece)

Phthiriinae Subfamily Analysis

Phthiria pulicaria (Mikan) Poecilognathus loewi (Painter) Neacreotrichus atratus (Coquillett) Acreotrichus antecedens Walker Acreophthiria americana (Coquillett) Pygocona flavicincta (Hull) Australiphthiria hilaris (Walker) Tmemophlebia coquilletti (Johnson) Relictiphthiria psi (Cresson) Euryphthiria grandis Evenhuis

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TABLE III. Data matrix for the Usiinae Analysis

			Character																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14*	15	16*	17	18	19	20	21	22
hypanc	(HYP)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aenea	(AEN)	1	1	0	1	0	0	1	0	1	0	1	1	0	+**	0	+	0 °	0	1	0	0	1
versicolor	(VER)	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1
lutescens	(LUT)	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1
incisus	(INC)	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1
humilis	(HUM)	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	1	4	1
sedophila	(SED)	0	0	0	0	1	1	0	0	0	0	1	0	0	+	1	0	0	0	0	1	1	1
mus	(MUS)	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	1
mitis	(MIT)	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	1
flavifemoris	(FLA)	1	1	0	0	0	1	0	0	0	0	1	0	0	+	1	0	0	1	0	1	2	1
cinereus	(CIN)	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	3	1
Greece sp.	(GRÉ)	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	4	1

character deleted in final analysis. polymorphic for that taxon. *

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TABLE IV. Data matrix for the Phthiriinae Analysis

			Character																											
Taxon		1	2	3	4*	5*	6	7	8*	9	10	11	12*	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28*	29
hypanc	(HYP)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
pulicaria	(PUL)	0	0	1	0	+*	* 0	0	+	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
atratus	(ATR)	0	0	1	+	1	0	0	+	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
antecedens	(ANT)	0	0	1	1	1	0	2	+	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
americana	(AME)	0	0	1	1	1	0	0	+	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1
flavicincta	(FLV)	0	0	1	0	1	0	1	+	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
hilaris	(HIL)	0	0	1	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1
coquilletti	(COQ)	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1	1
psi	(PSI)	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	1	1	0	1	0	0	1	1
grandis	(GRA)	1	0	1	0	1	1	0	0	0	1	0	+	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1	1
loewi	(LOE)	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	+	1

character deleted in final analysis (see text for discussion). polymorphic character for that taxon.

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