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THE GENERA OF THE FAMILY NEMESTRINIDAE (DIPTERA: BRACHYCERA)

NELSON BERNARDI

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Anteriormente os artigos zoológicos do Museu Paulista eram publicados na Revista do Museu Paulista. Com a fundação do Departamento de Zoologia, os volumes 1, 2 e 3 dos Arquivos de Zoologia traziam as indicações, respectivamente, de volumes 24, 25 e 26 da Revista do Museu Paulista. Esta prática foi abandonada, visto continuar esta revista sua publicação como Nova Série, dedicada a assuntos estranhos à Zoologia.

Scientific publications

The Museu de Zoologia publishes two periodicals, *Arquivos de Zoologia* (publication started 1940, volumes 1-14 under the name *Arquivos de Zoologia do Estado de São Paulo*) and *Papéis Avulsos de Zoologia* (publication started 1941, volumes 1-19 under the name *Papéis Avulsos do Departamento de Zoologia da Secretaria da Agricultura de São Paulo*). Papers are individually published and show the date of distribution to authors and bibliographical centers, being eventually assembled into volumes.

Prior to 1940, the zoological papers of the Museu Paulista were published in the Revista do Museu Paulista. When the Departamento de Zoologia was founded, volumes 1, 2 and 3 of Arquivos de Zoologia had the indication "volumes 24, 25 and 26" of the Revista do Museu Paulista. Such practice was subsequently abandoned, as that periodical continued publication as a "New Series" (Nova Série).

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THE GENERA OF THE FAMILY NEMESTRINIDAE (DIPTERA: BRACHYCERA)

NELSON BERNARDI [1]

CONTENTS

INTRODUCTION

The relative scarcity of nemestrinids in collections, plus the fact that the larvae of many species are acridiophagous, stimulated an interest in the study of the family, not only in search of a deeper knowledge of the group itself, but also in view of its practical importance for biological control.

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[1] Museu de Zoologia, Universidade de São Paulo.

Many dipterists have paid attention to the family, but few engaged in working on its suprageneric classification and intergeneric relationships. Outstanding students of the Nemestrinidae included Lichtwardt, Bequaert, and Paramonov, especially the first two. Out of 254 extant species, 60 were described by Lichtwardt, 33 by Paramonov and 20 by Bequaert. The many works by Bequaert, on the whole, are the most important. In my opinion, however, the best single paper is the revision of the Australasian fauna by Mackerras (1925); it is an excellent model for dipterists interested in nemestrinids in other regions.

Much useful information is scattered throughout the literature, but no comprehensive work has so far been attempted, and this is why the present research was undertaken. I have attempted to work out the evolutionary and geographical history of the Nemestrinidae as well as a better classification of the family. As a result of this project, two other papers have been published. In the first (Bernardi, 1972) the genus *Exeretoneura* Macquart was removed from the family, since it was concluded that it does not belong to the Nemestrinidae, and was better left "incertae sedis". Similarly, in the second paper (Bernardi, 1973), the Jurassic genus †*Rhagionemestrius* Ussatchov was removed from the family. Neither of these genera will be mentioned again in the present paper.

The purpose of the present work is to provide suitable answers to the following questions:

1) What is the evolutionary history of the Nemestrinidae?
2) What is the geographical history of the Nemestrinidae?
3) What is the best classification for the Nemestrinidae?

In attempting to answer these questions, morphological, paleontological and geographical data were used. Immature stages and biological data were not used, by reasons explained in the proper section.

The working unit is the genus. The fifteen Recent and the five fossil genera were studied in their morphology and distribution, the Recent genera of course were studied in greater detail. The genera are defined and possible inferences on their geographical history and phylogenetic relationships are presented. The conclusions of this study appear in the presentation of a formal classification of the family and in a general discussion in the third part of the work.

The three parts of the paper are as follows. In the first part general information is presented which is later systematized and discussed in the other two parts. The second part deals with the systematics of the family. Here are found the previous classifications, the proposed classification, keys for the identification of Recent genera and the study of each of the subfamilies and genera. For each subfamily a definition is given. For each genus are given: synonymy, important references, indication of illustrations, definition, distribution, comments (when necessary) and a catalog. The catalog includes references to the description of the species, type-localities (when many localities are given in the original description, without specific reference to the type-locality, all are presented; when neotype designation exists, type-localities for the type and the neotype are given), other useful references, range and synonymy (subspecies and varieties are treated as synonyms). In the third part the evolution of the family and conclusions on its zoogeography are discussed.

As I have seen practically all references on nemestrinids, I have given in the "References" almost all of them, even when they are not referred to in the text. This is intended to facilitate future research.

ACKNOWLEDGEMENTS

I am indebted to the following persons and institutions, for the expressed reasons:

Dr. P. E. Vanzolini, Director of the Museu de Zoologia, gave me helpful orientation on evolutionary and zoogeographical problems and in the preparation of the paper.

Dr. Nelson Papavero suggested the study of the Nemestrinidae, contributed many helpful suggestions during the whole research and made some observations on nemestrinids in the British Museum.

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Dr. Robert V. Peterson, of the Entomology Research Institute, Ottawa, Canada, revised the manuscript.

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Miss Heloisa Faria reproduced fig. 76.

During my brief stay in the United States and Canada, many friends and colleagues were extremely kind in providing working facilities and hospitality. They are: Dr. P. J. Darlington, Jr., Dr. H. E. Evans and Dr. F. M. Carpenter (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts), Dr. G. E. Shewell and Dr. J. M. Campbell (Entomology Research Institute, Ottawa, Canada), Dr. P. Wygodzinsky (American Museum of Natural History, New York) and, very especially, Dr. Lloyd V. Knutson (Systematic Entomology Laboratory, United States National Museum, Washington, D. C.).

Dr. D. H. Colless (Division of Entomology, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia) loaned the specimens of *Cyclopsidea hardyi*.

Dr. H. Oldroyd [British Museum (Natural History)] provided data on specimens from that institution.

Dr. Hugo de Souza Lopes provided some literature facilities.

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which I was able to do part of my work. It also provided grants "Biológicas 69/882" and "Biológicas 69/883", through which the Museu de Zoologia greatly enlarged its collection of Neotropical Diptera.

Finally, I gratefully thank my dear friend and professor Rev. Dr. Vincent James Mannoia and his family, who were missionaries in Brazil for many years. Dr. Mannoia was President of the Free Methodist Seminary in São Paulo, where I was his student. During my visit to the United States, in 1970, it was my privilege to spend Christmas in their home, in Ventnor, New Jersey.

PART I: GENERAL SECTION

1. Material and methods

During the course of this investigation the following collections were studied:

Museu de Zoologia, Universidade de São Paulo.
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
United States National Museum, Washington, D.C.
American Museum of Natural History, New York.
Entomology Research Institute, Canada Department of Agriculture, Ottawa.

In addition, I had the opportunity to study a couple of specimens of *Cyclopsidea hardyi*, from the Division of Entomology, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia.

The studied species are given in the following list, with the number of specimens examined in parentheses:

Hirmoneura: *annandalei* (1), *anthracoides* (12), *articulata* (28), *basalis* (3), *bellula* (32), *bradleyi* (23), *brandti* (2), *brevirostrata* (31), *brevirostris* (5), *cockerelli* (1), *exotica* (14), *flavipes* (3), *laotica* (3), *luctuosa* (16), *lurida* (10), *maculipennis* (24), *obscura* (4), *ochracea* (3), *orellanae* (3), *paraluctuosa* (1), *psilotes* (2), *punctipennis* (16), *ruizi* (2), *silvae* (2), *strobelii* (5), *texana* (54), *villosula* (4), *vitalisi* (25), unidentified specimens (130).

Trichophthalma: *albimacula* (1), *amoena* (38), *andina* (23), *bancrofti* (2), *barbarossa* (76), *bivittata* (20), *commutata* (9), *confusa* (1), *costalis* (9), *degener* (4), *eximia* (6), *fusca* (9), *glauciventris* (1), *harrisoni* (5), *herbsti* (1), *jaffueli* (142), *laetilinea* (3), *landbecki* (59), *leucophaea* (3), *murina* (4), *nicholsoni* (2), *nigripes* (7), *nigrovittata* (4), *niveibarbis* (10), *novaehollandiae* (9), *nubipennis* (149), *obscura* (3), *philippii* (9), *porteri* (1), *primitiva* (2), *punctata* (22), *rosea* (7), *rufonigra* (9), *scalaris* (27), *sexmaculata* (2), *subaurata* (22), *ursula* (1), unidentified specimens (78).

Prosoeca: *accincta* (10), *atra* (15), *beckeri* (3), *caffraria* (6), *circumdata* (6), *fusca* (1), *ganglbaueri* (14), *ignita* (1), *lata* (1), *longipennis* (5), *maculata* (4), *major* (1), *nitidula* (2), *peringueyi* (3), *rhodesiensis* (9), *sublineata* (1), *umbrosa* (5), *variabilis* (2), *variegata* (2), *westermanni* (2).

Stenobasipteron: *arnoldi* (1), *difficile* (3), *gracile* (21), *wiedemanni* (23).

Nemestrinus: *abdominalis* (12), *aegyptiacus* (9), *ariasi* (1), *ater* (11), *brandti* (2), *canaaniticus* (1), *capito* (2), *dedecor* (1), *eristalis* (3), *exalbidus* (4), *fasciatus* (6), *fascifrons* (5), *hermanni* (2), *hirsutus* (3), *hirtus* (3), *iranicus* (4), *laetus* (3), *melaleucus* (1), *modestus* (1), *nigrofemoratus* (3), *nigrovillosus* (2), *perezii* (2), *persicus* (6), *pieltaini* (1), *reticulatus* (1), *ruficaudis* (3), *rufipes* (15), *simplex* (5).

Stenopteromyia: *bolivari* (7).

Moegistorhynchus: *braunsi* (2).

Cyclopsidea: *hardyi* (2).

Neorhynchocephalus: *mendozanus* (48), *sackenii* (149), *sulphureus* (25), *tauscheri* (6), *vitripennis* (9), *volaticus* (216), unidentified specimens (67).

Fallenia: *fasciata* (12).

Trichopsidea: *clausa* (46), *costata* (6), *oestracea* (4).

Ceyloniola: *magnifica* (2).

Atriadops: *javanus* (15), *macula* (7), *vespertilio* (9), *westwoodi* (2).

Nycterimyia: *dohrni* (4), *horni* (1).

Nycterimorpha: *pyralina* (2), *speiseri* (6).

To this list must be added 307 specimens of Chilean *Hirmoneura* and *Trichophthalma* identified only to the generic level. In the systematic section, in the catalog of each genus, the species studied are preceded by an asterisk.

Table 1 gives the number of species studied per genus, the number of species recognized in the genus, and the number of specimens studied.

Ceyloniola and *Nycterimorpha* were not seen by me, but were examined by Drs. H. Oldroyd and N. Papavero at the British Musuem.

All the foregoing explanations refer to Recent species. Also, at Harvard University, I was fortunate to see three fossil specimens from Florissant (Oligocene), two †*Neorhynchocephalus melanderi* and one †*Palembolus florigerus*.

The paper by Rohdendorf (1968) is quoted several times in the text, but not from the Russian; I am quoting from an English translation by J. K. Peck-Kukalova, of which Dr. F. M. Carpenter, of Harvard University, kindly sent me a copy.

I have examined as many species of each genus as I could, always having in mind my goal, i. e., the study of the genera and not a specific revision. Of all the type-species, only *Moegistorhynchus longirostris* was not studied.

Male genitalia were drawn in three positions: dorsal, ventral and lateral. It was not possible to dissect the genitalia of *Ceyloniola* and

Table 1

Genus	Nº of species studied/recognized	Nº of specimens studied
Hirmoneura	28/46	459
Trichophthalma	37/64	780
Prosoeca	20/34	93
Stenobasipteron	4/5	48
Nemestrinus	28/66	112
Stenopteromyia	1/1	7
Moegistorhynchus	1/4	2
Cyclopsidea	1/1	2
Neorhynchocephalus	6/6	520
Fallenia	1/2	12
Trichopsidea	3/3	56
Ceyloniola	1/1	2
Atriadops	4/6	33
Nycterimyia	2/12	5
Nycterimorpha	2/2	8
Total (including unidentified material, as explained in the text)	139/254	2446

Nycterimorpha. In the definitions of the genera there are no descriptions of the genitalia, but references to the illustrations are given.

2. Immature stages and bionomical data.

As has already been stated in the introduction, data on the immature stages and on the biology of the nemestrinids were not used. The reason is that precise and comparable information does not exist. Until now only the subfamily Trichopsideinae has been well known in respect to its biology. The three genera of this subfamily are known to have acridiophagous larvae. In this connection, I refer the reader to Crouzel & Salavin (1943), Fuller (1938), Greathead (1958, 1963) Léonide (1962a, 1962b, 1963, 1964a, 1964b, 1968, 1969), Prescott (1955, 1960, 1961) and York & Prescott (1952).

Besides these data on the Trichopsideinae, there is only sufficient information on *Hirmoneura obscura*, whose larvae feed upon larvae and pupae of *Rhizotrogus solstitialis* (Coleoptera, Scarabaeidae) (Handlirsch, 1882, 1883). Two other species of *Hirmoneura*, *H. exotica*

(Bruch, 1917) and *H. articulata* (Stuardo Ortiz, 1935a), are also reported to feed upon scarabaeids.

From what is presently known, immature stage characters may become useful taxonomically in the future. The larvae of Trichopsideinae, for instance, form a respiratory tube; *Hirmoneura obscura* does not have such a structure. Besides that, there seems to be a difference in the number of the fleshy processes on the last abdominal segments of the larva and in the presence or absence of hooks on the spines of the abdominal pseudopods. One of the most important contributions arising from the study of immature Trichopsideinae is the confirmation of the subfamily based on adult morphology.

Adult nemestrinids have been observed on flowers of many different groups, and are known to live in open areas. Other than these, reliable biological data are wanting.

3. Morphology of taxonomic characters

Only the characters contributing to the phylogeny and classification will be dealt with here. Exclusion of other characters does not mean that they are unimportant, but that their importance has not yet been evaluated. Nevertheless, I believe that the characters used are the most important and deserve a greater weight in the elaboration of phylogeny and classification.

Table 2

Character	Primitive state	Specialized state
1 Shape of head	Hemispherical	Flattened
2 Proportion head/thorax	Head much smaller than thorax in volume	Head almost as large as thorax in volume
3 Face	Convex	Prominent
4 Frons	Normal	With depression below antennae
5 Eyes	Pilose	Bare
6 Ocelli	Present	Absent
7 Proboscis	Developed	Vestigial
8 Antennae	3rd segment and style separate	3rd segment and style fused
9 Post-scutellum	Normal, much smaller than scutellum	Almost as large as scutellum
10 Shape of leg	Normal	With femur or tibia enlarged
11 Tarsal proportion	1st segment of hind tarsus longer or as long as the last four together	1st segment of hind tarsus shorter than the last four together
12 Shape of abdomen	Wide and robust	Narrow and elongate
13 Ovipositor	Type 1	Type 2
14 Hypandrium	Present	Absent
15 Hypandrium	Free	Fused with gonopods
16 Hypandrium	Elongate	Sub-quadrate
17 Gonopods	Free	Fused together
18 Aedeagus	Free	Fused with gonopods
19 Wings	Hyaline	Opaque, with hyaline areas
20 Alula	Developed	Vestigial
21 Costa	Encircling the whole wing	Absent or reduced on hind margin
22 Radial phragma	Not individualized	Individualized
23 R3	Present	Absent
24 R4 and R5	Separate (3rd submarginal cell open)	Partially or totally fused (3rd submarginal cell closed or absent)
25 R4+R5 and M1	Separate (1st posterior cell open)	Fused (1st posterior cell closed)
26 R2	Ending on apical margin	Uniting R1 and R4, resembling a cross-vein
27 R2 and R4	Separate (2nd submarginal cell open)	Fused (2nd submarginal cell closed)
28 R2 and R4+R5	Separate	Fused
29 R5	Running towards hind margin	Running towards apical margin
30 R5 and M1	Separate (1st posterior cell open)	Fused (1st posterior cell closed)
31 R4+5 and M1+2	Fused for a short distance	Fused for a long distance
32 r-m	Present	Absent
33 M1 and M2	Running towards hind margin	Running towards apical margin
34 M1 and M2	Separate (2nd posterior cell open)	Totally or partially fused (2nd posterior cell absent or closed)
35 M3 and M4	Fused only on diagonal vein (discal and 5th posterior cells separate)	Fused before reaching diagonal vein (discal and 5th posterior cells in contact)
36 M4 and Cu1	Separated by m-cu	Fused (m-cu absent)
37 Cu1 and 1A	Separate (anal cell open)	Fused (anal cell closed)
38 M3+M4 (tip of diagonal vein)	Present (3rd and 5th posterior cells separate)	Absent (3rd and 5th posterior cells united)
39 Reticulation of wings	Absent	Present
40 Axillary cell	Normal	Enlarged

For the purpose of the present work it was necessary to decide on the degree of primitiveness, of a given character. This procedure was relatively easy. In relation to wing characters, Hennig (1954) made a thorough analysis of the subject and I have nothing to add to his paper. The male genitalia is easy to interpret in the majority of cases, because the basic plan is not very different from the Asilidae and related groups where we have the excellent paper by Karl (1959). Other characters either clearly disclose their condition (for instance, absence of ocelli in *Atriadops* is clearly a specialized condition) or may be placed in a scheme furnished by previously known characters. Characters and the interpretation of their condition are given in Table 2 and are discussed below.

Head wide, sometimes wider than the thorax. Its length (maximum distance, observed from above) varies from perfectly hemispheric (*Cyclopsidea*) to greatly flattened (Trichopsideinae and Atriadopsinae). Head in *Cyclopsidea* almost as large as the thorax in volume; in other genera it never reaches such proportions. The Atriadopsinae have a deep transversal depression on the face, just beneath the antennae. Face convex or projected forward in various degrees. Eyes large, occupying a large part of the head; their degree of separation varies from clearly holoptic to widely dichoptic. They may be heavily pilose to completely bare. Ocelli normally present, but missing in *Atriadops*. Proboscis very long (sometimes longer than the insect), short or vestigial. Antennae small, three-segmented, the segments varying in form. Third antennal segment followed by a segmented style. In the Atriadopsinae the third segment and the style are fused, forming a single piece. In the Trichopsideinae the style is reduced and segments are not easily observed. The style of *Cyclopsidea* has a characteristic expansion at the tip. The several antennal types are represented in figs. 1 through 13.

Thorax robust, but in *Cyclopsidea* relatively small. In the latter genus the post-scutellum is exceptionally well developed, being almost as large as the scutellum.

Legs long and slender, but *Nycterimyia* with femora incrassate and *Nycterimorpha* with the hind tibiae club-shaped. In the Hirmoneurinae, Nemestrininae, Cyclopsideinae and Trichopsideinae the first segment of the hind tarsus is longer or approximately as long as the last four together; in the Atriadopsinae the first segment is conspicuously shorter than the last four together, the fifth being longer than each one of the three intermediary.

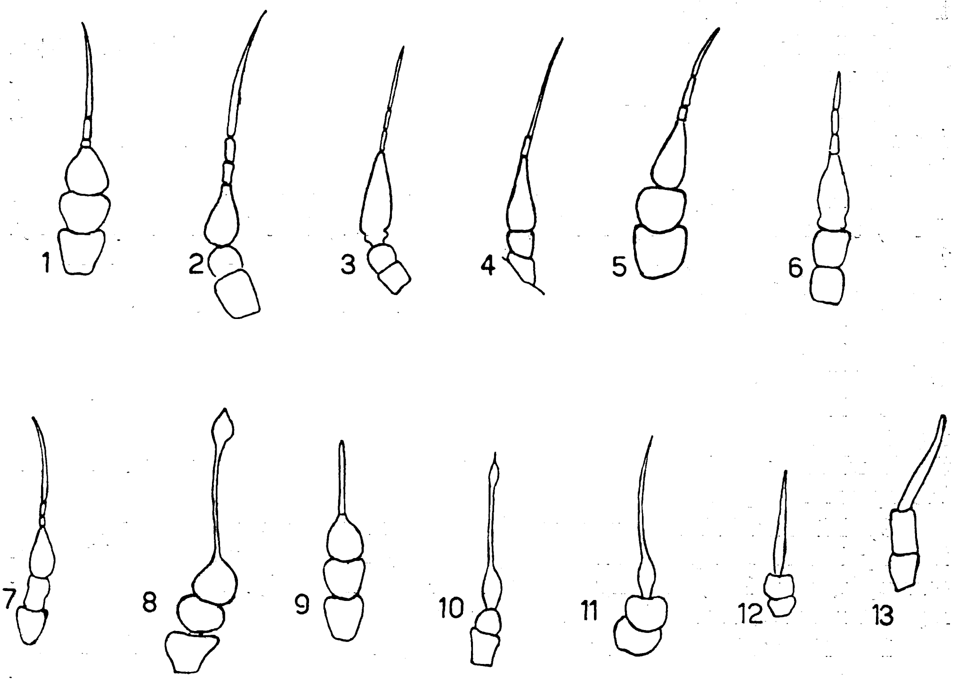
Abdomen usually wide, but in *Cyclopsidea* and *Nycterimorpha* narrow and long, with a characteristic form in each of the two mentioned genera.

There are two types of ovipositor:

Type 1: telescope-shaped, with many retractile segments and terminal valvulae short. Found in Hirmoneurinae, Nemestrininae and Cyclopsideinae.

Type 2: sabre-shaped, with two extremely long and slender valvulae. Found in Trichopsideinae and Atriadopsinae.

Male genitalia non-rotated. The nomenclature of the genital structures follows Karl (1959) and Wilcox & Papavero (1971). The epandrium (9th tergite) is a single piece, variable in shape and always free. The hypandrium (9th sternite) is a single ventral piece, usually longer than or as long as the gonopods. It is extremely reduced in *Hirmoneura obscura* (figs. 42-44) and absent in the majority of the species of the same genus (figs. 39-41). In the Nemestrininae it is well developed (figs. 45-62), in *Cyclopsidea* it seems to be fused with the gonopods (Mackerras, 1925: 557) and in the Trichopsideinae and Atriadopsinae it is absent. The gonopods are lateral structures, very variable in form. They may be free ventrally (*Hirmoneura*, figs. 39-44; Nemestrininae, figs. 45-62), fused with the hypandrium (*Cyclopsidea*) or fused together in some Trichopsideinae (figs. 63-65) and in the Atriadopsinae (figs. 69-74). The aedeagus is a simple or variously elaborate tube. It is free or fused with the gonopods (*Atriadops*, figs. 69-71). The



Antennae. 1, *Hirmoneura obscura;* 2, *Trichophthalma novaehollandiae;* 3, *T. rosea;* 4, *Stenobasipteron difficile;* 5, *Nemestrinus simplex;* 6, *Stenopteromyia bolivari;* 7, *Moegistorhynchus braunsi;* 8, *Cyclopsidea hardyi;* 9, *Fallenia fasciata;* 10, *Trichopsidea oestracea;* 11, *Atriadops javanus;* 12, *Nycterimyia papuana;* 13, *Nycterimorpha speiseri.* (Figs. 1 from Sack, 1933; figs. 2, 3, 8, 10, 11 from Mackerras, 1925; figs. 4, 12 from Bequaert, 1925a; fig. 7 from Bequaert, 1935b; fig. 13 from Hardy, 1924).

tenth tergite is always present, although sometimes concealed by the epandrium. It is followed by a pair of well developed cerci.

Wings large and generally hyaline, sometimes infuscated or opaque. Alula normal, narrow or vestigial. Venation very characteristic. In the following discussion, the veins are designated by letters and the cells by names.

1) The costa (C) normally encircles the whole wing, but may disappear on the apical margin; sometimes traces remain on the hind margin.

2) The radial sector has three branches: R2, R4 and R5. R3 is fused with R4 and both reach the apical margin together. This compound vein is called R4, for convenience.

3) R3 is present or absent, uniting R2 and R4 like a cross-vein. The two conditions may occur in the same genus (*Hirmoneura*). R3 may also exist as a stump arising from R4 and interrupted midway between R4 and R2 (†*Eohirmoneura*, fig. 16; *Ceyloniola*, fig. 35). It must be mentioned that it is difficult to interpret the true nature of R3. This vein is usually thought of as the true R3, but Hennig (1954) thinks it might be, in many Diptera, the result of a "reactivation" of the primitive R3 field.

4) R3 is usually united to R4, but it may also be fused with R4+5. The two conditions may occur in the same genus (*Neorhynchocephalus*).

5) The two posterior branches of the radial sector, R4 and R5, form a relatively short fork, whose branching point is not far away from r-m.

6) R4 and R5, primitively, after branching off, proceed independently to the apical margin. They may, however, fuse totally or partially. Then, when already fused (R4+R5), there may be another fusion (*Fallenia*, fig. 32).

7) R2 may unite with R4+R5 (*Nycterimorpha*, fig. 38) or fuse partially with R1 and R4, resembling a cross-vein between R1 and R4 (*Nycterimyia*, fig. 37). In these cases, especial cells are formed.

8) In the †Archinemestriinae, R5, M1 and M2 (†*Archinemestrius*, fig. 14) or M1 and M2 (†*Protonemestrius*, fig. 15) are bent towards the hind margin. In all other groups these veins are directed towards the apical margin.

9) M1 and M2 may run parallel to each other towards the margin, leaving the second posterior cell open; they may fuse partially (*Stenopteromyia*, fig. 27), closing the cell, or totally (*Nycterimyia*, fig. 37; *Nycterimorpha*, fig. 38), eliminating it.

10) M3 and M4 never reach the margin separately, i.e., the fourth posterior cell is always closed. These veins generally unite in the diagonal, but in *Nycterimorpha* (fig. 38) they fuse before reaching the diagonal, reducing the length of the fourth posterior and establishing contact between the discal and the fifth posterior cells.

11) r-m is present or absent, eliminated by the fusion of R4+5 and M1+2. When fusion occurs, it is either for a very short distance

(sometimes almost imperceptible) or for a long distance (*Nycterimyia*, fig. 37; *Nycterimorpha*, fig. 38).

12) m-cu may be present or absent. Interpretation of this vein is very difficult and doubtful (Hennig, 1954).

13) Cu1 and 1A in most cases are separated, leaving the anal cell open, but they may unite, closing the cell (*Fallenia*, fig. 32). The two conditions may be found in the same genus.

14) The axillary cell may be normal in size, or it may be very enlarged (*Ceyloniola*, fig. 35; *Atriadops*, fig. 36).

15) The so-called diagonal vein is the most conspicuous character of the nemestrinid venation. It is not a single vein, but results from the union of parts of various veins of the radial and medial fields. It extends from the base of the radial sector to the extremity or M3+M4 on the hind margin. Its composition is as follows: a) Rs; b) R4+5; c) r-m or R4+5+M1+2; d) M1+2; e) M2 (when M1 leaves the diagonal before M3 entering it) or M1+2+M3; f) M2+M3; g) M3 when M2 leaves the diagonal before M4 entering it) or M2+M3+M4; h) M3+M4. (The composition of the diagonal vein may be followed in figs. 14 through 38). There are some variations, however. In *Nycterimyia* (fig. 37), because of the total fusion of M1 and M2, M1+2+M3 is followed by M3. In *Nycterimorpha* (fig. 38), because of the same fusion and the fusion of M3 and M4 before the diagonal, after M1+2 comes M1+2+M3+M4, then M3+M4. In *Fallenia* (fig. 32), *Stenopteromyia* (fig. 27) and some *Neorhynchocephalus* the tip of the diagonal vein, formed by M3+M4, is absent. The same condition is found in †*Eohirmoneura carpenteri* (fig. 16).

16) According to Rohdendorf (1968: 181, 187) the radial phragma of the basial (*) is not distinctly individualized in the †Archinemestriinae, but in all other Nemestrinidae it is perfectly individualized, forming a strong oblique vein. This character, as far as I know, has never been mentioned by authors, including Hennig (1954). Anyway, according to Rohdendorf's interpretation, it indicates the primitiveness of the †Archinemestriinae in relation to other subfamilies.

4. Fossils

Twelve species of fossil Nemestrinidae have been described so far, five from the Oligocene of Florissant (Colorado, U. S. A.), six from the Jurassic of Karatau (Kazakhstan) and one from the Jurassic of Eichstätt (Germany). To those species must be added De Serres' reference to an undescribed and doutbfully characterized specimen from Aix (Southern France, Oligocene): "*Nemestrina* Latreille. Une espèce de la taille de la *Nemestrina reticulata* de Latreille" (in Bequaert & Carpenter, 1936: 399).

(*). The terms "radial phragma" and "basial", used by J. K. Peck-Kukalova in her translation, are unknown to me. I was unable to find these terms in the literature. They refer to a small region at the base of the wing, between R and M, which may have an oblique vein (Cf. figs. 14, 15 and 16).

The nemestrinid fauna of the Florissant shales was revised by Bequaert & Carpenter (1936). These authours ascribed all species to living genera: three to *Neorhynchocephalus*, one to *Hirmoneura* (considering †*Hirmoneurites* Cockerell a subgenus) and one to *Prosoeca* (considering †*Palembolus* Scudder a subgenus). I agree with the first two genera, but, as it will be explained in the systematic section, I prefer to consider †*Palembolus* a genus.

The fauna of Florissant does not add much to the systematics of the family, but shows that it must have been abundant in the Oligocene in that area, perhaps more so than now.

Much more important from the systematic and evolutionary points of view, as might be expected, is the Jurassic fauna. †*Prohirmoneura jurassica* Handlirsch is a very badly preserved fossil, but the wing venation shows clear similarities with living nemestrinids. The material from Karatau is much better preserved. Rohdendorf (1968) distributed it among two subfamilies (one extinct), three genera and six species. Two genera, †*Archinemestrius* and †*Protonemestrius*, were ascribed to the subfamily †Archinemestriinae. The third genus, †*Eohirmoneura*, is included in the Hirmoneurinae. This great diversification during the middle Mesozoic shows that the family was already abundant in the same area where it still is, though represented by different elements.

Hennig (1954), knowing only †*Prohirmoneura*, said that the confirmation of the existence of Nemestrinidae in the Jurassic would be very important in giving an idea of the age of various groups of Brachycera. Now this fact is confirmed by the fossils of Karatau.

5. Geographical distribution

The range of each genus is given in the systematic section and in maps 1 through 4. Table 3 shows the number of species per genus in each zoogeographic region.

Nemestrinidae occur in all regions, but there are some areas of higher concentration: from the Mediterranean to Turkestan, eastern Australia, southern Africa, Chile and Argentina. Areas with fewer species are: Oriental Region, eastern Africa north of the Zambezi, northwestern South America to the United States and southern Canada and many areas in the Palearctic Region. This is a very disjunct distribution. Areas from which the family is absent are widespread and can be seen better from the maps.

The most primitive extant subfamilies, Hirmoneurinae and Nemestrininae, are the most widely distributed. The Hirmoneurinae are represented by the single genus *Hirmoneura* (map 1).

The Nemestrininae do not have genera so widely distributed as *Hirmoneura*, but as a subfamily they have a very wide distribution. Genera are geographically segregated and where they occur they are dominant. *Nemestrinus* (we may add here *Stenopteromyia*, which has only one species and is related to *Nemestrinus*) has 87% of the Palearctic species. *Trichophthalma* has 84% of the Australian species and,

Table 3

Number of species, per genus, in the six zoogeographic regions

Genus	Ethiopian	Oriental	Palearctic	Nearctic	Neotropical	Australian
Hirmoneura	-	13	7	3	22	1(?)
Trichophthalma	-	-	-	-	20	43
Prosoeca	34	-	-	-	-	-
Stenobasipteron	5	-	-	-	-	-
Nemestrinus	-	-	66	-	-	-
Stenopteromyia	-	-	1	-	-	-
Moegistorhynchus	4	-	-	-	-	-
Cyclopsidea	-	-	-	-	-	1
Neorhynchocephalus	-	-	1	2	5	-
Fallenia	-	-	2	-	-	-
Trichopsidea	1	-	1	1	-	1
Ceyloniola	-	1	-	-	-	-
Atriadops	1	1	2	-	1	3
Nycterimyia	4	4	-	-	-	4
Nycterimorpha	1	1	-	-	-	1
TOTAL	49	20	80	6	48	54

in Chile and Argentina, 55%. *Prosoeca* has 69% of the African species and if we add to it the other two genera of Nemestrinidae that occur in the area, *Stenobasipteron* and *Moegistorhynchus,* the subfamily will have 88% of the South African species (map 2).

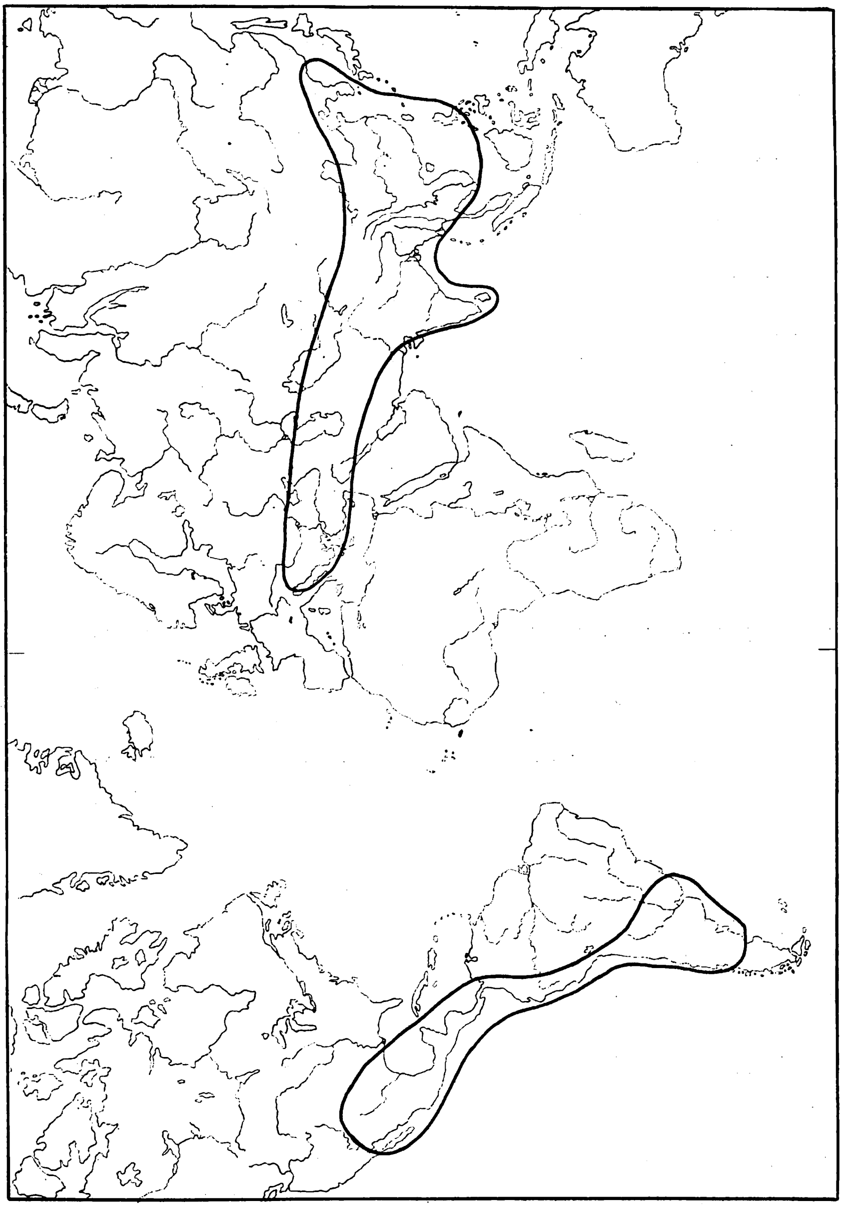
It is interesting to mention that *Hirmoneura* and the Nemestrininae largely exclude each other. Where both occur together, Nemestrininae are more abundant. Figures are as follows:

	Hirmoneura	Nemestrininae
Chile/Argentina	13	20
Mediterranean/Turkestan	5	67
Africa	0	43
Australia	1(?)	43
NW South America/S USA	7	0
Oriental Region	13	0

This might indicate a general competition between both groups, with different results in different areas. However, biological data are insufficient to warrant a thorough discussion of the matter.

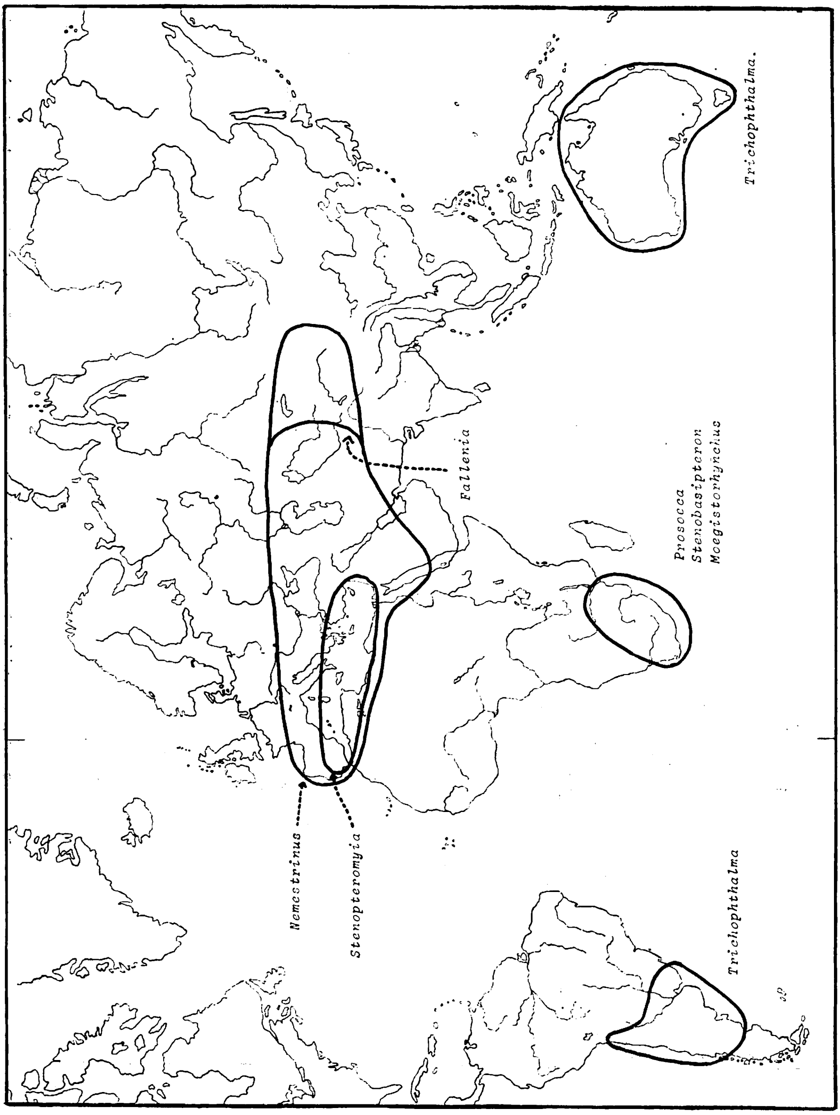
The Cyclopsideinae are the most restricted group, with a single and very rare species in Australia.

Only three genera make up the subfamily Trichopsideinae, which seems to be fairly sucessful in Recent times. The distribution is wide and, contrary to what happens with the Nemestrininae, the genera overlap geographically. *Fallenia* (map 2) extends from the Mediter-

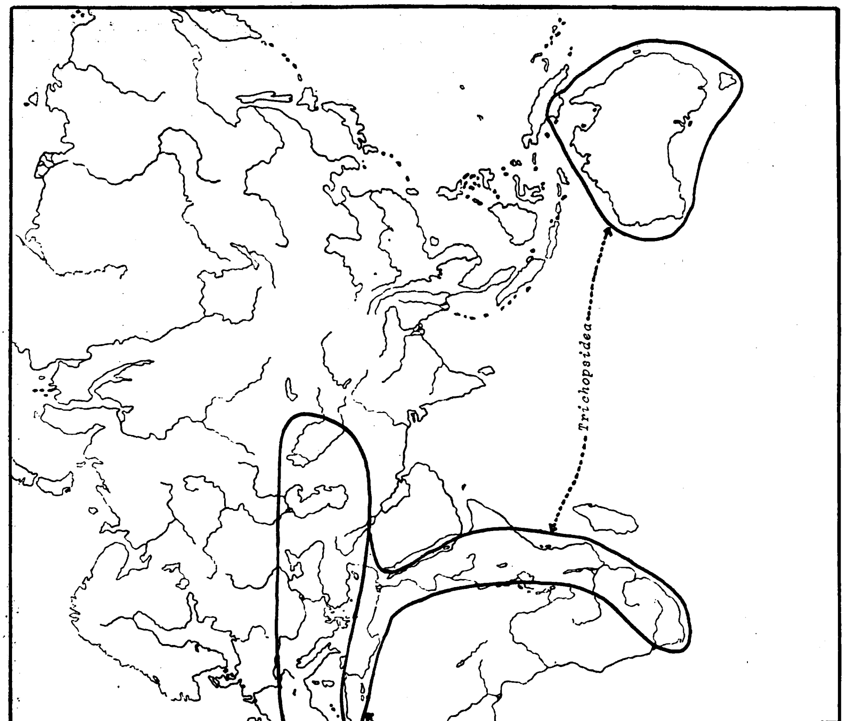


Map 1, Geographical distribution of *Hirmoneura.*

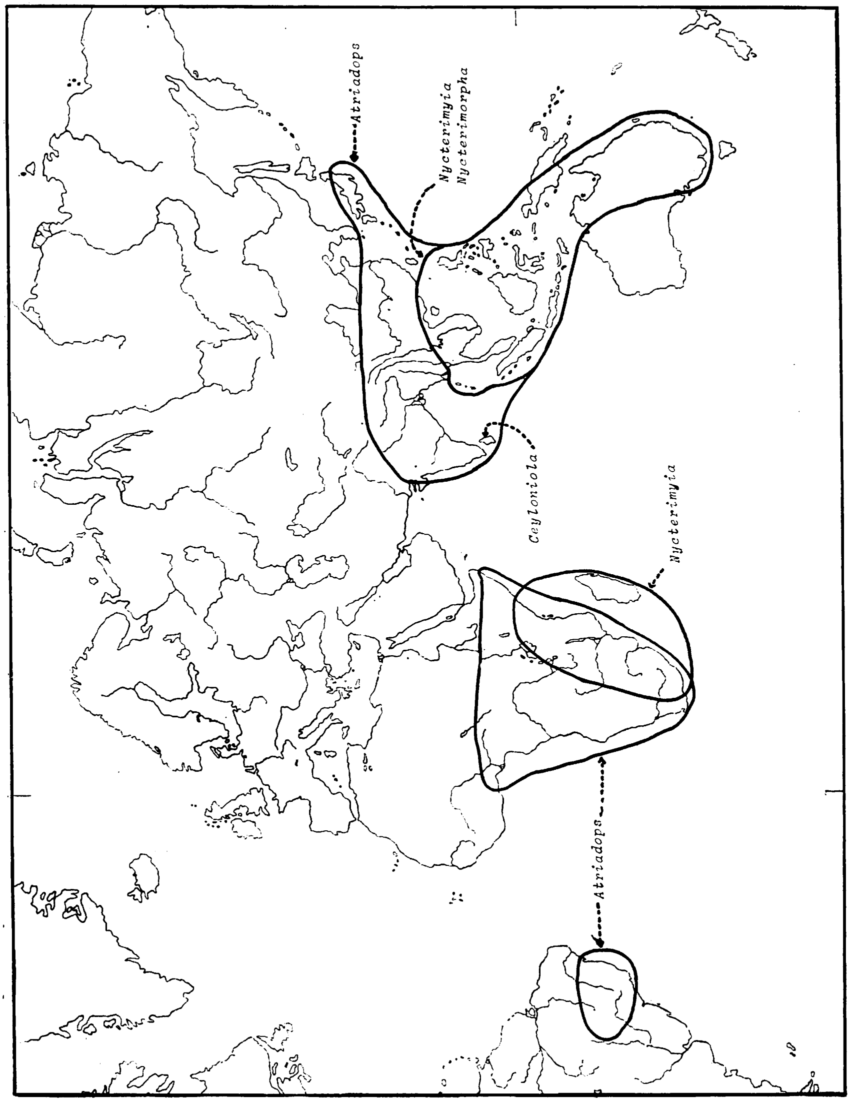
ranean to Turkestan. *Neorhynchocephalus* had at least three species in the Oligocene of Florissant and now it has six species, five American and one European (map 3). *Trichopsidea,* with only three species, has the widest distribution in the subfamily: one species is Australian, one North American and one lives in Europe and Africa (map 3). The last subfamily, Atriadopsinae (map 4), is the most restricted (with the exception of the Cyclopsideinae), but has more species than the Trichopsideinae. There are four genera, three of which relatively widely distributed. Here also, the genera overlap geographically. The subfamily occurs in Africa (with a species of *Nycterimyia* in Madagascar) and in the Oriental and Australian regions. In addition, there is one species in eastern and central Brazil. The subfamily, being the most specialized and the less widely distributed, seems to be an expanding group.



Map 2, Geographical distribution of *Trichophthalma, Prosoeca, Stenobasipteron, Moegistorhynchus, Nemestrinus, Stenopteromyia* and *Fallenia.*



Map 3, Geographical distribution of *Neorhynchocephalus* and *Trichopsidea*.



Map 4, Geographical distribution of *Ceyloniola, Atriadops, Nycterimyia* and *Nycterimorpha.*

PART II: SYSTEMATICS

1. Previous classifications

Only the classifications of Bequaert, Sack and Greathead will be dealt with.

Bequaert (1930, 1932a) proposed a classification in three subfamilies, separated as follows (in Bequaert & Carpenter, 1936):

"1 — Proboscis much reduced, more or less vestigial or aborted. Palpi either well developed, slender and hidden in deep grooves on both sides of the face, or vestigial. Ovipositor sabre-shaped. Alula usually vestigial or absent, very rarely well developed (*Nycterimyia* and *Ceyloniola*) .... Trichopsideinae

— Proboscis well developed, short or long. Palpi well developed. Alula always present, usually broad, rarely much narrowed 2

2 — Proboscis very short, always much shorter than the height of head, the labium ending in broad, soft labella. Face never prominent, deeply excavated below. Palpi usually distinctly three-segmented, resting in deep grooves on both sides of the face, close to the inner orbits. Ovipositor telescope-shaped, the terminal valvulae short .... Hirmoneurinae

— Proboscis long and slender, at least as long as the height of the head; the labium usually ending in narrow labella. Face convex and more or less prominent, sometimes snout-like. Palpi usually two-segmented (the third segment at most rudimentary), not placed in grooves along the sides of the face. Ovipositor either telescope-shaped or sabre-shaped .... Nemestrininae"

The genera included in Bequaert's classification were:

Hirmoneurinae: *Hirmoneura* Meigen (with the subgenera *Austrohirmoneura* Bequaert, *Hirmoneurilla* Bequaert, †*Hirmoneurites* Cockerell, *Hirmoneuropsis* Bequaert, *Hyrmophlaeba* Rondani, *Indohirmoneura* Bequaert, *Neohirmoneura* Bequaert and *Parahirmoneura* Bequaert).

Nemestrininae: *Nemestrinus* Latreille (including the subgenera *Heminemestrinus* Bequaert, *Nemestrellus* Sack, *Rhynchocephalus* Fischer and *Symmictoides* Bequaert), *Fallenia* Meigen, *Neorhynchocephalus* Lichtwardt, *Trichophthalma* Westwood (including the subgenera *Austrogastromyia* Bequaert, *Eurygastromyia* Lichtwardt and *Lichtwardtiomyia* Bequaert), *Stenopteromyia* Lichtwardt, *Prosoeca* Schiner (including the subgenus †*Palembolus* Scudder), *Moegistorhynchus* Macquart and *Stenobasipteron* Lichtwardt.

Trichopsideinae: *Atriadops* Wandolleck, *Cyclopsidea* Mackerras, *Nycterimorpha* Lichtwardt, *Nycterimyia* Lichtwardt, *Ceyloniola* Strand, *Trichopsidea* Westwood (including the subgenera *Dicrotrypana* Bigot, *Symmictus* Loew and *Parasymmictus* Bigot).

Sack (1933), studying only the Palearctic fauna, accepted only two subfamilies: "Rüssel verlängert, mindestens von halber Thoraxlänge ...... Nemestrininae Rüssel kurz, meist in der Behaarung des Gesichts verborgen oder ganz rudimentär .... Hirmoneurinae"

The division of genera by Sack was as follows:

Nemestrininae: *Nemestrellus* Sack, *Nemestrinus* Latreille, *Heminemestrinus* Bequaert, *Rhynchocephalus* Fischer, *Symmictoides* Bequaert, *Neorhynchocephalus* Lichtwardt, *Stenopteromyia* Lichtwardt and *Fallenia* Meigen.

Hirmoneurinae: *Symmictus* Loew, *Hirmoneura* Meigen and *Atriadops* Wandolleck.

Greathead (1967) accepted the system proposed by Bequaert, but gave the group a new treatment, with special attention to the male genitalia. He thus defined the subfamilies:

Nemestrininae: "Proboscis well developed; palpi robust usually porrect, face wide, bare, or with only sparse short hairs, projecting. Wing venation not reduced and with a marked tendency to the development of a reticulated wing tip. Body rather bare, with fine scattered hairs and a pattern formed by tomentum and bare shiny areas. Abdomen flattened. Hypopygium with parameres separate, telomeres elongate usually bifid, aedeagus sharply bent upwards and with accessory structures applied to it, no blade-like accessory structure applied to the ventral surface of the apical tergites. Ovipositor telescopic, valves usually short".

Trichopsideinae: "Proboscis tending to be reduced or rudimentary. Palpi narrow, pendant. Face wide covered with dense hairs, not prominent. Wing venation tending to reduction of the number of veins at the apex, and to atrophy of the veins at the posterior margin. Body covered with silky mainly decumbent hairs which tend to form bands across the hind margin of the tergites. Abdomen inflated, tending to be circular in cross section. Hypopygium with parameres meeting ventrally, telomeres triangular or elongate but simple, aedeagus tubular protruding posteriorly between the telomeres, with a blade-like accessory structure applied to the ventral surface of the apical tergites. Ovipositor not telescopic, valves usually very long".

Hirmoneurinae: "Proboscis short fleshy, palpi erect. Face narrow not markedly hairy. Wing venation not modified by reticulation of the apex or reduction of veins. Body sparsely covered with erect hairs and tomentum, and without a distinct pattern. Abdomen flattened. Hypopygium with parameres separated by a pair of accessory structures sheathing the aedeagus, no distinctly sclerotized structures in the terminal depression between the hypopygium and ninth tergite".

Greathead divided the genera this way:

Nemestrininae: *Nemestrinus* Latreille, *Prosoeca* Schiner, *Stenobasipteron* Lichtwardt and probably *Trichophthalma* Westwood and *Moegistorhynchus* Macquart.
Trichopsideinae: group 1: *Trichopsidea* Westwood, *Neorhynchocephalus* Lichtwardt; group 2: *Fallenia* Meigen; group 3: *Atriadops* Wandolleck, *Nycterimyia* Lichtwardt and probably *Nycterimorpha* Lichtwardt.

Hirmoneurinae: *Hirmoneura* Meigen.

Of the three classifications, Sack's was the weakest and Greathead's the best. Sack's system, based on a single character of secondary importane, the proboscis, was completely artificial. Bequaert, although also relying in large measure on the proboscis, was correct in recognizing that *Hirmoneura*, on the one hand, and his Trichopsideinae, on the other, were completely independent groups. In spite of this, his classification was very artificial, especially in separating *Neorhynchocephalus* and *Fallenia* from *Trichopsidea* and uniting those two genera with the Nemestrininae. As to his Trichopsideinae, although they might have been subdivised, if one excludes *Cyclopsidea*, they form a much more natural group than Sack's Hirmoneurinae. When Bequaert presented his system, *Cyclopsidea* was known only from the male, which he placed in the Trichopsideinae. Had he known the presence of an ovipositor of type 1 in this genus and perhaps he would have erected a new subfamily for it, since he would not have been able to place it in the Nemestrininae.

Greathead did not mention *Stenopteromyia*, *Cyclopsidea* and *Ceyloniola*. According to his concepts, *Stenopteromyia* would easily be included among the Nemestrininae and *Ceyloniola* among the Trichopsideinae, but *Cyclopsidea* would fall in none of the subfamilies. Greathead's contribution was, nevertheless, extremely important, because his groupings were natural, although his Trichopsideinae could be divided, as we shall see.

Bequaert considered the Hirmoneurinae the most primitive subfamily, followed by the Nemestrininae and Trichopsideinae. Even considering the fact that this Trichopsideinae included at least three different groups, his order was correct. Greathead's order was: Nemestrininae, Trichopsideinae, Hirmoneurinae. However, since he did not give any explanation, it is impossible to know if this order reflected his ideas about the family phylogeny or not. I do not believe it did. Anyway, it was inadequate.

In 1968, Rohdendorf erected a new subfamily, †Archinemestriinae, for two genera of the Jurassic of Karatau (Kazakhstan), based especially on the radial phragma of the basial and the bend of some veins that terminate on the hind margin. This step taken by Rohdendorf was very important. The †Archinemestriinae are the most primitive group in the family and help very much in understanding the evolution of Recent groups.

2. Proposed classification

Taking into consideration the works of Bequaert, Greathead and Rohdendorf, and adding my own observations, I propose some changes in the systematic treatment of the Nemestrinidae. My proposed classification is as follows:

1) Subfamily †Archinemestriinae Rohdendorf
   Genera: †*Archinemestrius* Rohdendorf and †*Protonemestrius* Rohdendorf.

2) Subfamily Hirmoneurinae Loew
   Genera: †*Eohirmoneura* Rohdendorf and *Hirmoneura* Meigen.

3) Subfamily Nemestrininae Macquart
   Genera: *Trichophthalma* Westwood, *Prosoeca* Schiner, *Stenobasipteron* Lichtwardt, †*Palembolus* Scudder, *Nemestrinus* Latreille, *Stenopteromyia* Lichtwardt and *Moegistorhynchus* Macquart.

4) Subfamily Cyclopsideinae, new subfam.
   Genus: *Cyclopsidea* Mackerras.

5) Subfamily Trichopsideinae Bequaert
   Genera: *Neorhynchocephalus* Lichtwardt, *Fallenia* Meigen and *Trichopsidea* Westwood.

6) Subfamily Atriadopsinae, new subfam.
   Genera: *Ceyloniola* Strand, *Atriadops* Wandolleck, *Nycterimyia* Lichtwardt and *Nycterimorpha* Lichtwardt.

7) Genus "incertae sedis": †*Prohirmoneura* Handlirsch.

This classification employs characters not used so far, such as the proportions of the segments of the hind tarsus, depression of the face, opacity of the wings and some characters of wing venation. I have tried to give up completely the idea that certain characters are peculiar to certain categories, i. e., certain characters are of generic rank, others of subfamily rank, etc. This idea undoubtedly obscures the phylogenetic relationships and produces artificial groupings, as can be seen in the classifications of Sack and Bequaert. I have tried to discover the apparent evolutionary trends within the family, ascribing them to subfamily rank.

I believe the divisions I have made are justified. *Cyclopsidea* undoubtedly requires a subfamily of its own, because it is a completely isolated branch within the family. The Atriadopsinae might perhaps be divided into two tribes, each with two genera, but I do not think it necessary at this time. In the other subfamilies, any subdivisions would, I think, be doubtful and unnecessary, at least for the time being.

The concept of nemestrinid genera requires some comments. They are, in general, well delimited, but in the Nemestrininae separation of some genera is not clear. Nevertheless, all groups here called genera are undoubtedly natural groups. I do not underestimate what could be called "taxonomic intuition". Sometimes the systematist knows that certain groups are natural and distinct, but he is not always able to express that in terms of characters. In the case of the nemestrinine genera just mentioned, previous authors neither gave definitions for them nor put them in keys, although there was no doubt as to identity of the genera. I have tried to define them, but sometimes with not too much firmess. In other subfamilies diagnostic characters are abundant. As a result, there is no homogeneity in the generic concepts in all subfamilies. Because of the evolutionary history of the family, different groups representing different radiations in different areas and different times did not develop the same amount of morphological difference.

The work of the systematist is, essentially, choosing and weighing characters. I have tried to use only those characters really useful and, in my opinion, unquestionable. Highly variable characters, useless for the definition of genera and subfamilies, and in the understanding of phylogenetic relationships, such as color, pilosity, pollinosity and others, were not used. This does not mean that these characters do not have importance. It may be possible, after good generic revisions, to show limits of variation and such characters may then be used for generic diagnoses. It will be noted that my definitions are brief. On the other hand, not all characters were used in all groups, either because it was not yet possible to study them in all groups or because they do not always have the same importance in all groups.

3. Identification keys

Keys include only Recent genera. I decided to make a generic key for the world and separate keys for each zoogeographic region. Regional keys are more trustworthy and easier to use. In the general key, sometimes characters restricted to one sex had to be included. This key still has to be tested.

KEY TO WORLD GENERA

1. Proboscis well developed, longer than head 2
Proboscis reduced, clearly shorter than head, or vestigial 9

2. R3 present 3
R3 absent 6

3. R4 and R5 almost totally fused, forming a small triangular cell (3rd submarginal) in the middle of the wing, that may be occasionally absent; diagonal vein incomplete (3rd and 5th posterior cells fused); M1 fused with R4+R5 (1st posterior cell closed); M2 strongly bent forward, almost reaching

R4+R5+M1, sometimes reaching it and closing the 2nd posterior cell; anal cell closed (fig. 32) .... *Fallenia*

R4 and R5 free or, at most, fused for a short distance; diagonal vein complete (incomplete in some *Neorhynchocephalus*); M1 and R4+R5 free; M2 normally bent, approximately parallel to other veins; anal cell open (closed in some *Neorhynchocephalus*) 4

4. Claws exceptionally long and slender; pulvilli and empodia long; hypandrium sub-quadrate, much shorter than gonopods, high in lateral view, with a ventral tuft of hairs (figs. 60-62); South Africa .... *Moegistorhynchus*

Claws, pulvilli and empodia normal; hypandrium absent or elongate, free, longer than gonopods, thin in lateral view, without tuft of hairs; Palearctic or New World 5

5. Face swollen, often prominent; ovipositor type 1; hypandrium elongate, free, longer than gonopods (figs. 54-56); behind R1, five veins reach the apical margin; M1 and M2 free (2nd posterior cell open); diagonal vein complete (3rd and 5th posterior cells separate); often supernumerary cross-veins present on the apical third of wing (figs. 24-26); exclusively Palearctic genus .... *Nemestrinus*

Face slightly convex; ovipositor type 2; hypandrium absent, gonopods fused, forming a single ventral piece (figs. 63-65); behind R1, four or five veins reach the apical margin; M1 and M2 free or partially fused (2nd posterior cell open or closed); diagonal vein complete or incomplete (3rd and 5th posterior cells separate or united); no supernumerary cross-veins (fig. 30-31); New World genus, with a single Palearctic species (*N. tauscheri*) .... *Neorhynchocephalus*

6. Behind R1, three veins reach the apical margin; R2 and R4 fused (2nd submarginal cell closed); diagonal vein incomplete (3rd and 5th posterior cells united) (fig. 27) .... *Stenopteromyia*

Behind R1, five veins reach the apical margin; all cells beyond diagonal vein open; diagonal vein complete 7

7. Eyes densely pilose; Australia, Chile, Argentina and Uruguay .... *Trichophthalma*

Eyes bare; South Africa 8

8. Wings transparent, but strongly infuscated, characteristic in shape; costa strongly developed; alula much reduced (fig. 23) .... *Stenobasipteron*

Wings hyaline, normal; alula normal, with tendency to reduction in some species (fig. 22) .... *Prosoeca*

9. Head without depression below the antennae; antennae with three segments, followed by style; 1st segment of hind tarsus longer or as long as the last four together; wings hyaline 10

Head with a strong depression below the antennae; 3rd antennal segment fused with style, forming a single piece (figs. 11-13); 1st segment of hind tarsus clearly shorter than the last four together, the 5th longer than each one of the three intermediary; wings opaque, leathery, with reduced hyaline areas 11

10. Behind R1, five veins reach apical margin (fig. 18) .... *Hirmoneura*

Behind R1, four veins reach the apical margin (fig. 29) .... *Cyclopsidea*

Behind R1, two or three veins reach the apical margin (figs. 33, 34) .... *Trichopsidea*

11. Axillary cell well developed; m-cu present; all cells beyond diagonal vein open; hind margin normal 12

Axillary cell narrow; m-cu absent; beyond the diagonal vein there is a closed cell, just above the discal cell, formed by fusions in the radial field; hind margin wavy, projecting at least in the region of the anal cell 13

12. Ocelli present; R4 and R5 free (3rd submarginal cell open); R3 present as a stump projecting from the bend of R4, interrupted midway between R4 and R2 (fig. 35); restricted to Ceylon .... *Ceyloniola*

Ocelli absent; R4 and R5 totally fused (3rd submarginal cell absent); R3 absent (fig. 36); Africa, Oriental Region, Australia, Brazil .... *Atriadops*

13. Alula narrow, but present; M3 and M4 reach the diagonal vein (the 4th posterior cell separates completely the discal and the 5th posterior cells); behind R1, three veins reach the apical margin (fig. 37) .... *Nycterimyia*

Alula absent; M3 and M4 fuse before reaching the diagonal vein (4th posterior cell reduced in length and discal and 5th posterior cells in contact); behind R1, two veins reach the apical margin (fig. 38) .... *Nycterimorpha*

KEY TO NEARCTIC GENERA

1. Proboscis well developed, longer than head .... *Neorhynchocephalus*

Proboscis shorter than head, or vestigial 2

2. Behind R1, five veins reach the apical margin ...... *Hirmoneura*

Behind R1, three veins reach the apical margin (3rd submarginal and 2nd posterior cells closed) .... *Trichopsidea*

KEY TO NEOTROPICAL GENERA

1. Proboscis well developed, longer than head 2
Proboscis shorter than head or vestigial 3

2. Eyes densely pilose .... *Trichophthalma*
Eyes bare .... *Neorhynchocephalus*

3. Behind R1, five veins reach the apical margin; ocelli present .... *Hirmoneura*
Behind R1, four (or three) veins reach the apical margin (fig. 36); ocelli absent .... *Atriadops*

KEY TO PALEARCTIC GENERA

1. Proboscis well developed, longer than head 2
Proboscis shorter than head or vestigial 5

2. R3 absent; R2 and R4 fused (2nd submarginal cell closed); M1 and M2 fused (2nd posterior cell closed) (fig. 27) .... *Stenopteromyia*
R3 present; R2 and R4 separate (2nd submarginal cell open); M1 and M2 separate or fused (2nd posterior cell open or closed) . 3

3. R4 and R5 almost totally fused, forming a small triangular cell (3rd submarginal) in the middle of the wing, that may be occasionally absent; diagonal vein incomplete (3rd and 5th posterior cells united); M1 fused with R4+R5 (1st posterior cell closed); M2 strongly bent forward, almost reaching R4+R5+M1, sometimes reaching it and closing the 2nd posterior cell; anal cell closed (fig. 32) .... *Fallenia*
R4 and R5 free or, at most, fused for a short distance; diagonal vein complete or incomplete (3rd and 5th posterior cells separate or united); M1 and R4+R5 free; M2 normally bent, approximately parallel to other veins; anal cell open (may be closed in *Neorhynchocephalus*) 4

4. Face swollen, often prominent; ovipositor type 1; hypandrium elongate, longer than gonopods (figs. 54-56); behind R1, five veins reach the apical margin; M1 and M2 free (2nd posterior cell open; diagonal vein complete (3rd and 5th posterior cells separate); often supernumerary cross-veins present at apical third of wing (figs. 24-26) .... *Nemestrinus*
Face slightly convex; ovipositor type 2; hypandrium absent, gonopods separate, almost meeting ventrally; behind R1, four or five veins reach the apical margin; M1 and M2 free or fused

(2nd posterior cell open or closed); diagonal vein incomplete (3rd and 5th posterior cells united) ...... *Neorhynchocephalus*

5. Behind R1, five veins reach the apical margin (fig. 18) *Hirmoneura.*
Behind R1, less than five veins reach the apical margin 6

6. Wings hyaline; ocelli present; axillary cell narrow (fig. 34) .... *Trichopsidea*
Wings opaque; ocelli absent; axillary cell wide (fig. 36) .... *Atriadops*

KEY TO ETHIOPIAN GENERA

1. Proboscis well developed, longer than head 2
Proboscis vestigial 4

2. Apical third of wing reticulate, due to presence of supernumerary cross-veins (fig. 28) .... *Moegistorhynchus*
Apical third of wing not reticulate 3

3. Wings transparent, but strongly infuscated, characteristic in shape; Costa strongly developed; alula much reduced (fig. 23) .... *Stenobasipteron*
Wings hyaline, normal; alula normal, with tendency to reduction in some species (fig. 22) .... *Prosoeca*

4. Wings hyaline .... *Trichopsidea*
Wings opaque, with or without hyaline areas 5

5. Ocelli absent; axillary cell strongly enlarged; m-cu present; hind margin normal; all cells beyond diagonal vein open; without hyaline areas (fig. 36) .... *Atriadops*
Ocelli present; axillary cell much narrowed; m-cu absent; hind margin wavy, projected at the diagonal vein and at the anal cell; there is a closed cell beyond the diagonal vein, just above the discal cell, formed by fusions in the radial field; hyaline areas present (fig. 37) .... *Nycterimyia*

KEY TO ORIENTAL GENERA

1. Wings hyaline .... *Hirmoneura*
Wings opaque, with hyaline areas 2

2. Axillary cell strongly enlarged: m-cu present; all cells beyond diagonal vein open; hind margin normal 3
Axillary cell very narrow; m-cu absent; there is a closed cell, beyond the diagonal vein, just above the discal cell, formed by fusions

in the radial field; posterior margin wavy, projectin at least in the anal cell region 4

3. Ocelli present; R4 and R5 free (3rd submarginal cell open); R3 present as a stump projecting from the bend of R4, interrupted midway between R4 and R2 (fig. 35) .... *Ceyloniola*

Ocelli absent; R4 and R5 totally fused (3rd submarginal cell absent); R3 absent (fig. 36) .... *Atriadops*

4. Alula narrow, but present; M3 and M4 reach the diagonal vein separately (4th posterior cell separating completely the discal and the 5th posterior cells); behind R1, three veins reach the apical margin (fig. 37) .... *Nycterimyia*

Alula absent; M3 and M4 fuse before reaching the diagonal vein (4th posterior cell reduced in length and discal and 5th posterior cells in contact); behind R1, two veins reach the apical margin (fig. 38) .... *Nycterimorpha*

KEY TO AUSTRALIAN GENERA

1. Proboscis well developed, at least as long as head. *Trichophthalma*

Proboscis shorter than head or vestigial 2

2. Head hemispheric, conspicuously wider than thorax and almost as large in volume; post-scutellum conspicuously enlarged, almost as large as scutellum .... *Cyclopsidea*

Head flattened, not so wide as thorax and much smaller in volume; post-scutellum normally developed 3

3. Wings hyaline 4

Wings opaque, with hyaline areas 5

4. Behind R1, five veins reach the apical margin; (the presence of this genus in Australia is doubtful) .... *Hirmoneura*

Behind R1, three veins reach the apical margin (fig. 33) .... *Trichopsidea*

5. Ocelli absent; axillary cell very wide; m-cu present; all cells beyond diagonal vein open (fig. 36) .... *Atriadops*

Ocelli present; axillary cell very narrow; m-cu absent; there is a closed cell beyond the diagonal vein, formed by fusions in the radial field 6

6. Alula narrow, but present; M3 and M4 reach the diagonal vein separately (4th posterior cell separating completely the discal and the 5th posterior cells); behind R1, three veins reach the apical margin (fig. 37) .... *Nycterimyia*

Alula absent; M3 and M4 fuse before reaching the diagonal vein (4th posterior cell reduced in length and discal and 5th posterior cells in contact); behind R1, two veins reach the apical margin (fig. 38) .... *Nycterimorpha*

4. Subfamily †Archinemestriinae Rohdendorf

"Description. Basial without distinctly individualized radial phragma. The darkening on corresponding place without distinct outlines. Vein C on anterior margin thickened, after passing apex on posterior margin it becomes thinner. R1 thick, strong, markedly stronger than Sc and posterior veins. Sc markedly shorter than R1 and terminating on the anterior margin approximately at the level of the cross vein rm, at the end of the second third of the wing length. M1 and M2 curved backwards at their ends and reaching the wing margin behind the apex. Area M1 and R2+3 without cross veins. Diagonal vein not straight, shaped zigzag posteriorly. Proboscis short, more rarely equal to head length".

"Relations. This Jurassic group is characterized by slightly prolongated wings with little specialized venation. Radial phragma in the basial is little individualized, the diagonal vein is not straight. Also the bends of veins and their terminations on the posterior margin are characteristic. All features mentioned above separate the subfamily from all other representantives of the family so far known" (Rohdendorf, 1968: 181).

Genus †**Archinemestrius** Rohdendorf

(Fig. 14)

†*Archinemestrius* Rohdendorf, 1968: 181. Type-species, †*karatavicus* Rohdendorf (orig. des.).

"Description. The wing is in apical part slightly curved backwards, with irregularly undulated posterior margin. Sc shorter than 2/3 of the wing length. Cross vein rm absent because of the anastomoses R4+5 with M1+2. Cell R4 bent and strongly broadened at the apex: veinlet R5 curved backwards, terminating on the posterior margin side by side to M1 behind the wing apex. M1 strongly curved at its end, parallel to R5 in its distal part. M2 short, slightly curved backwards: cell M1 broadening towards apex, much broader than the cell R5. Cell M2 short, almost triangular: end of M2 situated at the middle distance between the apex and the end of M3+4. Diagonal veinlet well indicated in its anterior half and pronouncedly zig-zag in the posterior part from the end of discoidal cell to the posterior wing margin. The free end of M3+4 (end of the diagonal vein) is equal to the section M3 (last but one section of the diagonal vein). Basial without the strong radial phragma, with stout medial part and dark spot next to radial stem. Head short, apparently lacking the long proboscis. Eyes holoptic (male?). There are three very small ocelli. Antennae thin and short, composed of not less than four homonomous joints. Thorax somewhat broader than the head. Abdomen broadened at its base, gradually narrowing towards the apex, composed of not less than eight segments" (Rohdendorf, 1968: 181-182).

"Relations. The genus differs distinctly from the other genus by the wing shape and by the bend of distal portions of veins" (Rohdendorf, 1968: 182).

Distribution: Jurassic of Karatau (Kazakhstan).

Catalog:

†*karatavicus* Rohdendorf, 1968: 182, text-fig. 1, pl. 22, fig. 1. Type-locality: Kazakhstan, Karatau (Jurassic).

Genus †**Protonemestrius** Rohdendorf

(Fig. 15)

†*Protonemestrius* Rohdendorf, 1968: 182. Type-species, †*martynovi* Rohdendorf (orig. des.)

"Description. Apical part of the wing not curved; posterior margin slightly undulated, sometimes regularly convex. Sc equal to 2/3 of the wing length or slightly longer. Cross vein rm short, but well developed, veins R and M do not fuse. Cell R4 broadened at the apex and slightly bent: vein R5 slightly curved and terminating in the very apex. M1 slightly bent, in the discal part markedly diverging from the end of R5, less frequently parallel to it. M2 long, meeting M1, curved backwardly at the very end. Cell M1 narrowed towards the apex and at the end usually markedly broadened. Cell M2 long, slightly shorter than the cell M1. Diagonal vein zigzag, not straight. Free end of diagonal vein (M3+4) of various length, equal to or longer than the last but one section (M3). Basial without strong radial phragma, with broad darkening, distinct oblique veinlet absent. Head slightly prolongated, with prominent proboscis. Thorax not particularly broad. Legs with slightly broadened femora and narrow tibiae and tarsi; hind tibiae with short spurs, tarsi with bristles. Abdomen broad at the base (first three segments), narrowing towards the distal end, composed of not less than nine segments" (Rohdendorf, 1968: 182-183).

"Relations. This genus approaches the Hirmoneurinae and Nemestrininae by the character of M and of the apical section of veins and differs distinctly from the genus *Archinemestrius* (Rohdendorf, 1968: 183).

Distribution: Jurassic of Karatau (Kazakhstan).

Catalog:

†*bequaerti* Rohdendorf, 1968: 185, text-fig. 4, pl. 22, fig. 4. Type-locality: Kazakhstan, Karatau (Jurassic).

†*handlirschi* Rohdendorf, 1968: 184, text-fig. 3, pl. 22, fig. 3. Type-locality: Kazakhstan, Karatau (Jurassic).

†*longinasus* Rohdendorf, 1968: 186, text-fig. 5, pl. 22, fig. 5. Type-locality: Kazakhstan, Karatau (Jurassic).

†*martynovi* Rohdendorf, 1968: 183, text-fig. 2, pl. 22, fig. 2. Type-locality: Kazakhstan, Karatau (Jurassic).

5. Subfamily Hirmoneurinae Loew

Definition: head large, hemispherical, as wide as or wider than thorax, but much smaller in volume; face convex; proboscis very short, always much shorter than head, antennae three-segmented, with segmented style. Thorax normal in relation to the insect's size; scutellum normal; 1st segment of hind tarsus longer or as long as the last four together. Alula present, wide or narrow. Wings hyaline or infuscated, but transparent; M1 and M2 running towards the apical margin. Venation complete, without reduction. Ovipositor type 1. Hypandrium reduced (much shorter than half the gonopods) or absent.

Genus †**Eohirmoneura** Rohdendorf

(Fig. 16)

†*Eohirmoneura* Rohdendorf, 1968: 187. Type-species, †*carpenteri* Rohdendorf (orig. des.).

"Description. Sc reaching the level of the distal end of discoidal cell. Diagonal vein angulous, not reaching the posterior margin. R4 at the base angulous, with short offshoot (rudimentary R3?), not reaching R2+3. M1 area divided into two cells by a strong cross vein, contacting veins M1 and M2. Cross vein rm straight, not particularly short. Apex between M1 and M2".

"Relations. New genus differs from the genus *Hirmoneura* by indistinctly developed angulous diagonal vein, not reaching the wing margin, short Sc and by original angulous bend of the base; the venation resembles the Oligocene subgenus *Hirmoneura* (*Hirmoneurites*)" (Rohdendorf, 1968: 187).

Distribution: Jurassic of Karatau (Kazakhstan).

Catalog:

†*carpenteri* Rohdendorf, 1968: 188, text-fig. 6, pl. 22, fig. 6. Type-locality: Kazakhstan, Karatau (Jurassic).

Genus **Hirmoneura** Meigen

(Figs. 1, 18-19, 39-44, map 1)

Hirmoneura Meigen, 1820: 132. Type-species, *obscura* Wiedemann (mon.).

Hyrmophlaeba Rondani, 1863: 51. Type-species, *Hirmoneura brevirostris* Macquart (orig. des.).

†*Hirmoneurites* Cockerell, 1910: 283. Type-species, †*willistoni* Cockerell (mon.).

Neohirmoneura Bequaert, 1920: 306 (as subgenus). Type-species, *Hirmoneura flavipes* Williston (orig. des.)

Austrohirmoneura Bequaert, 1932a: 15 (as subgenus). Type-species, *Hermoneura bellula* Philippi (orig. des.).

Hirmoneurilla Bequaert, 1932a: 15 (as subgenus). Type-species, *Hermoneura punctipennis* Philippi (orig. des.)

Hirmoneuropsis Bequaert, 1932a: 15 (as subgenus). Type-species, *Hirmoneura brevirostrata* Bigot (orig. des.).

Indohirmoneura Bequaert, 1932a: 14 (as subgenus). Type-species, *Hirmoneura coffeata* Lichtwardt (orig. des.).

Parahirmoneura Bequaert, 1938: 292 (as subgenus). Type-species, *Hirmoneura brandti* Bequaert (orig. des.).

Hermoneura, emendation.

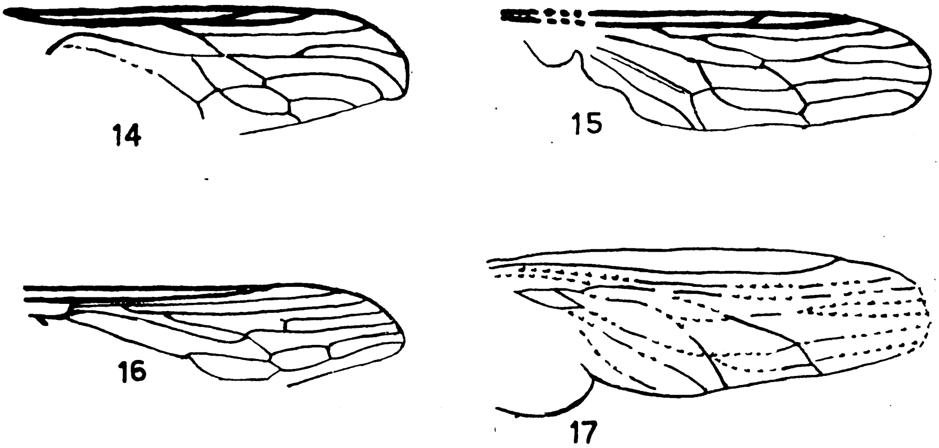
Hirmonevra, emendation.

Hyrmoneura, error.

Hirmophlaeba, error.

Hirmophloeba, error.

Hyrmophloeba, error.



Wing venation. 14, †*Archinemestrius karatavicus;* 15, †*Protonemestrius martynovi;* 16, †*Eohirmoneura carpenteri;* 17, †*Prohirmoneura jurassica.* (Figs. 14-16 from Rohdendorf, 1968; fig. 17 from Handlirsch, 1908).

Refs.: Angulo, 1971: 52; Bequaert, 1932a: 14, 1938: 292; Paramonov, 1953: 255, 1956: 235; Sack, 1933; 38; Stuardo Ortiz, 1932: 63.

Definition: head large, almost hemispherical or slightly flattened, approximately as wide as thorax, but smaller in volume; proboscis reduced, always much shorter than head. Eyes varying from completely bare to densely pilose. Antennae with three short segments and a segmented style. Alula normal, sometimes very narrow. R3 present or absent; R4 and R5 always free (3rd submarginal cell open); M1 and M2 always free (2nd posterior cell open); 1st and 2nd posterior cells sometimes divided by a cross-vein (when this occurs in both cells, a second diagonal vein, short, parallel to the first, is formed); r-m present or absent (if fusion between R4+5 and M1+2 occurs, it is just incipient); Cu1 and 1A free (anal cell open). Male genitalia: figs. 39-44. Hypandrium absent in most species, but in *H. obscura* it is greatly reduced, much shorter than half the length of gonopods; gonopods free. Ovipositor type 1.

Distribution:

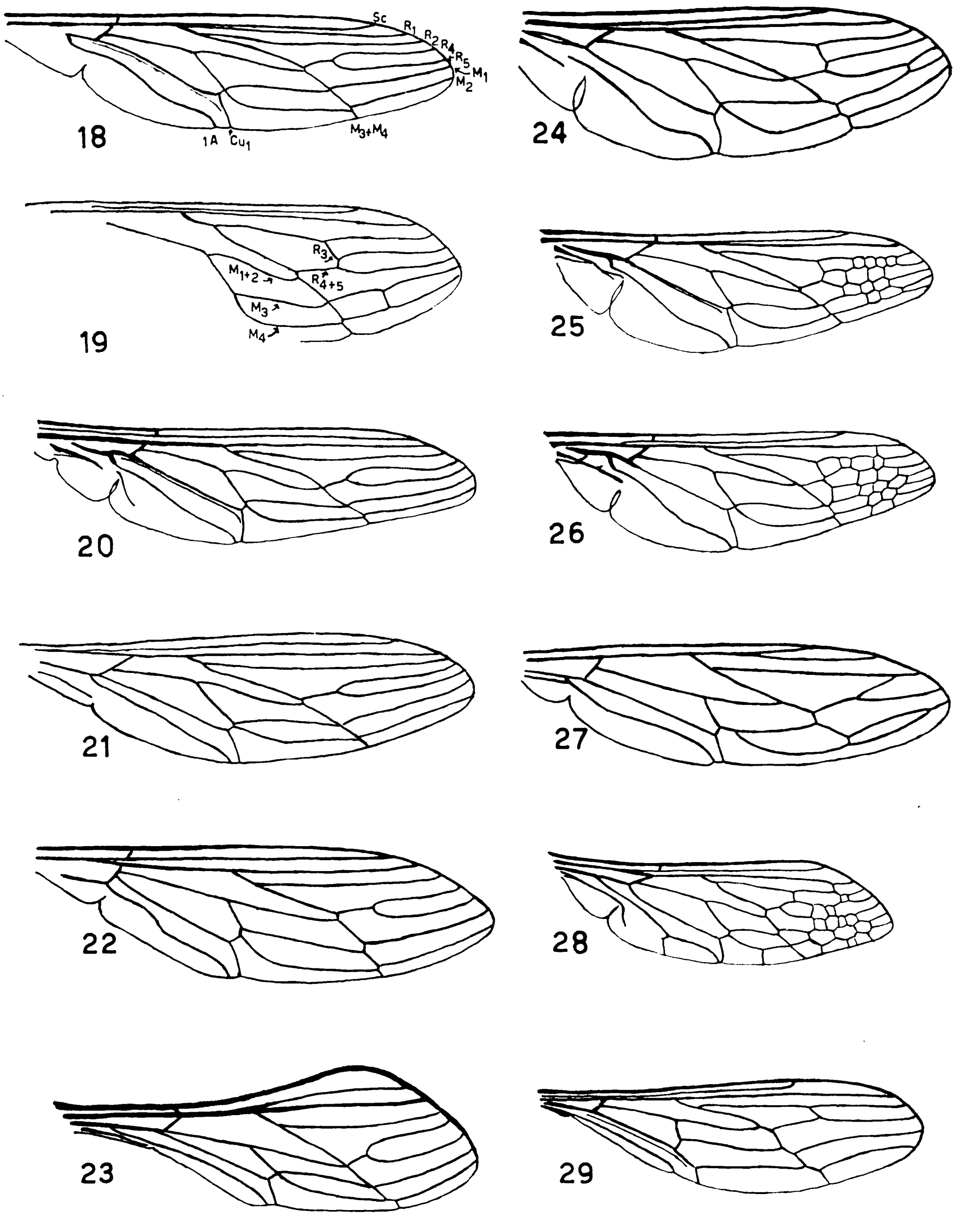
1) United States (Colorado, Arizona, Texas), Mexico, Guatemala, Nicaragua, Panama, Colombia, Ecuador, Peru (Lima), Chile (Tarapacá to Valdivia), Argentina (Catamarca to Santa Cruz), Uruguay.

2) Yugoslavia, Austria, Romania, Greece, Turkey, Syria, Iran and Turkestan.

3) Nepal, India, Ceylon, Burma, Thailand, Laos, Vietnam, China (Chekiang), Formosa, Russia (Khabarovsk), Philippines.

4) Australia (one doubtful reference, without precise locality).

Comments: Bequaert (1932a) divided *Hirmoneura* into several subgenera, which I am provisionally rejecting, as did Paramonov (1953). The genus is possibly polyphyletic, but threre are not yet sufficient data to make a sound subdivision. The groups proposed by Bequaert have been based on the presence or absence of R3, of supernumerary crossveins, on the pilosity of the eyes and on holopticity or dichopticity of the eyes. However, these groups are not geographically segregated. Study of the male genitalia may perhaps reveal a good deal of reliable informations. Meanwhile, I prefer to keep *Hirmoneura* as a single genus. Angulo (1971) represented all Chilean species of *Hirmoneura* as having a distinct and free hypandrium. I cannot agree with him since I have dissected many species of this genus, including Chilean species and the only species found to have a hypandrium was *H. obscura;* in all other species the hypandrium was absent, leaving a free space between the gonopods. Curiously enough, he even considered *Neorhynchocephalus mendozanus* to have a hypandrium (see his fig. 75), which is completely unbelievable.



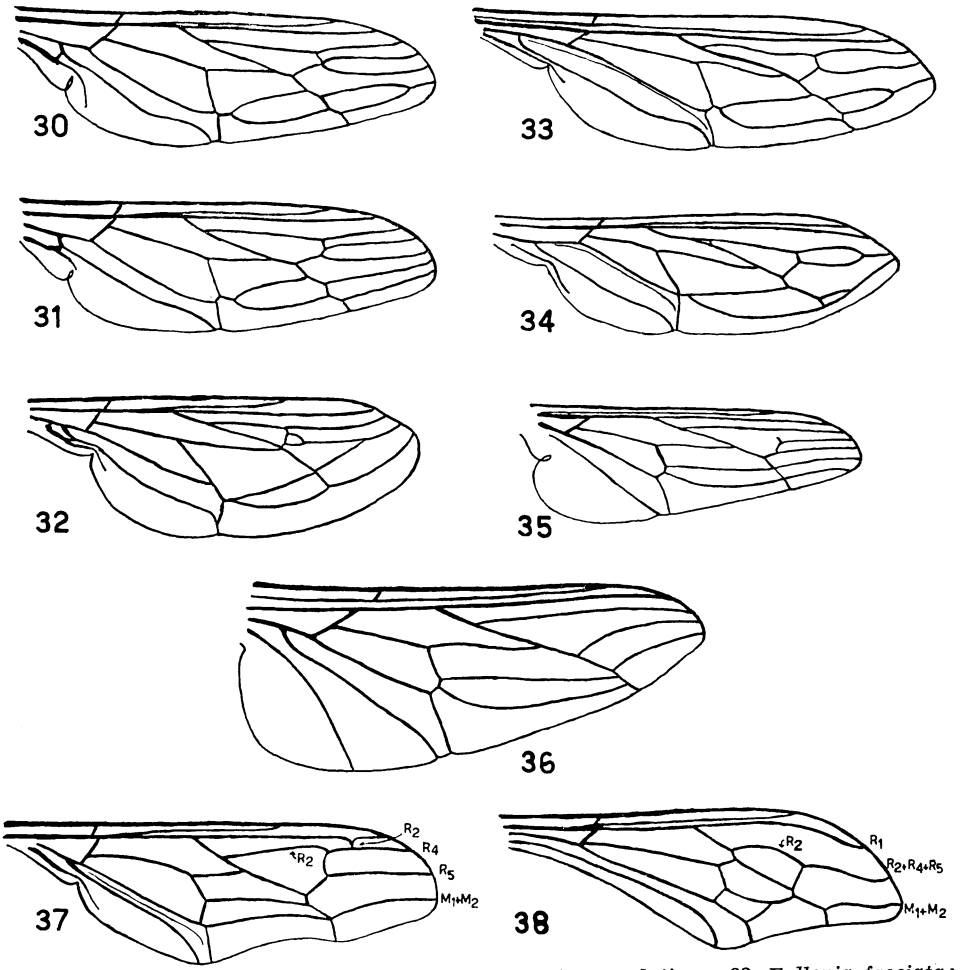
Wing venation. 18, *Hirmoneura obscura;* 19, †*H. willistoni;* 20, *Trichophthalma bancrofti;* 21, †*Palembolus florigerus;* 22, *Prosoeca sublineata;* 23, *Stenobasipteron wiedemanni;* 24, *Nemestrinus caucasicus;* 25, *N. brandti;* 26, *N. iranicus;* 27, *Stenopteromyia bolivari;* 28, *Moegistorhynchus brevirostris;* 29, *Cyclopsidea hardyi.* (Figs. 19, 21 from Bequaert & Carpenter, 1936; figs. 20, 29 from Mackerras, 1925; fig. 22 from Bequaert, 1925b; fig. 24 from Ionescu & Weinberg, 1962; figs. 25, 26 from Bequaert, 1938; fig. 28 from Bequaert, 1935b).

Catalog:

ales (Newman), 1841: 220 (*Rhynchocephalus*). Type-locality: Australia. Distr.: Australia. Refs.: Hardy, 1924: 452; Mackerras, 1925: 510 (see under *Trichophthalma costalis*); Paramonov, 1953: 256.

andicola Lichtwardt, 1925: 393, fig. 1. Type-locality: Argentina, Salta, 2500 m. Distr.: Argentina (Salta).

**annandalei* Lichtwardt, 1913: 333. Type-locality: India, Western Himalayas (Simla, 7000 ft; Kufti, Simla Hills, 8000 ft). Distr.: India. Ref.: Bequaert, 1935a: 129.



Wing venation. 30, *Neorhynchocephalus sackeni;* 31, *N. volaticus;* 32, *Fallenia fasciata;* 33, *Trichopsidea oestracea;* 34, *T. costata;* 35, *Ceyloniola magnifica;* 36, *Atriadops macula;* 37, *Nycterimyia dohrni;* 38, *Nycterimorpha speiseri.* (Figs. 30-31 from Bequaert, 1957; fig. 32 from Sack, 1933; fig. 33 from Mackerras, 1925; fig. 34 from Greathead, 1960; fig. 35 from Lichtwardt, 1909c; fig. 38 from Hennig, 1954).

**anthracoides* Philippi, 1865: 663. Type-locality: Chile, Santiago, "Andibus humilioribus". Neotype: Chile, Santiago, Peñalolen (Angulo, 1971: 53). Distr.: Chile (Valparaiso to Santiago). Ref.: Angulo, 1971: 53, figs. 27, 29, 34.

albistria Schiner, 1868: 109. Type-locality: Chile.

**articulata* Philippi, 1865: 660. Type-locality: Chile, Colchagua. Neotype: Chile, Santiago, Manquehue (Angulo, 1971: 56). Distr.: Peru (Lima), Chile (Tarapacá to Malleco), Argentina (Catamarca, Mendoza). Ref.: Angulo, 1971: 56, figs. 35, 36, 41.

cinerea Philippi, 1865: 660. Type-locality: Chile, Coquimbo (Illapel), Colchagua.

clinerea Hunter, 1901: 150 (error).

austeni Lichtwardt, 1909c: 643. Type-locality: India, Assam, Khasi Hills. Distr.: India. Ref.: Bequaert, 1935a: 125.

**basalis* Lichtwardt, 1910b: 595, fig. 3. Type-locality: India (Ecuador was given initially as type-locality, but see Lichtwardt, 1913: 334 and Bequaert, 1935a: 133, for correction). Distr.: India, Burma, Thailand. Refs.: Bequaert, 1935a: 133; Lichtwardt, 1913: 334.

**bellula* Philippi, 1865: 662. Type-locality: Chile, Coquimbo, Illapel. Neotype: Chile, Valparaiso, Las Palmas, Quillota (Angulo, 1971: 60). Distr.: Chile (Coquimbo to Valdivia). Ref.: Angulo, 1971: 60, figs. 37, 39, 42.

**bradleyi* Bequaert, 1920: 301, unnumbered text-fig. Type-locality, U.S.A., Texas, Anhalt, Comal Co. Distr.: U. S. A. (Texas), Mexico (Nuevo Leon). Ref.: Bequaert, 1957: 134, fig. 1.

novileonis Bequaert, 1950a: 8. Type-locality: Mexico, Nuevo León, Monterrey.

**brandti* Bequaert, 1938: 292, fig. 1a-e. Type-locality: Iran, Fort Sine-Sefid, about 2200 m, road from Chiraz to Kazeroun. Distr.: Turkmenistan, Iran. Ref.: Paramonov, 1956: 236.

**brevirostrata* Bigot, 1857: 280, pl. 6, figs. 1, 1a-b. Type-locality: Chile. Distr.: Chile (Valparaiso to Bio-Bio). Ref.: Angulo, 1971: 63, figs. 38, 40, 43.

bigoti Schiner, 1868: 108 (unjustified change of name for *brevirostrata* Bigot).

brevirostris Hunter, 1901: 149, nec Macquart, 1845 (error).

**brevirostris* Macquart, 1846a: 229 (1846b: 101), pl. 20, fig. 1, 1a. Type-locality: Mexico, Yucatan, Merida. Distr.: Mexico (Guerrero to Yucatan) to Nicaragua. Refs.: Cockerell, 1908a: 252, pl. 16, fig. 2; Bequaert, 1930: 295.

brunnea Lichtwardt, 1909c: 645. Type-locality: Ceylon (Rambodde; Tricomali). Distr.: Ceylon. Ref.: Bequaert, 1935a: 128.

carbonifera Angulo, 1971: 66. Type-locality: Chile, Tarapacá, Cariquima. Distr.: Chile (Tarapacá).

cingulata Lichtwardt, 1909c: 644. Type-locality: India. Distr.: India. Ref : Bequaert, 1935a: 125.

**cockerelli* Bequaert, 1935a: 125, figs. 1a-c. Type-locality: Thailand, Doi-Setep. Distr.: Thailand.

coffeata Lichtwardt, 1909c: 644. Type-locality: Ceylon, Rambodde. Distr.: Ceylon. Ref.: Bequaert, 1935a: 128.

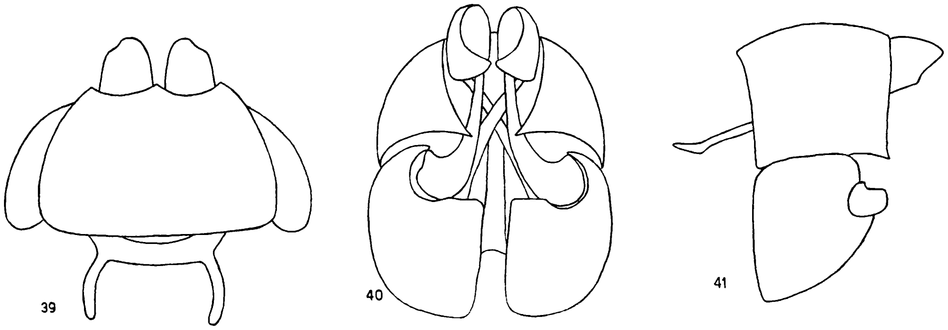
cuprofulgida Angulo, 1971: 67, figs. 44, 45, 50. Type-locality: Chile, Coquimbo, Socos. Distr.: Chile (Atacama to Coquimbo).

ecuadorensis Bequaert, 1932a: 16. Type-locality: Ecuador, "Cordilleren von Ecuador". Distr.: Ecuador.

**exotica* Wiedemann, 1824: 20. Type-locality: Uruguay, Montevideo, Montevideo. Distr.: Uruguay, Argentina (Chaco to Santa Cruz). Refs.: Bruch, 1917: 427; Stuardo Ortiz, 1943: 385, pl. 16, figs. a-d.

**flavipes* Williston, 1886: 292. Type-locality: U.S.A. Distr.: U. S. A. (Arizona, ? Florida). Ref.: Bequaert, 1934: 176.

**laotica* Bequaert, 1935a: 134, fig. 3. Type-locality: Laos, Pang Bo. Distr.: Laos.



Male genitalia of *Hirmoneura luctuosa*. 39, dorsal view; 40, ventral view; 41, lateral view.

**luctuosa* Philippi, 1865: 661. Type-locality: Chile, Santiago, near Santiago. Neotype: Chile, Santiago, El Canelo (Angulo, 1971: 69). Distr.: Peru, Chile (Tarapacá to Maule). Refs.: Bequaert, 1932a: 16 (*H. punctipennis* var. *luctuosa*) ; Angulo, 1971: 69, figs. 46, 48, 51.

luctuos Hunter, 1901: 150 (error).

**lurida* Rondani, 1868: 33, pl. 4, fig. 10. Type-locality: Argentina, Mendoza, San Carlos. Distr.: Chile (Atacama to Santiago), Argentina (Chaco to Mendoza). Ref.: Angulo, 1971: 72, figs. 47, 49, 52.

**maculipennis* Macquart, 1850a: 403 (1850b: 99) pl. 9, fig. 10. Type-locality: Chile. Distr.: Chile (Coquimbo to Malleco). Ref.: Angulo, 1971: 75, figs. 53, 54, 59.

fusca Rondani, 1863: 51. Type-locality: Chile.

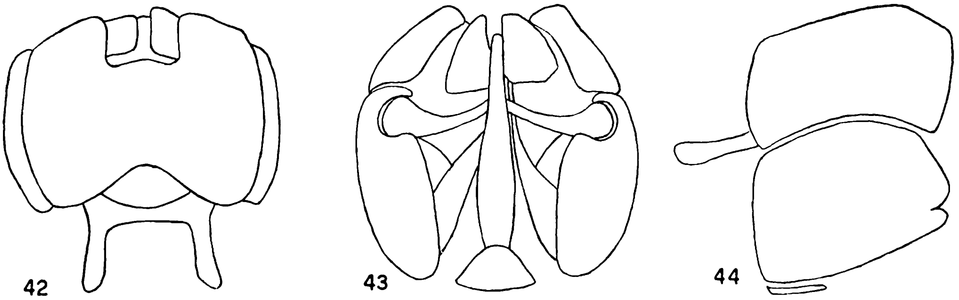
modesta Philippi, 1865: 662. Type-locality: Chile, Santiago, "radicem Adium".

**obscura* Meigen, 1820: 132, pl. 16, figs. 7-11. Type-locality: Yugoslavia, Dalmatia. Distr.: Austria, Yugoslavia, Romania, Greece, Turkey, Syria. Refs.: Handlirsch, 1882: 224, 1883: 11, figs. 1-15; Sack, 1933: 39, text-figs. 6, 28, pl. 1, fig. 10; Paramonov, 1956: 240; Weinberg, 1966: 9, pl. 3, figs. c-d.

**ochracea* Lichtwardt, 1909c: 643. Type-locality: Burma, Tan Plateau, 4000 ft. Distr.: Burma, Laos. Ref.: Bequaert, 1935a: 131.

oldenbergi Lichtwardt, 1925: 392. Type-locality: Russia, Khabarovsk, Vladivostok. Distr.: Russia (Khabarovsk) (Paramonov, 1956: 242, gives also "Far East, Stiller Sea, Posjet Bay"). Ref.: Paramonov, 1956: 241.

opaca Lichtwardt, 1909c: 643. Type-locality: India, Kangra Valley, northwestern Himalayas, 4500 ft. Distr.: India, Nepal. Refs.: Brunetti, 1920: 150, text-fig. 8, pl. 2. fig. 22; Bequaert, 1935a: 127.



Male genitalia of *Hirmoneura obscura*. 42, dorsal view; 43, ventral view; 44, lateral view.

montana Maxwell-Lefroy & Howlett, 1909, Indian Insect Life, p. 597 (apud Bequaert, 1935a: 127), nomem nudum.

**orellanae* Stuardo Ortiz, 1936: 170, pl. 16, fig. 4. Type-locality: Chile, Coquimbo, Cuncumán. Distr.: Chile (Atacama to Santiago). Ref.: Angulo, 1971: 78, figs. 55, 58, 61.

orientalis Lichtwardt, 1909c: 645. Type-locality: Formosa, Kosempo. Distr.: Formosa. Ref.: Bequaert, 1935a: 130.

**paraluctuosa* Angulo, 1971: 80, figs. 56, 57, 60. Type-locality: Chile, Linares, Estero de Leiva, Cord. Parral. Dist.: Chile (Coquimbo to Aysen).

philippina Banks, 1922: 518, pl. 1, figs. 1-9. Type-locality: Philippines, Mindanao, Lanao, Kolambugan, 8° 10' N. 123° 55' E. Distr.: Philippines. Ref.: Bequaert, 1935a: 130.

pipistrella Angulo, 1971: 83, figs. 63, 67. Type-locality: Chile, Curicó, La Jaula, Los Queñes. Distr.: Chile (Valparaiso to Curicó).

**psilotes* Osten Sacken, 1886: 74. Type-locality: Mexico. Distr.: Mexico, Guatemala. Ref.: Bequaert, 1934: 174.

**punctipennis* Philippi, 1865: 660. Type-locality: Chile (Santiago and Colchagua). Neotype: Chile, Santiago, La Obra (Angulo, 1971: 84). Distr.: Peru, Chile (Tarapacá to Talca). Ref.: Angulo, 1971: 84, figs. 62, 65, 68.

**ruizi* Stuardo Ortiz, 1936: 172, pl. 16, fig. 2. Type-locality: Chile, Talca, Las Mercedes. Distr.: Chile (Coquimbo to Malleco). Ref.: Angulo, 1971: 87, figs. 64, 66, 69.

**silvae* Stuardo Ortiz, 1936: 171, pl. 16, fig. 3. Type-locality: Chile, Ñuble, Termas de Chillán, Gruta de los Pangues, 1700 m. Distr.: Chile (Linares to Ñuble). Ref.: Angulo, 1971: 90, figs. 70, 71, 76.

**strobelii* Rondani, 1868: 34, pl. 4, fig. 11. Type-locality: Argentina (Santa Fé and Córdoba). Neotype: Argentina, Santa Fé, Rosario (Angulo, 1971: 92). Distr.: Chile (Santiago to Cautin), Argentina (Córdoba to Santa Fé). Ref.: Angulo, 1971: 92, figs. 72, 74, 77.

simplex Bigot, 1881, 20. Type-locality: Chile.

strobelli Kertész, 1909: 27 (error).

**texana* Cockerell, 1908a: 253. Type-locality: U. S. A., Texas, New Braunfels. Distr.: U. S. A. (Arizona, Texas) to Panama. Ref.: Bequaert, 1934: 178.

arizonensis Bequaert, 1934: 180. Type-locality: U. S. A., Arizona, San Diego Canyon, west side of Baboquivari Mts., 25 mi SE of Sells, Pima Co.

tienmushanensis Ouchi, 1939: 239, fig. 1. Type-locality: China, Chekiang, Tienmushan. Distr.: China (Chekiang).

turkestanica Paramonov, 1956: 238. Type-locality: Tadzhikistan (Varzob; Kondara), Kirghizistan (Bulaki, 26 km N of the city of Turkestan). Distr.: Tadzhikistan, Kirguizistan.

vicarians Schiner, 1868: 109. Type-locality: South America (Bequaert, 1932a: 19, remembers the possibility of the type-locality being on the coast of Colombia, maybe Cartagena. Distr.: Venezuela, Brazil (Rio Grande do Sul). Ref.: Bequaert, 1932a: 19.

**villosula* Loew, 1873: 103. Type-locality: Uzbekistan, Samarkand. Distr.: Uzbekistan. Refs : Paramonov, 1956: 239; Sack, 1933: 40.

**vitalisi* Bequaert, 1935a: 132, fig. 2. Type-locality: South Vietnam, Giaray. Distr.: Thailand, South Vietnam.

vsevolodi Paramonov, 1956: 239. Type-locality: Tadzhikistan (surroundings of Tavil-Dara; Kuak). Distr.: Tadzhikistan.

†*willistoni* (Cockerell), 1910: 283, fig. 3 (†*Hirmoneurites*). Type-locality: U. S. A., Colorado, Florissant (Oligocene).

6. Subfamily Nemestrininae Macquart

Definition: head from considerably flattened to hemispherical; face convex or prominent; proboscis at least as long as the head; antennae three-segmented, with segmented style. Thorax normal in relation to the insect's size; scutellum normal. 1st segment of hind tarsus longer or as long as the last four together. Alula present, wide or narrow. Wings hyaline, sometimes with darker areas or infuscated, but transparent. M1 and M2 running towards apical margin. Venation complete (reduced in *Stenopteromyia*). Ovipositor type 1. Hypandrium well developed, free, elongate, longer than gonopods, flattened in side view (in *Moegistorhynchus* it is sub-quadrate, approximately half the length of gonopods, high in lateral view).

Genus **Trichophthalma** Westwood

(Figs. 2-3, 20, 45-47, map 2)

Trichophthalma Westwood, 1835: 448 (as subgenus of *Nemestrina*). Type-species, *Nemestrina bivittata* Westwood (Lichtwardt, 1910a: 371).

Trichopthalma, error.

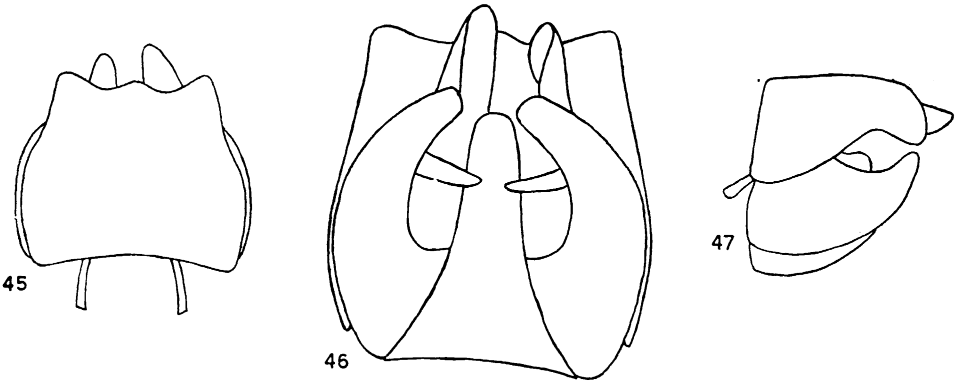
Trichopthalmus, error.

Refs.: Angulo, 1971: 47 (*Eurygastromyia*), 97 (*Trichophthalma*); Bequaert, 1932a: 29; Edwards, 1930: 180; Hardy, 1924: 449; Mackerras, 1925: 492; Paramonov, 1953: 257; Stuardo Ortiz, 1935b: 216.

Definition: head almost hemispherical, slightly flattened; eyes large, densely pilose, very near to each other in both sexes, holoptic or nearly so in the male. Proboscis well developed, at least as long as head; antennae with first two segments cylindrical, subequal, or first slightly longer, the third large, conical, followed by a long, segmented style. Alula developed; wing long and narrow. R3 absent; R4 and R5 free (3rd submarginal cell open); M1 and M2 free (2nd posterior cell open); R4+5 fused for a very short distance with M1+2; m-cu present; M3+M4, on tip of diagonal vein, in normal position, in line with remainder of diagonal or slightly displaced basewards. Male genitalia: figs 45-47. Ovipositor type 1.

Distribution: Australia (all states, including Tasmania), Chile (Coquimbo to Magallanes), Argentina (Rio Negro to Santa Cruz), Uruguay.

Comments: Lichtwardt (1910b) erected the genus *Eurygastromyia* for the American species, but Edwards (1930) and subsequent authors have correctly kept those species in *Trichophthalma*. Mackerras (1925) divided the Australian species into three groups, which, together with the American group, form the four categories considered subgenera by Bequaert (1932a). The latter author, however, kept two American species, *T. amoena* and *T. niveibarbis,* in the Australian subgenus *Trichophthalma*. This seems inadequate to me and I am keeping both species in *Eurygastromyia*. Recently, Angulo (1971) reestablished the genus *Eurygastromyia* for *T. philippi* and *T. sexmaculata,* based on the spermatheca and the aedeagus. I think this procedure inadequate



Male genitalia of *Trichophthalma costalis.* 45, dorsal view; 46, ventral view; 47, lateral view.

and unnecessary and hereby reject it. The Australian fauna was well studied by Mackerras (1925) and Paramonov (1953), but the South American one still needs a convenient treatment. The four subgenera may be identified by the following key:

1. 3rd antennal segment long, subcylindrical, with a sulcus at the base, sometimes not very clear, but distinguishable 2
   3rd antennal segment short, conical, pyriform or bulbous, without basal sulcus 3

2. Tip of diagonal vein (M3+M4) displaced basad, not in line with remainder of diagonal; Australia .... *Trichophthalma*
   Tip of diagonal vein (M3+M4) in line with remainder of diagonal; Chile, Argentina, Uruguay .... *Eurygastromyia*

3. 2nd palpal segment very large, swollen, club-shaped; Australia .... *Austrogastromyia*
   2nd palpal segment slender, small not thicker than lst; Australia. .... *Lichtwardtiomyia*

Catalog:

Subgenus **Austrogastromyia** Bequaert

Austrogastromyia Bequaert, 1932a: 30. Type-species, *Hirmoneura novaehollandiae* Macquart (orig. des.)

**bancrofti* Mackerras, 1925: 533, figs. 3a-b, 7a. Type-locality: Australia, Queensland, Eidsvold. Distr : Australia (Queesland, New South Wales). Ref.: Paramonov, 1953: 273.

doddi Paramonov, 1953: 274. Type-locality: Australia, Queensland, Meringa. Distr.: Australia (Queensland).

froggatti Paramonov, 1953: 274. Type-locality: Australia, Queensland, Cairns. Distr.: Australia (Queensland).

**nigrovittata* Mackerras, 1925: 531, figs. 4e-f, 5d, Type-locality: Australia, New South Wales, Barrington Tops. Distr.: Australia (Queensland, New South Wales).

**novaehollandiae* (Macquart), 1840: 18 (1841: 297), pl. 2, fig. 7a-c. (*Hirmoneura*), nec 1846a: 225, 1846b: 101, nec 1850a: 403, 1850b: 99. Type-locality: Australia. Distr.: Australia (South Australia, Queensland, New South Wales, Victoria). Refs.: Mackerras, 1925: 531, figs. 2b, d-e; Paramonov, 1953: 274.

funesta Walker, 1849: 231. Type-locality: Australia.

gigas Newman, 1841: 220. Type-locality: Australia, New South Wales, near Sydney.

**scapularis* Bigot, 1881: 18. Type-locality: Australia. Distr.: Australia (Queensland, New South Wales, A.C.T., Victoria). Refs.: Mackerras, 1925: 534, fig. 6k (*nigripes*); Paramonov, 1953: 272.

nigripes (Macquart), 1840a: 20, 1841: 298 (*Hirmoneura*). Type-locality: unknown. (According to Paramonov, *nigripes* is certinly an artifact).

pallipes Paramonov, 1953: 273. Type-locality: Australia, Queensland (Stradbroke I.; Mt. Tambourine; McPherson R.; Biloela), New South Wales (Lake Macquarie; Tooloom; Kendall; Blue Mts.).

Subgenus **Eurygastromyia** Lichtwardt

Eurygastromyia Lichtwardt, 1910b: 601 (as genus). Type-species, *Trichophthalma philipii* Rondani (Edwards, 1930: 180).

Heurygastromyia, error.

Refs.: Angulo, 1971: 47 (*Eurygastromyia*), 97 (*Trichophthalma*); Bequaert, 1932a: 29; Edwards, 1930: 180.

**amoena* Bigot, 1881: 20 (originally misspelled *amaena*). Type-locality: Chile. Neotype: Chile, Llanquihue, Casa Pangue (Angulo, 1971: 100). Distr.: Chile (Santiago to Magallanes), Argentina (Rio Negro, Chubut). Ref.: Angulo, 1971: 100, figs. 79, 80, 87.

niveicincta Lichtwardt, 1910b: 610 (*Eurygastromyia*). Type-locality: Argentina, Chubut, Valle del Lago Blanco.

**andina* (Philippi), 1862: 388 (*Hermoneura*). Type-locality: Chile, Ñuble, Termas de Chillán. Neotype: Chile, Cautin, Cherquenco (Angulo, 1971: 102). Distr.: Chile (Valparaiso to Llanquihue). Ref.: Angulo, 1971: 102, figs. 81, 83, 86.

**barbarossa* (Bigot), 1857: 281 (*Hirmoneura*). Type-locality: Chile Neotype: Chile, Osorno, Puerto Octay (Angulo, 1971: 104). Distr.: Chile (Coquimbo to Chiloe), Uruguay. Ref.: Angulo, 1971: 104, figs. 82, 84, 85.

zonalis Rondani, 1863: 52. Type-locality: Chile.

nemestrinoides Jaennicke, 1867: 335, pl. 43, fig. 6 (*Hirmoneura*). Type-locality: Chile.

vicarians Schiner, 1868: 111. Type-locality: Chile.

vicarius Hunter, 1901: 150 (error).

**commutata* (Philippi), 1865: 658 (*Hermoneura*). Type-locality: Chile, Valdivia. Neotype: Chile, Talca, Fdo. El Radal, Cord. Talca. (Angulo, 1971: 109). Distr.: Chile (Coquimbo to Aysen). Ref.: Angulo, 1971: 109, figs. 88, 89, 94.

chilensis Blanchard, 1852: 383, pl. 3, figs. 11, 11b-c (*Hirmoneura*), nec Macquart, 1840.

communata Angulo, 1971: 109 (error).

**eximia* (Philippi), 1865: 656 (*Hermoneura*). Type-locality: Chile, Valdivia, Ranco Lake. Neotype: Chile, Valdivia, Rofuco (Angulo, 1971: 111). Distr.: Chile (Curicó to Osorno). Ref.: Angulo, 1971: 111, figs. 90, 92, 95.

**herbsti* (Lichtwardt), 1910b: 605 (*Eurygastromyia*). Type-locality: Chile, Concepcion, Malleco (Termas de Tolluaca). Neotype: Chile, Concepcion, Penco (Angulo, 1971: 114). Distr.: Chile (Aconcagua to Cautin). Ref.: Angulo, 1971: 114, figs. 91, 93, 96.

inexpectata Angulo, 1971: 117, fig. 97. Type-locality: Chile, Linares, Estero de Leiva, Cordillera de Parral. Distr.: Chile (Linares to Ñuble).

**jaffueli* Stuardo Ortiz, 1936: 172, pl. 16, fig. 1. Type-locality: Chile, Ñuble, Termas de Chillán. Distr.: Chile (Santiago to Aysen). Ref.: Angulo, 1971: 119, figs. 98, 99, 102.

**landbecki* (Philippi), 1865: 658 (*Hermoneura*). Type-locality: Chile, Colchagua, near Llico. Neotype: Chile, Colchagua, Nancagua (Angulo, 1971: 122). Distr.: Chile (Valparaiso to Osorno). Ref.: Angulo, 1971: 122, figs. 100, 101, 103.

speciosa Pirion, 1930: 171 (nomen nudum).

morenii Stuardo Ortiz, 1939: 81. Type-locality: Argentina ("Patagonia", Santa Cruz; San Jorge, "Patagonia"). (See Stuardo's comments). Distr.: Argentina (Chubut, Santa Cruz).

**murina* (Lichtwardt), 1910b: 607 (*Eurygastromyia*). Type-locality: Argentina, Chubut, Valle del Lago Blanco. Distr.: Chile (Coquimbo to Aysen), Argentina (Chubut, Santa Cruz). Ref.: Angulo, 1971: 126, figs. 104, 105, 110).

**niveibarbis* (Bigot), 1857: 282 (*Hirmoneura*). Type-locality: Chile. Neotype: Chile, Santiago, Peñalolen (Angulo, 1971: 128). Distr.: Chile (Coquimbo to Llanquihue). Ref.: Angulo, 1971: 128, figs. 106, 108, 111.

pictipennis Philippi, 1865: 657 (*Hermoneura*). Type-locality: Chile, Valdivia.

amaena Röder, 1882: 511, nec Bigot, 1881.

glauciventris Edwards, 1930: 183, fig. 11. Type-locality: Chile, Llanquihue, Casa Pangue.

**nubipennis* Rondani, 1863: 52. Type-locality: Chile. Neotype: Chile, Malleco, Pto. Balloco (Angulo, 1971: 131). Distr.: Chile (Coquimbo to Chiloe), Argentina (Neuquen). Ref.: Angulo, 1971: 131, figs. 107, 109, 112.

picta Philippi, 1865: 657 (*Hermoneura*). Type-locality: Chile, Valdivia.

**philippii* Rondani, 1863: 53. Type-locality: Chile. Neotype: Chile, Llanquihue, Casa Pangue (Angulo, 1971: 48). Distr.: Chile (Arauco to Llanquihue), Argentina (Rio Negro). Ref.: Angulo, 1971: 48, figs. 26, 31, 33 (*Eurygastromyia*).

balteata Philippi, 1865: 656, pl. 25, figs. 23, 23a (*Hermoneura*). Type-locality: Chile, Valdivia.

baltea Hunter, 1901: 150 (error).

**porteri* Stuardo Ortiz, 1935b: 245, fig. 55. Type-locality: Chile, Santiago, Peñalolen, Casa de Piedra, 1600 m. Distr.: Chile (Santiago to Ñuble). Ref.: Angulo, 1971: 136, figs. 113, 114, 117.

**scalaris* Bigot, 1881: 19. Type-locality: Chile. Neotype: Chile, Ñuble, Termas de Chillán (Angulo, 1971: 139). Distr.: Chile (Linares to Malleco). Ref.: Angulo, 1971: 139, figs. 115, 116, 118.

**sexmaculata* Edwards, 1930: 184. Type-locality: Chile, Llanquihue, Casa Pangue. Distr.: Chile (Llanquihue), Argentina (Rio Negro). Ref.: Angulo, 1971: 50, figs. 28, 30, 32 (*Eurygastromyia*).

**subaurata* (Westwood), 1835: 448 (*Nemestrina*). Type-locality: Chile, Valparaiso. Distr.: Chile (Coquimbo to Chiloe). Ref.: Angulo, 1971: 141, figs. 119, 120, 123.

chilensis Macquart, 1840: 19 (1841: 297), pl. 2, fig. 8. (*Hirmoneura*).

flaviventris Blanchard, 1852: 384, pl. 3, figs. 12, 12a (*Hirmoneura*).

bombyliformis Schiner, 1868: 111. Type-locality: Chile.

tigrina Angulo, 1971: 144. Type-locality: Chile, Magallanes, Bahia Municiones. Distr.: Chile (Magallanes), Argentina (Chubut).

**ursula* (Philippi), 1865: 659 (*Hermoneura*). Type-locality: Chile, Valdivia. Distr.: Chile (Valparaiso to Valdivia). Ref.: Angulo, 1971: 145, figs. 121, 122, 124.

Subgenus **Lichtwardtiomyia** Bequaert

Lichtwardtiomyia Bequaert, 1932a: 29. Type-species, *Nemestrina costalis* Westwood (orig. des.).

bivitta Walker, 1857: 135. Type-locality: Australia. Distr.: Australia (South Australia, Queensland, New South Wales, Victoria). Refs.: Mackerras, 1925: 523; Paramonov, 1953: 285 (ssp. *nigricosta*).

nigricosta Mackerras, 1925: 524. Type-locality: Australia, New South Wales, Barrington Tops.

calabyi Paramonov, 1953: 276, fig. 5b: Type-locality: Australia, South Australia, Immarna. Distr.: Australia (South Australia).

**confusa* Mackerras, 1925: 521, fig. 6d. Type-locality: Australia, New South Wales, Berowra. Distr.: Australia (Queensland, New South Wales, Victoria). Ref.: Paramonov, 1953: 283.

**costalis* (Westwood), 1835: 448 (*Nemestrina*). Type-locality:Australia. Distr.: Australia (West Australia, South Australia, Queensland, New South Wales, Victoria). Refs.: Mackerras, 1925: 510, figs. 2e, 4a-c; Paramonov, 1953: 277 (*costalis*), 278 (*apicalis*).

albibasis Walker, 1857: 134. Type-locality: Australia.

heydenii Jaennicke, 1867: 336, pl. 43, fig. 7 (*Hirmoneura*). Type-locality: Australia.

fuscipennis Thomson, 1869: 447. Type-locality: Australia, New South Wales, Sydney.

ochropa Thomson, 1869: 447. Type-locality: Australia, New South Wales, Sydney.

apicalis Mackerras, 1925: 512. Type-locality: Australia, West Australia, Perth.

soror Paramonov, 1953: 277. Type-locality: Australia, West Australia, City Beach.

**degener* Walker, 1949: 233. Type-locality: Australia, West Australia. Distr.: Australia (West Australia). Refs.: Mackerras, 1925: 539, 6h (*leucophaea*); Paramonov, 1953: 281.

leucophaea Mackerras, 1925: 529, nec Walker, 1849.

longirostris Mackerras, 1925: 530. Type-locality: Australia, West Australia, Perth.

dubiosa Mackerras, 1925: 527. Type-locality: Australia, New South Wales, Meldrum. Distr.: Australia (New South Wales, Victoria). Ref.: Paramonov, 1953, 284.

fortei Paramonov, 1953: 287. Type-locality: Australia, West Australia, Capel. Distr.: Australia (West Australia).

fullerae Paramonov, 1953: 274. Type-locality: Australia, Queensland (Stanthorpe), New South Wales (Crookhaven), A.C.T. (near Canberra). Distr.: Australia (Queensland, New South Wales). Ref.: Mackerras, 1925: 515 (*obscura*), partim.

obscura Mackerras, 1925: 515, partim, nec Westwood, 1835.

fulva Walker, 1849: 235. Type-locality: Australia, West Australia. Distr.: Australia (West Australia, Queensland, New South Wales, Victoria). Refs.: Mackerras, 1925: 520; Paramonov, 1953: 280.

**fusca* Mackerras, 1925: 516, fig. 6j. Type-locality: Australia, Queensland, Gayndah. Distr.: Australia (Queensland, New South Wales). Ref.: Paramonov, 1953: 275, fig. 5a.

glauerti Paramonov, 1953: 286. Type-locality: Australia, West Australia, Yallingup. Distr.: Australia (West Australia).

griseola Paramonov, 1953: 283. Type-locality: Australia, West Australia, Katanning. Distr.: Australia (West Australia).

griseolineata Mackerras, 1925: 528. Type-locality: Australia, South Australia. Distr.: Australia (South Australia). Ref.: Paramonov, 1953: 286.

**harrisoni* Mackerras, 1925: 525. fig. 6f. Type-locality: Australia, New South Wales, Barrington Tops. Distr.: Australia (Queensland, New South Wales). Ref.: Paramonov, 1953: 286.

intermedia Mackerras, 1925: 517. Type-locality: Australia, Queensland, Russel I. Distr.: Australia (Queensland: Russell I., Stradbroke I.) Ref.: Paramonov, 1953: 277.

**leucophaea* Walker, 1849: 233. Type-locality: Australia, West Australia. Refs.: Mackerras, 1925: 529, fig. 6h (partim); Paramonov, 1953: 281.

heydenii Hardy, 1924: 453, nec Jaennicke, 1867.

lutea Paramonov, 1953: 280. Type-locality: Australia, New South Wales, Crookhaven. Distr.: Australia (New South Wales, Victoria).

mackerrasi Paramonov, 1953: 275. Type-locality: Australia, Queensland, Stradbroke I. Distr.: Australia (Queensland: Stradbroke I.).

**nicholsoni* Mackerras, 1925: 525, fig. 6g. Type-locality: Australia, New South Wales, Kosciusko. Distr.: Australia (New South Wales). Ref.: Paramonov, 1953: 284.

obscura (Westwood), 1835:448 (*Nemestrina*). Type-locality: "Africa" (?). Distr.: Australia (Queensland). Ref.: Bequaert, 1932a: 31; Paramonov, 1953: 274 (under *fullerae*).

orientalis Mackerras, 1925: 519, fig. 6b. Type-locality: Australia, New South Wales, Barrington Tops. Distr.: Australia (West Australia, Queensland, New South Wales, Victoria). Ref.: Paramonov, 1953: 280.

**punctata* (Macquart), 1846a: 229, 1846b: 101 (*Hirmoneura*). Type-locality: Australia, Tasmania. Distr.: Australia (South Australia, Queensland, Victoria, Tasmania). Refs.: Mackerras, 1925: 517, fig. 6a; Paramonov, 1953: 279.

quadricolor Walker, 1849: 234. Type-locality: Australia, Tasmania.

nigriventris Macquart, 1850a: 402, 1850b 98, pl. 9, fig. 9 *(Hirmoneura)*. Type-locality: Australia, Tasmania.

novaehollandiae Macquart, 1850a: 403, 1850b: 99, nec 1846a: 229, 1946b: 101.

minima Mackerras, 1925: 519. Type-locality: Australia, New South Wales, Barrington Tops.

regina Paramonov, 1953: 282. Type-locality: Australia, West Australia, Booanya. Distr.: Australia (West Australia).

ruficosta Mackerras, 1925: 522. Type-locality: Australia, West Australia, King George's Sound. Distr.: Australia (West Australia). Ref.: Paramonov, 1953: 285.

**rufonigra* Mackerras, 1925: 513, fig. 6a-c. Type-locality: Australia, New South Wales, Barrington Tops. Distr.: Australia (New South Wales). Ref.: Paramonov, 1953. 278.

subcostalis Mackerras, 1925: 514. Type-locality: Australia, South Australia, Tulka. Distr.: Australia (South Australia). Ref.: Paramonov, 1953: 278.

transversa Paramonov, 1953: 278. Type-locality: Australia, Queensland, Eidsvold. Distr.: Australia (Queensland).

trilinealis Mackerras, 1925: 526. Type-locality, Australia, New South Wales, Kosciusko. Distr.: Australia (New South Wales). Ref.: Paramonov, 1953: 285.

Subgenus **Trichophthalma** Westwood

**albimacula* Walker, 1849: 234. Type-locality: Australia. Distr.: Australia (West Australia, Queensland, New South Wales). Ref.: Mackerras, 1925: 539, fig. 9c, pl. 50, fig. 3; Paramonov, 1953: 270.

  occidentalis Paramonov, 1953: 270. Type-locality: Australia, West Australia, Yelbeni.

alulata Paramonov, 1953: 269. Type-locality: Australia, West Australia, Mingenew. Distr.: Australia (West Australia).

**bivittata* (Westwood), 1835: 448 *(Nemestrina)*. Type-locality: Australia (according to Bequaert, 1932b: 166, the type came from New South Wales). Distr.: Australia (West Australia, Queensland, New South Wales, Victoria). Refs.: Bequaert, 1932b: 166: Mackerras, 1925: 537, fig. 9b *(eques)*, 538 *(bivittata)*; Paramonov, 1953: 266.

  eques Schiner, 1868: 110. Type-locality: Australia, New South Wales, Sydney.

  wheeleri Bequaert, 1932b: 164. Type-locality: Australia, West Australia, Mullewa.

  coerulea Paramonov, 1953: 267. Type-locality: Australia, New South Wales (National Park; Gundamain; Port Hacking, near Sydney).

grisea Mackerras, 1925: 542. Type-locality: Australia, West Australia, Armadale. Distr.: Australia (West Australia). Ref.: Paramonov, 1953: 271.

**laetilinea* Walker, 1857: 134. Type-locality: Australia. Distr.: Australia (Queensland, New South Wales, Victoria). Refs.: Mackerras, 1925: 543, fig. 9e; Paramonov, 1953: 270.

**primitiva* Walker, 1857: 134. Type-locality: Australia. Distr.: Australia (Queensland, New South Wales). Ref.: Makerras, 1925: 541, fig. 9d.

  tabanina Thomson, 1869: 476. Type-locality: Australia, New South Wales, Sydney.

ricardoae Lichtwardt, 1910a: 385. Type-locality: Australia, South Australia, Adelaide. Distr.: Australia (South Australia, Queensland, New South Wales). Refs.: Mackerras, 1925: 544, fig. 9f; Paramonov, 1953: 270.

richardoae Hardy, 1924: 455 (error).

**rosea* (Macquart), 1846a: 228, 1846b: 100 *(Hirmoneura)*. Type-locality: Australia, New South Wales, Sydney. Distr.: Australia (Queensland, New South Wales). Refs.: Mackerras, 1925: 536, figs. 1, 2a, 2f, 3c, 4g-i, 7b, 8, 9a, pl. 50, figs. 1-2; Paramonov, 1953: 266.

aurora Walker, 1849: 342. Type-locality: Australia, New South Wales.

monotaenia Schiner, 1868: 110. Type-locality: Australia, New South Wales.

thomsoni Paramonov, 1953: 271 (new name for *bivittata* Thomson, nec Westwood). Type-locality: Australia, New South Wales, Sydney. Distr.: Australia. (New South Wales).

bivittata Thomson, 1869: 476, nec Westwood, 1835. Type-locality: Australia, New South Wales, Sydney.

variolosa Lichtwardt, 1910a: 386. Type-locality: Australia, South Australia, Adelaide. Distr.: Australia (South Australia). Ref.: Mackerras, 1925: 540.

variosa Hardy, 1924: 451 (error).

waterhousei Paramonov, 1953: 270. Type-locality: Australia, New South Wales (Blackheath, Blue Mts.; Medlow; Balli). Distr.: Australia (New South Wales).

Genus **Prosoeca** Schiner

(Figs. 22, 48-50, map 2)

Prosoeca Schiner, 1867: 306. Type-species, *Nemestrina westermanni* Wiedemann (orig. des.).

Definition: eyes bare. R3 present. Alula normal, with tendency to reduction in some species. Otherwise, similar to *Nemestrinus*, excepting reticulation of wings. Male genitalia: figs. 48-50. Ovipositor type 1.

Distribution: Malawi, Rhodesia, Lesotho, South Africa.

Comments: see under †*Palembolus* and *Moegistorhynchus*.

Catalog:

**accincta* (Wiedemann), 1830: 631 *(Nemestrina)*. Type-locality: South Africa, Cape. Distr.: South Africa (Transvaal, Natal, Cape). Refs.: Bezzi, 1924: 188; Hull, 1961: 413.

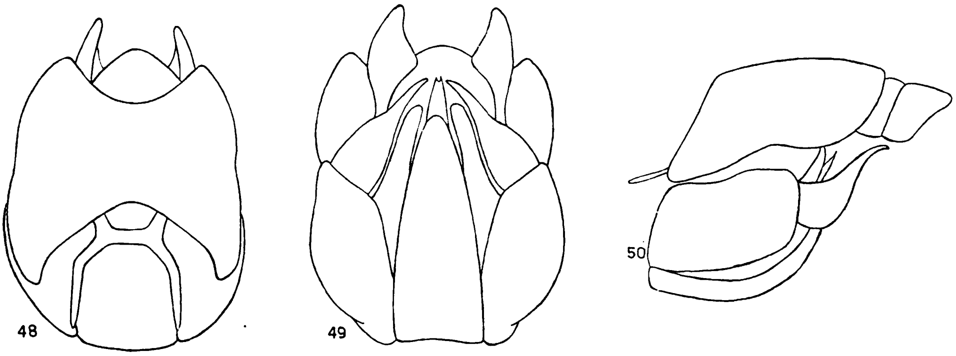
**atra* (Macquart), 1846a: 228, 1846b: 100 *(Hirmoneura)* Type-locality: South Africa, Cape. Distr.: South Africa (Cape, Natal). Ref.: Bezzi, 1924: 185.

**beckeri* Lichtwardt, 1920: 98. Type-locality: South Africa, Cape, Saldanha Bay. Distr.: South Africa (Transvaal, Cape). Refs.: Bequaert, 1925a: 7; Bezzi, 1924: 182.

**caffraria* Lichtwardt, 1910b: 620. Type-locality: South Africa, Transvaal (Zontpansberg; Uitphome). Distr.: South Africa (Transvaal, Natal). Refs.: Bezzi, 1924: 185; Hull, 1961: 413.

**circumdata* Lichtwardt, 1910b: 620. Type-locality: South Africa, Natal (Howick; Durban; Port Shepstone). Distr.: South Africa (Transvaal, Natal). Refs.: Bezzi, 1924: 186.

connexa Bezzi, 1924: 188. Type-locality: South Africa, Natal, Durban. Distr.: South Africa (Transvaal, Natal).



Male genitalia of *Prosoeca westermanni*. 48, dorsal view; 49, ventral view; 50, lateral view.

flavipennis Lichtwardt, 1910b: 618. Type-locality: unknown. Refs.: Bezzi, 1924: 182.

**fusca* (Loew), 1860: 252 *(Nemestrina)*. Type-locality: South Africa, Cape. Distr.: South Africa (Natal, Cape).

**ganglbaueri* Lichtwardt, 1910b: 616. Type-locality: South Africa, Cape, Algoa Bay. Distr.: South Africa (Transvaal, Cape), Lesotho. Ref.: Bezzi, 1924: 178.

handlirschi Lichtwardt, 1910b: 621. Type-locality: South Africa, Cape, Robinson's Pass. Distr.: South Africa (Cape). Ref.: Bezzi, 1924: 187.

**ignita* Bezzi, 1924: 183. Type-locality: South Africa, Transvaal, (Woodbush Ville; New Agatha). Distr.: South Africa (Transvaal).

**lata* Lichtwardt, 1910b: 618. Type-locality: South Africa, Natal, Port Shepstone. Distr.: South Africa (Transvaal, Natal, Cape).

lichtwardti Bezzi, 1924: 185. Type-locality: South Africa, Cape, Paarl. Distr.: South Africa (Cape).

**longipennis* (Loew), 1858: 367 (*Nemestrina*). Type-locality: South Africa, Cape. Distr.: South Africa (Cape).

longirostris (Macquart), 1846a: 227, 1846b: 99 *(Hirmoneura)*. Type-locality: South Africa, Cape, Capetown. Distr.: South Africa (Cape).

**maculata* (Wiedemann), 1828: 581 *(Nemestrina)*. Type-locality: South Africa, Cape. Distr.: South Africa (Cape).

**major* Bezzi, 1924: 181. Type-locality: South Africa, Cape, Gt. Wintershoek, Tulbagh, 5000 ft. Distr.: South Africa (Cape).

**nitidula* Bezzi, 1924: 178. Type-locality: South Africa, Cape, Capetown. Distr.: South Africa (Cape).

oldroydi Hull, 1958: 129. Type-locality: South Africa, Natal, Durban. Distr.: South Africa (Natal).

olivacea Brunetti, 1929: 4. Type-locality: South Africa, Natal, Willowgrange. Distr.: South Africa (Natal).

ornata Lichtwardt, 1910b: 622. Type-locality: South Africa, Cape, Simonstown. Distr.: South Africa (Cape).

**peringueyi* Lichtwardt, 1920: 98. Type-locality: South Africa, Cape, Namaqualand, Klipfontein. Distr.: South Africa (Cape). Ref.: Bezzi, 1924: 175.

pygmea Hull, 1958: 130. Type-locality: South Africa, Cape, Mitchell's Pass, 100 mi from Capetown. Distr.: South Africa (Cape).

quinque Lichtwardt, 1920: 101. Type-locality: South Africa, Cape, Dunbrody. Distr.: South Africa (Cape). Ref.: Bezzi, 1924: 187.

**rhodesiensis* Bequaert, 1925a: 4. Type-locality: Rhodesia, Matopos. Distr.: Malawi, Rhodesia.

robusta Bezzi, 1924: 180. Type-locality: South Africa, Cape, Grahamstown. Distr.: South Africa (Cape).

rubicunda Bezzi, 1924: 177. Type-locality: South Africa, Cape, Caledon District, Oudebush. Distr.: South Africa (Cape).

**sublineata* Bequaert, 1925b: 185, fig. 1. Type-locality: South Africa, Cape, Caledon District, Palmiet River Mouth. Distr.: South Africa (Cape).

**umbrosa* Lichtwardt, 1910b: 620. Type-locality: South Africa, Natal, Howick. Distr.: South Africa (Natal).

**variabilis* (Loew), 1858: 368 *(Nemestrina)*. Type-locality: South Africa, Cape. Distr.: South Africa (Natal, Cape). Ref.: Bezzi, 1924: 187.

**variegata* (Loew), 1858: 368 *(Nemestrina)*. Type-locality: South Africa, Cape. Distr.: South Africa (Cape).

**westermanni* (Wiedemann), 1821: 185 *(Nemestrina)*. Type-locality: South Africa, Natal, Howick (Lichtwardt, 1920: 100). Distr.: South Africa (Natal, Cape). Refs.: Bezzi, 1924: 184; Lichtwardt, 1920: 100.

willowmorensis Lichtwardt, 1910b: 617. Type-locality: South Africa, Cape, Willowmore. Distr.: South Africa (Cape).

zuluensis Lichtwardt, 1920: 100. Type-locality: South Africa, Transvaal, Zoutpansberg. Distr.: South Africa (Transvaal, Natal). Ref.: Bezzi, 1924: 184.

Genus **Stenobasipteron** Lichtwardt

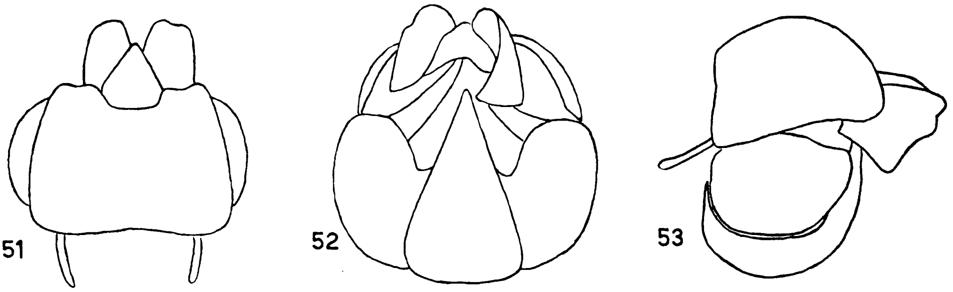
(Figs. 4, 23, 51-53, map 2)

Stenobasipteron Lichtwardt, 1910b: 614. Type-species, *wiedemanni* Lichtwardt (present designation).

Refs.: Bequaert, 1925a: 17, 1927: 256.

Definition: eyes bare. R3 present. Alula very narrow. Wings transparent, but infuscated, and characteristic in shape; costa strongly developed, especially on anterior margin. Otherwise, similar to *Nemestrinus,* excepting reticulation of wings. Male genitalia: figs. 51-53. Ovipositor type 1.

Distribution: Malawi, Rhodesia, South Africa.



Male genitalia of *Stenobasipteron wiedemanni.* 51, dorsal view; 52, ventral view; 53, lateral view.

Comments: the shape of the male genitalia, the shape and characteristic coloration of the wings separate fairly well this genus from *Prosoeca,* but even then they are very similar.

Catalog:

**arnoldi* Bequaert, 1925a: 8, fig. 1a. Type-locality: Rhodesia, Matopos Mts., Mt. Bambata. Distr.: Rhodesia.

**difficile* Bequaert, 1925a: 11, fig. 1b. Type-locality: Rhodesia, Vumbu Mts., Cloudlands, 6000 ft. Distr.: Rhodesia. Ref.: Bequaert, 1927: 356.

**gracile* Lichtwardt, 1910b: 615. Type-locality: Rhodesia, Mashonaland, Mazoe. Distr.: Malawi, Rhodesia, South Africa (Cape, Transvaal). Refs.: Bequaert, 1925a: 14, fig. 1c, 1927: 357.

minimum Bezzi, 1924: 171. Type-locality: South Africa, Cape, Capetown, Table Mt. Distr.: South Africa (Cape).

**wiedemanni* Lichtwardt, 1910b: 614, figs. 7-8. Type-locality: South Africa, Cape (Capetown), Natal (Malveru; Karkloof). Distr.: Rhodesia, South Africa (Natal, Cape). Refs.: Bequaert, 1927: 357; Greathead, 1967: fig. 7.

Genus †**Palembolus** Scudder

(Fig. 21)

†*Palembolus* Scudder, 1878: 526. Type-species, †*florigerus* Scudder (mon.). Ref.: Bequaert & Carpenter, 1936: 406.

Definition: "The venation is almost exactly as in most living species of the genus *Prosoeca*: a) there are only two complete submarginal cells, the first and second being fused; b) the two branches of the third and the upper branch of the fourth longitudinal vein are curved upward at the tips (a feature characteristic of several, but not all, species of *Prosoeca*) ; c) the fourth longitudinal reaches the diagonal, a short distance beyond the branching off of the third longitudinal, so that the first submarginal cell does not touch the discal cell; d) the diagonal vein extends beyond the second and fourth posterior cells to the hind margin of the wing; e) the base of the fourth posterior cell is much narrowed and removed far from the anal cell; f) the apical portion of the wing has no accessory cross-veins; g) the submarginal and posterior cells all open broadly on the apical margin of the wing; h) the sixth longitudinal vein is almost straight; i) the costa encircles the wing completely".

"The presence of the very long proboscis places *P. florigerus* without possible doubt in the subfamily Nemestrininae. The presence of only two submarginal cells, combined with the bare eyes, eliminate the following genera: *Stenobasipteron, Trichophthalma, Fallenia, Neorhynchocephalus, Moegistorhynchus* and *Nemestrinus*. In body characters and particularly in venation, *P. florigerus* shows close relationship to *Stenobasipteron* and *Prosoeca,* the two genera nowadays restricted to South and South Central Africa. *Stenobasipteron* has the alula very narrow, the base of the wing becoming long and stalk-like; otherwise it is like *Prosoeca.* The two genera are, moreover, rather poorly defined, some species of *Prosoeca* showing a decided tendency to narrowing of the alula. On the whole *florigerus* seems to be nearer *Prosoeca,* for although the alula is markedly narrowed, the base of the wing is yet broad, not in least stalk-like. We are unable to point out a character by means of which *Palembolus florigerus* might be separated generically from all living species of *Prosoeca;* for even the wide frons of the male is found in some species of *Prosoeca.* It should be noted, though, that the development of the facial snout is unusual; in the living fauna it is duplicated only by certain species of *Nemestrinus* (such as *N. simplex* Loew). In *Prosoeca* and *Stenobasipteron* the face may be more or less prominent. Moreover, quite possibly, the appearance of the snout-like face was exaggerated in *florigerus* by pressure during preservation".

"The relationship of *florigerus* seems to be best expressed by referring it to the modern genus *Prosoeca,* retaining *Palembolus* in a subgeneric sense. From the living species of *Prosoeca* proper, *Palem-*

bolus differs only in the narrow alula and the quite prominent face". (Bequaert & Carpenter, 1936: 407).

Distribution: Oligocene of Florissant (U. S. A., Colorado).

Comments: in spite of Bequaert and Carpenter's considerations, I prefer to keep †*Palembolus* as a separate genus, because zoogeography is thus better explained. Systematists usually do not like to use geographical characters, but I think in this case my procedure is justified, although provisional. Morphological similarities, in the case of †*Palembolus* based almost exclusively in venation characters, are not to be considered conclusive in uniting this genus with *Prosoeca*. In the Recent fauna, for instance, it is impossible to separate generically many species of *Nemestrinus* and *Neorhynchocephalus* based on such characters, although the two genera belong to distinct subfamilies. The genus *Prosoeca* is a homogeneous group of species, representing a South African radiation; there are no traces of it outside southern Africa. Summing up, it does not seem reasonable to me to place an Oligocene North American fossil in an exclusively South African genus, on the basis of characters that cannot be trusted.

Catalog:

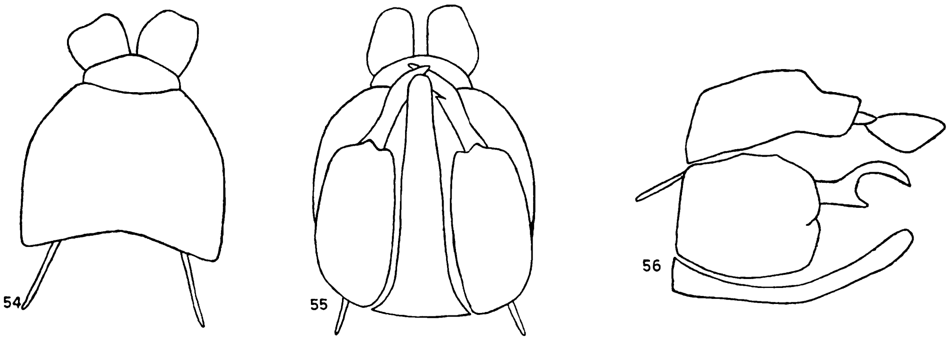
*†*florigerus* Scudder, 1878: 528. Type-locality: U. S. A., Colorado, Florissant (Oligocene). Ref.: Bequaert & Carpenter, 1936: 406, figs. 6, 7 (5).

Genus **Nemestrinus** Latreille

(Figs. 5, 24-26, 54-56, map 2)

Nemestrinus Latreille, 1802: 437. Type-species, *reticulatus* Latreille (mon.).
Rhynchocephalus Fischer, 1806: 217. Type-species, *caucasicus* Fischer (mon.).
Andrenomyia Rondani, 1850: 189. Type-species, *Nemestrina albofasciata* Wiedemann (orig. des.) = *Rhynchocephalus caucasicus* Fischer.
Heminemestrinus Bequaert, 1932a: 21 (as subgenus). Type-species, *Nemestrina dedecor* Loew (orig. des.).
Symmictoides Bequaert, 1932a: 21 (as subgenus). Type-species, *Nemestrina simplex* Loew (orig. des.).
Nemestrellus Sack, 1933: 7. Type-species, *Nemestrina abdominalis* Olivier (orig. des.).
Nemestrina, error.
Refs.: Bequaert, 1932a: 20, 1938: 294; Paramonov, 1944a: 56, 1945: 279, 1951: 118; Sack, 1933: 7, 14, 21, 24, 33.

Definition: head wide, varying from considerably flattened to strongly prominent; proboscis well developed, longer than head; 3rd antennal segment generally longer than first two, the 1st a little shorter; style segmented. Eyes bare. Alula wide in the majority of species, sometimes narrow. R3 present; R4 and R5 free (3rd submarginal cell open); M1 and M2 free (2nd posterior cell open); r-m present or absent; Cu1 and 1A free (anal cell open). The genus has a strong tendency to develop supernumerary cross-veins, which vary from complete absence to a very intensive reticulation, going from the marginal cell to the 3rd posterior and, sometimes, to the 4th and 5th posterior and discal cells. Male genitalia: figs. 54-56. Ovipositor type 1.



Male genitalia of *Nemestrinus aegyptiacus*. 54, dorsal view; 55, ventral view; 56, lateral view.

Distribution: Spain, France, Romania, Bulgaria, Ukrania, southern Russia, Caucasus, Turkey, Morocco, Algier, Tunis, Libya, Sicily, Greece, Egypt, Ethiopia, Arabia, Israel, Iran, Turkestan, Chinese Turkestan, Mongolia, Tibet.

Comments: Sack (1933) divided *Nemestrinus* into five genera and Paramonov (1944a, 1945, 1951) into three. Bequaert (1932a) accepted only one genus with four subgenera, trying to show, with this division, the progressive complication of the venation, but he himself recognized the existence of intermediates (1938: 294). As there are no clear-cut limits, I believe there is no reason to accept subgenera. The above mentioned tendency is perfectly obvious without a formal recognition of artificial groups. The genus needs a revision, with special attention to the male genitalia; perhaps this will reveal some natural groupings. With our present knowledge, there is no basis for a sound subdivision.

Catalog:

*_abdominalis_ Olivier, 1811: 171. Type-locality: Egypt. Distr.: Algier, Tunis, Egypt, Israel, Ethiopia. Refs.: Bequaert, 1938: 300; Sack, 1933:9, pl. 1, fig. 1 (*Nemestrellus*).

    osiris Wiedemann, 1828: 561. Type-locality: Egypt.

*_aegyptiacus_ Wiedemann, 1828: 249. Type-locality: Egypt. Distr.: Morocco, Algier, Tunis, Libya, Sicily, Egypt, Arabia. Refs.: Bequaert, 1938: 302; Lichtwardt, 1909a: 118; unnumbered text-fig.; Sack, 1933:15, text-fig. 10, pl. 1, fig. 2, pl. 3, fig. 21.

jullieni Efflatoun, 1925: 357, unnumbered text-fig. Type-locality: Egypt (Wadi Hoff, east of Helouan; Wadi Um-Elek, branch of Wadi Hoff; Wadi Abu-Handal).

tripolitana Lichtwardt, 1907: 443. Type-locality: Libya, Tripoli.

albomaculatus (Paramonov), 1951: 121 (*Rhynchocephalus*). Type-locality: Kazakhstan, Kzyl Orda, Perovsk. Distr.: Kazakhstan.

amoenus Lichtwardt, 1907: 448. Type-locality: Turkestan, Talas River, 120 km from Aulicata. Distr.: Turkestan.

**ariasi* Lichtwardt, 1912: 541. Type-locality: Spain, Madrid. Distr.: Spain. Refs.: Arias, 1913b: 17, unnumbered text-fig., pl. 1, figs. 1-2; Sack, 1933: 26, pl. 2, fig. 18, pl. 3, fig. 29 (*Rhynchocephalus*).

**ater* Olivier, 1811: 171. Type-locality: Egypt. Distr.: Spain, Algier, Tunis, Egypt, Israel. Ref.: Sack, 1933: 9, pl. 3, fig. 22 (*Nemestrellus*).

nigra Wiedemann, 1828: 560. Type-locality: Egypt.

bombiformis Portschinsky, 1892: 203, pl. 1, fig. 3. Type-locality: Georgia, Elbruz. Distr.: Georgia, Armenia. Refs.: Bequaert, 1938: 296 (under *hirtus*); Sack, 1933: 26 (*Rhynchocephalus*).

**brandti* Bequaert, 1938: 298, fig. 2. Type-locality: Iran, Keredj, 50 km from Teheran. Distr.: Caucasus, Iran. Ref.: Paramonov, 1945: 291 (as subspecies of *marginatus*).

**canaaniticus* Lichtwardt, 1907: 446. Type-locality: Israel, Jerusalem. Distr.: Israel. Ref.: Sack, 1933: 16, pl. 3, fig. 26.

candicans Villeneuve de Janti, 1936: 12. Type-locality: Southwestern Mongolia. Distr.: Mongolia.

**capito* Loew, 1873: 116. Type-locality: Kazakhstan (Kyzyl Kum; Syr Darya). Distr.: Turkestan. Refs.: Paramonov, 1945: 291; Sack, 1933: 22, text-figs. 12-13, pl. 3, fig. 28 (*Heminemestrinus*).

caucasicus (Fischer), 1806: 220, pl. 15, figs. 1-3, 5-7, 10-13 (*Rhynchocephalus*). Type-locality: Caucasus. Distr.: Bulgaria, Romania, Ukrania, southern Russia, Caucasus, Iran, Turkestan. Refs.: Ionescu & Weinberg, 1962: 638, figs. 1-3; Paramonov, 1951: 120 (*Rhynchocephalus*).

analis Olivier, 1811: 172. Type-locality: "environs de la mer Caspienne".

adamsii Fischer, 1812: 188, pl. 15, figs. 1-3, 5-7, 10-13, pl. 15b, fig. 5 (unjustified change of name).

albofasciatus Wiedemann, 1828: 251. Type-locality: unknown.

anthophorinus Portschinsky, 1881: 136. Type-locality: Causasus, Etschmiadzin.

chinganicus Paramonov, 1945: 295. Type-locality: Chingan Mountains (Turkestan?).

cinereus Olivier, 1811: 171. Type-locality: Arabia. Distr.: Arabia.

*_dedecor_ Loew, 1873: 115. Type-locality: Turkmenistan. Distr.: Turkmenistan, Turkey. Refs.: Bequaert, 1938: 300; Paramonov, 1945: 293; Sack, 1933: 23 (_Heminemestrinus_).

nivea Lichtwardt, 1907: 440. Type-locality: Turkmenistan, Ashkhabad.

*_eristalis_ Loew, 1873: 110. Type-locality: Turkmenistan. Distr.: Turkmenistan, Uzbekistan. Refs.: Paramonov, 1945: 288; Sack, 1933: 17.

escalerai Arias, 1913a: 150 Type-locality: Morocco, Marrakesh. Distr.: Morocco. Ref.: Sack, 1933: 19 (_Nemestrellus_).

*_exalbidus_ Lichtwardt, 1907: 441. Type-locality: Israel, Jerusalem. Distr.: Egypt, Israel, Iran. Refs.: Bequaert, 1938: 300; Sack, 1933: 10 (_Nemestrellus_).

*_fasciatus_ Olivier, 1811: 171. Type-locality: Egypt. Distr.: Morocco, Algier, Egypt, Israel, Syria. Refs.: Bequaert, 1938: 295; Sack, 1933: 28, text-figs. 1, 14, pl. 3, fig. 30 (_Rhynchocephalus_).

*_fascifrons_ Bigot, 1888: 8. Type-locality: Tunis. Distr.: Tunis, Egypt, Israel. Ref.: Sack, 1933: 10, pl. 2, fig. 12, pl. 3, fig. 23 (_Nemestrellus_).

flavipes Lichtwardt, 1907: 449. Type-locality: "Central Asia", Togus Tjurae, Kogard Tau. Distr.: Turkestan. Ref.: Sack, 1933: 28, text-fig. 15, pl. 3, fig. 31 (_Rhynchocephalus_).

fraudator Loew, 1873: 108. Type-locality: Uzbekistan, Zeravshan Valley. Distr.: Turkestan. Ref.: Sack, 1933: 17.

graecus Lichtwardt, 1907: 450. Type-locality: Greece (Peloponese, Erymanthus; Peloponese, without other data). Distr.: Greece. Ref.: Sack, 1933: 29, text-fig. 16, pl. 1, fig. 4 (_Rhynchocephalus_).

gussakovskiji (Paramonov), 1944a: 57 (_Symmictoides_). Type-locality: Tadzhikistan (Rujdasht, 300 m, near Stalinabad; Rushan, Kalaj-Wamar, 1900 m). Distr.: Tadzhikistan.

*_hermanni_ Lichtwardt, 1909a: 116. Type-locality: Algier (Biskra; also Algier, without other data). Distr.: Algier. Ref.: Sack, 1933: 10, pl. 2, fig. 13 (_Nemestrellus_).

*_hirsutus_ Bequaert, 1932a: 25, fig. 2. Type-locality: Uzbekistan, Samarkand. Distr.: Uzbekistan. Refs.: Bequaert, 1938: 297; Paramonov, 1944a: 57 (_Symmictoides_); Sack, 1933: 34, pl. 3, fig. 35 (_Symmictoides_).

*_hirtus_ Lichtwardt, 1909a: 121. Type-locality: Kirghizistan, Lake Issykkul. Distr.: Turkestan, Chinese Turkestan. Refs.: Bequaert, 1938: 296; Paramonov, 1951: 125 (_Rhynchocephalus_); Sack, 1933: 29 (_Rhinchocephalus_).

innotatus Loew, 1871: 54. Type-locality: Uzbekistan, Zeravshan Valley. Distr.: Uzbekistan. Refs.: Paramonov, 1945: 288; Sack, 1933: 18.

*_iranicus_ Bequaert, 1938: 306, fig. 4. Type-locality: Iran, Fars, Fort Sine-Sefid, 2200 m, road from Chiraz to Kazeroun. Distr.: Iran.

kiritshenkoi Paramonov, 1945: 294, Type-locality: Northern Iran. Distr.: Iran.

kozlovi (Paramonov), 1951: 124 (*Rhynchocephalus*). Type-locality: China, "Nanj-Shanj, Pinfanj" (Chinese Turkestan?).

**laetus* Loew, 1873: 113. Type-locality: Iran, Astrabad. Distr.: Caucasus, Iran, Turkestan. Refs.: Bequaert, 1932a: 28, 1938: 301; Sack, 1933: 11, text-fig. 8, pl. 2, fig. 14, pl. 3, fig. 24 (*Nemestrellus*).

lichtwardti Bequaert, 1932a: 21 (new name for *Nemestrina cinerea* Lichtwardt, nec Olivier). Type-locality: Tibet ("zwischen See Itsche und Fluss Orogyn, Nord Zaidam"). Distr.: Tibet, Mongolia. Refs.: Paramonov, 1945: 289; Sack, 1933: 23 (*Heminemestrinus*).

cinerea Lichtwardt, 1907: 449, nec Olivier, 1810. Type-locality: Tibet ("zwischen See Itsche und Fluss Orogyn, Nord Zaidam").

marginatus Loew, 1873: 119. Type-locality: Kazakhstan, Kyzyl Kum. Distr.: Turkestan, Chinese Turkestan, Tibet, Mongolia. Refs.: Paramonov, 1945: 290; Sack, 1933: 23 (*Heminemestrinus*).

tarimensis Paramonov, 1945: 291. Type-locality: Chinese Turkestan, Tarim, Nia Oasis.

**melaleucus* Loew, 1873: 103. Type-locality: Kazakhstan (Bairakum; Syr-Darya). Distr.: Turkestan. Refs.: Paramonov, 1951: 121 (*Rhynchocephalus*); Sack, 1933: 30, text-fig. 17, pl. 2, fig. 20 (*Rhynchocephalus*).

**modestus* Lichtwardt, 1919: 276. Type-locality: Turkestan, Karagaitau. Distr.: Turkestan. Refs.: Bequaert, 1938: 296; Sack, 1933: 30, text-fig. 18 (*Rhynchocephalus*).

mollis Loew, 1871: 54. Type-locality: Uzbekistan, Zeravshan Valley. Distr.: Turkestan. Refs.: Bequaert, 1932a: 22, fig. 1d-e; Paramonov, 1951: 122 (*Rhynchocephalus*); 1933: 31, text-fig. 19, pl. 3, fig. 32 (*Rhynchocephalus*).

mongolicus (Paramonov), 1951: 125 (*Rhynchocephalus*). Type-locality: Mongolia, Northern Gobi, Cholt. Distr.: Mongolia.

naso Loew, 1873: 104. Type-locality: Turkmenistan. Distr.: Turkestan. Refs.: Bequaert, 1932a: 24; Paramonov, 1951: 122 (*Rhynchocephalus*); Sack, 1933: 31, text-fig. 20 (*Rhynchocephalus*).

**nigrofemoratus* Lichtwardt, 1907: 449. Type-locality: Kirghizistan, Naryn. Distr.: Turkestan. Refs.: Bequaert, 1938: 296; Paramonov, 1951: 126 (*Rhynchocephalus*); Sack, 1933: 32, pl. 3, fig. 33 (*Rhynchocephalus*).

**nigrovillosus* Lichtwardt, 1909a: 114. Type-locality: Spain. Distr.: Morocco, Spain. Ref.: Arias, 1913b: pl. 2, figs. 1-2.

nitidissimus Strobl, in Czerny & Strobl, 1909: 144. Type-locality: Spain, Alicante.

trautmanni Gil Collado, 1934: 325. Type-locality: Spain, Almeria.

nitidus Lichtwardt, 107: 441. Type-locality: Turkestan, Talas, 120 km from Aulicata. Distr.: Turkestan. Ref.: Sack, 1933: 18.

obscuripennis Portschinsky, 1887: 3, pl. 1, fig. 3. Type-locality: Armenia, Ordubad, Surmali. Distr.: Armenia.

pallipes Olivier, 1811: 171. Type-locality: "Java" (Bequaert, 1932a: 22, thinks this species was based on Egyptian material). Ref.: Bequaert, 1932a: 21.

javanus Macquart, 1840b: 17. Type-locality: "Java" (the same observation holds here).

**perezii* Dufour, 1850: 135, pl. 5, fig. 2. Type-locality: Spain, near Madrid. Distr.: Spain, France. Refs.: Arias, 1913b: 13, pl. 1, figs. 1-2; Sack, 1933: 12 (*Nemestrellus*).

**persicus* Lichtwardt, 1909a: 19. Type-locality: Iran. Distr.: Iran, Turkestan. Refs.: Bequaert, 1932a: 27; Paramonov, 1945: 288; Sack, 1933: 19, pl. 1, fig. 3, pl. 3, fig. 27.

**pieltaini* (Gil Collado), 1934: 321, figs. 1-2 (*Nemestrellus*). Type-locality: Morocco, Imasinen. Distr.: Morocco.

pollinosus Paramonov, 1945: 294. Type-locality: "Ak-Dzhark" (?).

pubescens Lichtwardt, 1919: 274. Type-locality: Turkey, Konia. Distr.: Turkey, Turkestan. Refs.: Paramonov, 1945: 289; Sack, 1933: 24 (*Heminemestrinus*).

pulcherrimus (Paramonov), 1951: 124 (*Rhynchocephalus*). Type-locality: Mongolia, Altai, Iche-Bogdo. Distr.: Mongolia.

**reticulatus* Latreille, 1802: 437. Type-locality: the insect "a été apporté du Levant" (Latreille, 1805: 319); according to the edition of 1809:307, Egypt and Syria. Distr.: Greece, Turkey, Caucasus, Egypt, Arabia, Syria. Refs.: Bequaert, 1932a: 28, 1938: 302, fig. 3, Paramonov, 1945: 285; Sack, 1933: 19, text-fig. 11, pl. 2, fig. 17.

cinctus Macquart, 1840a: 294, pl. 2, fig. 1, 1840b: 16, pl. 2, fig. 1. Type-locality: Arabia.

kindermanni Bischof, 1905: 172. Type-locality: Turkey, Illany Dagh, 1300 m.

latreillei Fischer, 1812: 184, pl. 15b, figs. 1-2 (unjustified change of name).

rjabovi Paramonov, 1945: 295. Type-locality: Turkmenistan, Ashkhabad. Distr.: Turkmenistan.

roederi Bequaert, 1932a: 22, fig. 1a-c. Type-locality: Turkestan, Fergana, Osch. Distr.: Turkestan. Ref.: Sack, 1933: 32, text-fig. 21, pl. 3, fig. 34 (*Rhynchocephalus*).

roseus Paramonov, 1945: 295. Type-locality: "Northern China". Distr.: Northern China.

rubriventris Loew, 1873: 112. Type-locality: Kazakhstan, Kyzyl Kum. Distr.: Turkestan, Mongolia. Ref.: Sack, 1933: 19.

**ruficaudis* Lichtwardt, 1907: 447. Type-locality: Kirghizistan, Naryn. Distr.: Turkestan. Refs.: Bequaert, 1938: 296 (under *hirtus*);

Paramonov, 1951: 125 (*Rhynchocephalus*); Sack, 1933: 32, text-fig. 22 (*Rhynchocephalus*).

ruficornis Macquart, 1840: 15, pl. 2, fig. 5, 1841: 293, pl. 2, fig. 5. Type-locality: Egypt. Distr.: Egypt. Ref.: Sack, 1933: 12 (*Nemestrellus*).

**rufipes* Olivier, 1811: 171. Type-locality: Egypt. Distr.: Algier, Egypt, Syria. Refs.: Bequaert, 1938: 301; Sack, 1933: 12, text-figs. 7-9, pl. 2, fig. 15 (*Nemestrellus*).

lateralis Wiedemann, 1828: 560. Type-locality: Egypt.

rufotestaceus Lichtwardt, 1907: 442. Type-locality: Turkestan, Talas River, 120 km from Aulicata. Distr.: Turkestan. Ref.: Sack, 1933: 20.

signatus Lichtwardt, 1907: 446. Type-locality: Israel, Jerusalem. Distr.: Israel. Ref.: Sack. 1933: 20.

**simplex* Loew, 1873: 105. Type-locality: Uzbekistan, Samarkand. Distr.: Turkestan, Tibet. Refs.: Bequaert, 1938: 297; Paramonov, 1944a: 57 (*Symmictoides*); Sack, 1933: 34, pl. 1, fig. 5, pl. 3, fig. 36 (*Symmictoides*).

sinensis Sack, 1933: 21. Type-locality: "Northern China". Distr.: Northern China.

striatus Lichtwardt, 1907: 443. Type-locality: Libya, Tripoli. Distr.: Algier, Libya. Ref.: Sack, 1933: 13 (*Nemestrellus*).

surcoufi Arias, 1914: 85, figs. 1-2. Type-locality: Tunis. Distr.: Tunis. Ref.: Sack, 1933: 13, pl. 2, fig. 16 (*Nemestrellus*).

transfasciatus (Paramonov), 1951: 123 (*Rhynchocephalus*). Type-locality: Uzbekistan, Bukhara, Darvaz, Vis'harvi. Distr.: Uzbekistan.

variicolor Lichtwardt, 1919: 276. Type-locality: Turkestan, Karagaitau. Distr.: Turkestan. Refs.: Bequaert, 1938: 296 (under *hirtus*); Sack, 1933: 33 (*Rhynchocephalus*).

Genus **Stenopteromyia** Lichtwardt

(Figs. 6, 27, 57-59, map 2)

Stenopteromyia Lichtwardt, 1909b: 509. Type-species, *Nemestrina bolivari* Strobl (orig. des.).

Ref.: Sack, 1933: 35.

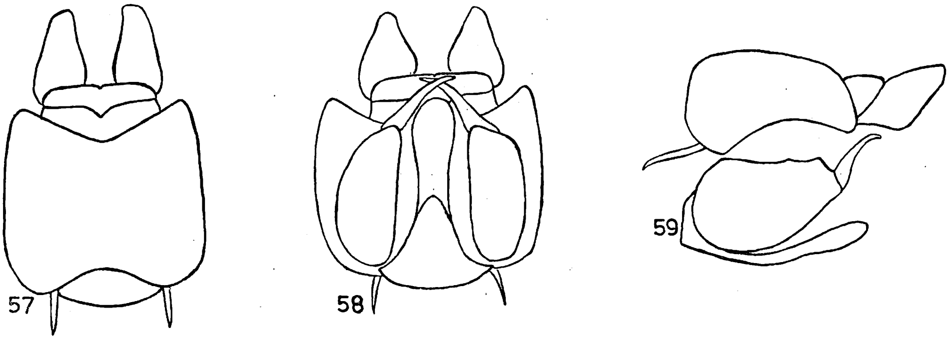
Definition: eyes bare. R3 absent; R2 and R4 fused (2nd submarginal cell closed), M1 and M2 fused (2nd posterior cell closed); diagonal vein incomplete (3rd and 5th posterior cells united). Male genitalia: figs. 57-59. Ovipositor type 1. Otherwise as *Nemestrinus*, except for reticulation of wings.

Distribution: Spain, Greece, Israel.

Comments: this genus is clearly related to *Nemestrinus*, differing in the specialization of the wings.

Catalog:

*_bolivari_ (Strobl), 1905: 280 (_Nemestrina_). Type-locality: Spain, La Coruña, Villa Rutis. Distr.: Spain, Greece, Israel. Refs.: Arias, 1913b: 22, pl. 5, figs. 1-2; Lichtwardt, 1909b: 509, fig. 1; Sack, 1933: 35, text-fig. 24, pl. 1, fig. 7.



Male genitalia of _Stenopteromyia bolivari_. 57, dorsal view; 58, ventral view; 59, lateral view.

Genus **Moegistorhynchus** Macquart

(Figs. 7, 28, 60-62, map 2)

Moegistorhynchus Macquart, 1840: 12, 1841: 290. Type-species, _Nemestrina longirostris_ Wiedemann (orig. des.).

Maegistorhynchus, error.

Megistorhynchus, error.

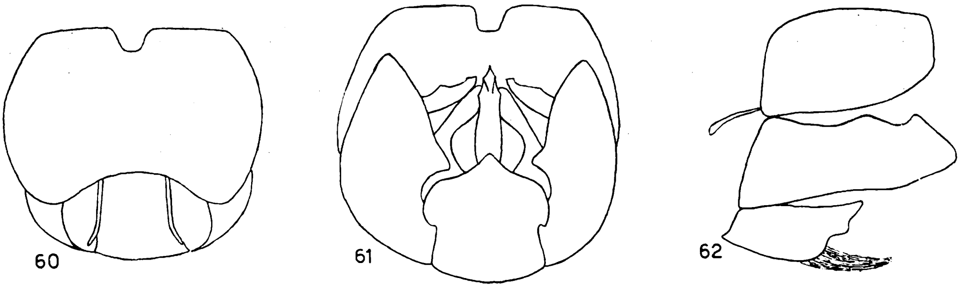
Megistorrhynchus, error.

Ref.: Bequaert, 1935b: 491.

Definition: claws exceptionally long and slender; pulvilli and empodia long. Hypandrium sub-quadrate, much shorter than gonopods, high in lateral view and with a ventral tuft of hairs. Male genitalia: figs. 60-62. Ovipositor type 1. Otherwise as _Nemestrinus_, including reticulation of wings.

Distribution: South Africa.

Comments: "Macquart's original diagnosis of this genus will not help much in separating it from either _Nemestrinus_ or _Prosoeca_. All three genera have a protruding face with bare eyes. The reticulate apex of the wing will separate _Moegistorhynchus_ from _Prosoeca_, as well as from other South African nemestrinids, but this character is also found in many species of _Nemestrinus_. The unusual length of the proboscis of the genotype is not present in another species of the genus. The



Male genitalia of *Moegistorhynchus braunsi.* 60, dorsal view; 61, ventral view; 62, lateral view.

fork of the sixth longitudinal vein (Bezzi's anal vein) dividing the axillary cell into two (as mentioned by Macquart and used by Bezzi in his key) is a very variable feature: of eleven specimens seen, only four have this supernumerary cross-vein complete; in the others there is either no trace of it, or there are one to three short or long stumps on the sixth longitudinal. Possibly these differences are of specific value. It seems to me that if the two known species of *Moegistorhynchus* were Palearctic (instead of South African), they would perhaps be regarded as forming merely a subgenus of *Nemestrinus*".

"Attention may be called to the unusually long and slender claws and the long pulvilli and empodia, as well as the vertex being wide in both sexes. These two peculiarities are present in all *Moegistorhynchus*, being evidently of more than specific value" (Bequaert, 1935b: 491). I cannot judge these last characters proposed by Bequaert, but the male genitalia undoubtedly separates this genus from all other Nemestrininae.

Catalog:

**braunsi* Bequaert, 1935b: 495, figs. 1c, 2a-c. Type-locality: South Africa, Cape, Stellenbosch. Distr.: South Africa (Cape).

brevirostris (Wiedemann), 1821: 156 (*Nemestrina*). Type-locality: South Africa, Cape, Capetown. Distr.: South Africa (Cape). Ref.: Bequaert, 1935b: 492, fig. 1b.

longirostris (Wiedemann), 1919: 13 (*Nemestrina*). Type-locality: South Africa, Cape, Capetown. Distr.: South Africa (Cape). Ref.: Bequaert, 1935b: 493, Lichtwardt, 1910b: 612, fig. 6.

perplexus Bequaert, 1935b: 498, figs. 1a, 2d. Type-locality: South Africa, Cape, Clan Williams. Distr.: South Africa (Cape).

7. Subfamily Cyclopsideinae, new subfam.

Definition: head very large in relation to the size of the insect, pronouncedly hemispherical, wider than thorax and almost as large in volume; face convex; proboscis vestigial; antennae three-segmented, with apparently unsegmented style. Thorax small in relation to the insect's size; scutellum prominent, post-scutellum almost as large as scutellum. 1st segment of hind tarsus approximately as long as the last four together. Alula vestigial, wings hyaline, characteristic in shape. M1 and M2 running towards apical margin. Venation reduced at radial field. Hypandrium fused with gonopods. Ovipositor type 1.

Genus **Cyclopsidea** Mackerras

(Figs. 8, 29)

Cyclopsidea Mackerras, 1925: 557. Type-species, *hardyi* Mackerras (orig. des.).

Ref.: Paramonov, 1953: 255.

Definition: besides the characters given for the subfamily: eyes large, bare; palpi conical, very small; antennae small, with three subequal segments, the third continuing into a slender style, widened at the tip. Costa well developed, encircling the whole wing; R3 present; R4 and R5 totally fused (3rd submarginal cell absent); R4+5 and M1+2 fused, eliminating r-m; M1 and M2 free (2nd posterior cell open); M4 and Cu1 fused, eliminating m-cu; Cu1 and 1A free (anal cell open). Abdomen elongate, tapering. Male genitalia: Mackerras, 1925: fig. 17c-f.

Distribution: Australia (West Australia, Queensland, New South Wales, South Australia).

Comments: only a few specimens of the single species of this genus are known. The male specimen I have studied (from the Commonwealth Scientific and Industrial Research Organization) had the genitalia already mounted on a slide, divided into two parts. Because of the mounting it was impossible to observe some important details, so that interpretation was difficult. Mackerras (1925: 557), in the original description, states: "ninth sternite large and continuous with the basistyles". Taking this statement into account, I am considering the hypandrium to be fused with the gonopods. This interpretation, however, I would like to see confirmed. Hennig (1954) gives an interpretation of venation different from mine. He considers R2 to be partially fused with R4, so that what I have called R3, he has interpreted as being the base of R4. This is a possible interpretation.

Catalog:

**hardyi* Mackerras, 1925: 559, fig. 17. Type-locality: Australia, Queensland, Inglewood. Distr.: Australia (West Australia, Queensland, New South Wales, South Australia). Ref.: Paramonov, 1953: 255.

8. Subfamily Trichopsideinae Bequaert

Definition: head flattened, slightly convex; face convex; proboscis well developed, longer than head, or vestigial; antennae three-segmented, with segmented style. Thorax normal in relation to the insect's size; scutellum normal. 1st segment of hind tarsus longer than or as long as the last four together. Alula wide, vestigial or absent; wings hyaline. Venation complete or more commonly reduced; M1 and M2 running towards the apical margin. Hypandrium absent; gonopods free or fused together. Ovipositor type 2.

Genus **Neorhynchocephalus** Lichtwardt

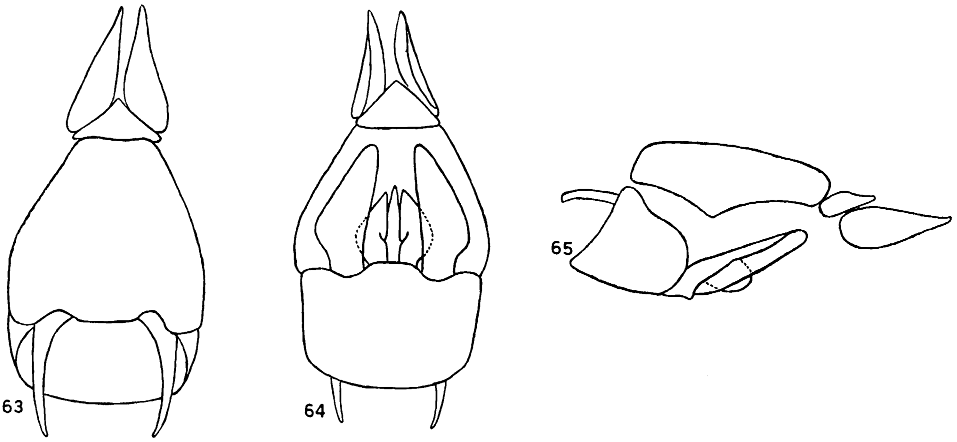
(Figs. 30-31, 63-65, map 3)

Neorhynchocephalus Lichtwardt, 1909b: 512. Type-species, *Rhynchocephalus volaticus* Williston (Bequaert, 1930: 287).

Nemestrinopsis Cockerell, 1910: 285 (as subgenus of *Rhynchocephalus*). Type-species, *Rhynchocephalus volaticus* Williston (orig. des.).

Refs.: Bequaert, 1930: 286, 1934: 162; Lichtwardt, 1910b: 592.

Definition: eyes bare; proboscis long; antennae short, with first two segments subequal, wider than high, the 3rd flattened, followed by a segmented style. Alula wide. Costa encircling the whole wing or, at least, leaving traces on the hind margin; apical portion of wing rarely presenting supernumerary cross-veins; R3 present; R4+5 and M1+2 fused, eliminating r-m; R4 and R5 free (3rd submarginal cell open); M1 and M2 free (2nd posterior cell open) or partially fused (2nd posterior cell closed); m-cu present or absent; Cu1 and 1A free (anal cell open). Male genitalia: figs. 63-65. Ovipositor type 2.



Male genitalia of *Neorhynchocephalus sulphureus*. 63, dorsal view; 64, ventral view; 65, lateral view.

Distribution: 1) Canada (British Columbia), United States (from Washington, Oregon and California to Michigan, Indiana, Georgia and Florida), Mexico, Guatemala, Honduras.

2) Chile (Aconcagua to Malleco), Argentina (Santiago del Estero and Misiones to Rio Negro), Paraguay, Brazil (Mato Grosso, Goiás and Minas Gerais to Rio Grande do Sul).

3) Southern Russia, Caucasus, Turkestan, southwestern Siberia, France, Spain, Greece, Turkey, Iran.

Comments: this genus may be distinguished with certainty from *Nemestrinus* only by the male genitalia and the female ovipositor. Externally both are very similar. Bequaert (1934: 164) remarks: "The only reliable characters separating *Neorhynchocephalus* from all species of *Nemestrinus* Latreille are the flattened or slightly convex face (in *Nemestrinus* always considerably swollen and often snout-like) and the long, sabre-shaped ovipositor of two slender curved valves (in *Nemestrinus* the ovipositor is telescope-shaped, of several retractile segments, the two terminal valves short and broad). Neither the venation of the wing nor the direction assumed by the proboscis are diagnostic. Some species of *Nemestrinus* (of the subgenus *Rhynchocephalus* Fischer; type, *N. caucasicus*) have the venation exactly like in *N. volaticus*. In most species of *Neorhynchocephalus* the proboscis is either directed downward or slanting backward; but I have seen many specimens of *N. volaticus* in which it slants forward. On the other hand, I have seen examples of *Nemestrinus fasciatus* (Olivier), in which the proboscis is directed vertically downward. In *Neorhynchocephalus* the frons below the ocelli is always considerably narrower in the male than in the female; the eyes being almost holoptic in the males of certain species. Although in most species of *Nemestrinus* the frons is not conspicuously narrowed in the males in others, such as *N. hirtus* Lichtwardt and *N. ruficaudis* (Lichtwardt), the frons of the male is relatively as narrow as in certain *Neorhynchocephalus*". In practice, however, there are no problems of identification, because only *Neorhynchocephalus tauscheri* is Palearctic, alongside with *Nemestrinus;* all other species are American. The two genera are considerably different in habitus.

Catalog:

*†*melanderi* (Cockerell), 1908c: 311 (*Hirmoneura*). Type-locality: U.S.A., Colorado, Florissant (Oligocene). Ref.: Bequaert & Carpenter, 1936: 403, figs. 5, 7 (3).

**mendozanus* (Lichtwardt), 1910b: 594 (*Rhynchocephalus*). Type-locality: Argentina, Mendoza (province). Distr.: Chile (Aconcagua to Malleco). Argentina (Mendoza, Rio Negro). Ref.: Angulo, 1971: 94, figs. 73, 75, 78.

†*occultator* (Cockerell), 1908b: 254 (*Hirmoneura*). Type-locality: U. S. A., Colorado, Florissant (Oligocene). Ref.: Bequaert & Carpenter, 1936: 402, figs. 4, 7 (1).

**sackenii* (Williston), 1880: 243, unnumbered text-fig. (*Rhynchocephalus*). Type-locality: U. S. A., Washington, Olympia. Distr.: Canada (British Columbia), U.S.A. (Washington, Oregon and California to Michigan, Illinois and Georgia), Mexico (Nayarit). Refs.: Bequaert, 1930: 291, 1934 169, 1950a: 9, 1957: 133, fig. 3; Cole & Lovett, 1924: 239, fig. 17 (*Rhynchocephalus*); Dietz, 1953: 38; Greathead, 1967: fig. 5; James, 1938: 21; Prescott, 1955: 392, figs. 1-6, 1960: 513, figs. 1-6, 1961: 557, figs. 1-9; York, 1955: 328; York & Prescott, 1952: 5.

sackeni, error.

subnitens Cockerell, 1908a: 250. Type-locality: U. S. A., Kansas, Clark Co.

**sulphureus* (Wiedemann), 1830: 631 (*Nemestrina*). Type-locality: Brazil, Minas Gerais, São João del Rei. Distr.: Brazil (Minas Gerais to Rio Grande do Sul), Paraguay, Argentina (Tucumán and Santiago del Estero to Rio Negro). Refs.: Bequaert, 1930: 294, 1934: 174; Crouzel & Salavin, 1943: 147, pls. 1-4, 33 figs.; Stuardo Ortiz, 1939: 81.

**tauscheri* (Fischer), 1812: 196 (*Rhynchocephalus*). Type-locality: Southern Russia, Sarepta. Distr.: Southern Russia, Caucasus, Turkestan, Siberia (Krasnoyarsk), France, Spain, Greece, Turkey, Iran. Refs.: Arias, 1913b: 20, pl. 4, figs. 1-2 (*Rhynchocephalus*); Oldroyd, 1967: 153, figs. 1-2; Sack, 1933: 35, text-fig. 23, pl. 1, fig. 6, pl. 3, fig. 37; Timon-David, 1952a: 119, figs. 1-2; Timon-David & Léonide, 1968: 188, pls. 7-8.

lativentris Portschinsky, 1887: 2. Type-locality: Iran, Astrabad.

**vitripennis* (Wiedemann), 1830: 631 (*Nemestrina*). Type-locality: Brazil. Distr.: Brazil (Mato Grosso, Goiás), Argentina (Misiones, Córdoba and San Juan to Rio Negro). Refs.: Bequaert, 1930: 294, 1934: 173; Crouzel & Salavin, 1948: 167.

vitreipennis Hunter, 1901: 149 (error).

**volaticus* (Williston), 1883: 71, fig. 4 (*Rhynchocephalus*). Type-locality: U. S. A., Florida, Georgina (Bequaert, 1934: 167, footnote). Distr.: U. S. A. (Arizona, Kansas and Illinois to Florida), Mexico (Baja California, Sinaloa and Nuevo Leon to Chiapas and Yuacatan), Guatemala, Honduras. Refs.: Bequaert, 1930: 209, 1934: 166, fig. 1 e-g, 1957: 133, fig. 2.

flavus Curran, 1931: 70. Type-locality: U. S. A., Kansas, Harper Co.

maculatus Curran, 1931: 69. Type-locality: U. S. A., Kansas, Lawrence.

mexicanus Bequaert, 1934: 171, fig. 1a-d. Type-locality: Mexico, Mexico City.

†*vulcanicus* (Cockerell), 1908c: 311 (*Hirmoneura*). Type-locality: U. S. A., Colorado, Florissant (Oligocene). Ref.: Bequaert & Carpenter, 1936: 401, figs. 3, 7 (4).

Genus **Fallenia** Meigen

(Figs. 9, 32, map 2)

Fallenia Meigen, 1820: 134. Type-species, *Cytherea fasciata* Fabricius (orig. des.).

Tallenia Bezzi, 1924: 165, (error).

Refs.: Bequaert, 1938: 309; Paramonov, 1944c: 39; Sack, 1933: 36.

Definition: eyes bare; proboscis long; antennae short, with first two segments subequal, wider than high, the third flattened. Alula very reduced. Costa encircling the whole wing; R3 present; R4+5 and M1+2 fused, eliminating r-m; R4 and R5 almost totally fused, forming a small triangular cell (3rd submarginal) in the middle of the wing, that may occasionally disappear; M1 and R4+R5 fused (1st posterior cell closed); M2 strongly bent forward, almost reaching R4+R5+M1, sometimes reaching it and closing the 2nd posterior cell; diagonal vein incomplete (3rd and 5th posterior cells united); Cu1 and 1A fused (anal cell closed). Male genitalia: as in *Trichopsidea*. Ovipositor type 2.

Distribution: Spain, France, Italy, Yugoslavia, Ukrania, Caucasus, Turkestan, Turkey, Algier, Tunis, Israel, Iran.

Comments: Paramonov (1924, 1944c) considered his *semenovi* a good species. Bequaert (1938) considered it to be a synonym of *fasciata*, remembering the great variability observed in other Nemestrinidae, taking the absence of the 3rd submarginal cell and the fusion of M2 with R4+R5+M1, closing the 2nd posterior cell, as simple variations. In some specimens of *fasciata* I have observed the disappearance of the 3rd submarginal cell due to reduction of the free section of either R4 or R5; perhaps the same result may be attained by a complete fusion of both veins. I was not able to observe the closure of the 2nd posterior cell. I will follow Paramonov, provisionally.

Catalog:

**fasciata* (Fabricius), 1805: 116 (*Cytherea*). Type-locality: Italy. Distr.: Spain, France, Italy, Yugoslavia, Ukrania, Caucasus, Turkestan, Turkey, Algier, Tunis, Israel, Iran. Refs.: Bequaert, 1938: 309; Greathead, 1967: fig. 10; Lichtwardt, 1909b: 513, fig. 4; Paramonov, 1944b: 40; Sack, 1933: 36, text-fig. 25, pl. 1, fig. 8, pl. 3, fig. 38; Séguy, 1926: 172, figs. 428, 433; Timon-David, 1948: 191.

semenovi Paramonov, 1924: 149. Type-locality: Iran, Pain-Gjatsch. Distr.: Iran. Refs.: Bequaert, 1938: 309 (as synonym of *fasciata*); Paramonov, 1944b: 39.

Genus **Trichopsidea** Westwood

(Figs. 10, 33-34, 66-68, map 3)

Trichopsidea Westwood, 1839: 151. Type-species, *oestracea* Westwood (mon.).

Symmictus Loew, 1858: 111. Type-species, *costatus* Loew (orig. des.).

Dicrotrypana Bigot, 1879: LXVII. Type-species, *flavopilosa* Bigot (mon.) = *Symmictus costatus* Loew.

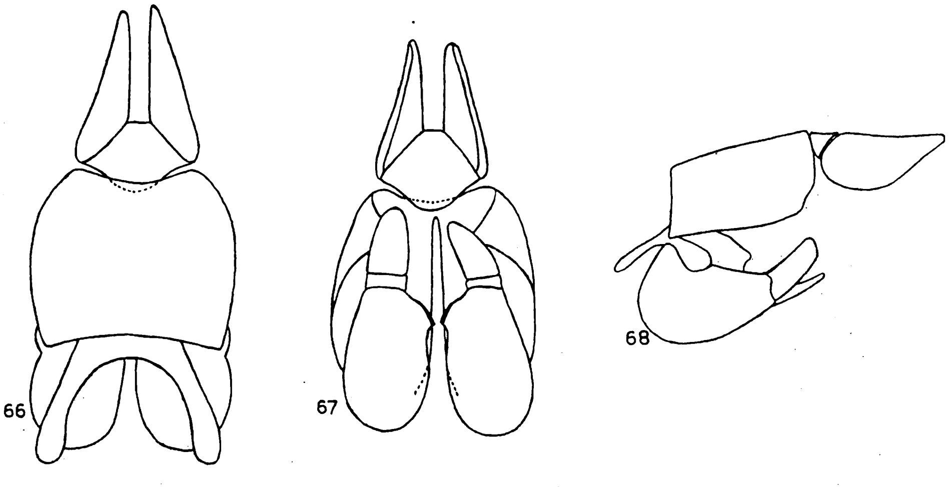
Parasymmictus Bigot, 1879: LXVII. Type-species, *Hirmoneura clausa* Osten Sacken (orig. des.).

Refs.: Bequaert, 1934: 180; Greathead, 1967: 306; Hardy, 1924: 456; Mackerras, 1925: 548.

Definition: eyes bare; proboscis extremely reduced, almost vestigial; 1st antennal segment cylindrical, the 2nd spherical or cylindrical, the 3rd globate. Alula vestigial or absent. Costa running to the apical margin; R3 present; R4 and R5 partially or totally fused (3rd submarginal cell closed or absent); R4+5 and M1+2 fused, eliminating r-m; R2 may fuse with R4+R5, closing the 2nd submarginal cell; M1 and M2 fused (2nd posterior cell closed); m-cu present; Cu1 and 1A free or fused (anal cell open or closed). Male genitalia: figs. 66-68. Ovipositor type 2.

Distribution:

1) Canada (British Columbia, Manitoba), U. S. A. (Washington, Montana and California to Florida).



Male genitalia of *Trichopsidea oestracea*. 66, dorsal view; 67, ventral view; 68, lateral view.

2) Spain, Caucasus, Turkestan, Algier, Ethiopia, Somaliland, Kenya, Mozambique, Botswana, South Africa.

3) New Guinea, Australia (West Australia, Queensland, New South Wales, Victoria, Tasmania).

Comments: this genus was divided, in the past, into four genera. Bequaert (1934: 180) reduced the four groups to subgenera, but considered even this doubtful. The works of Arias (1911, 1913) and Greathead (1960) established the synonymy of *costata* and *flavopilosa* on sound bases, reducing to three the number of species. I hereby propose that this division into subgenera be abandoned. As Bequaert himself remarked, if not for the disjunct distribution, it would be difficult even to separate the species.

Catalog:

**clausa* (Osten Sacken), 1877: 225 (*Hirmoneura*). Type-locality: U. S. A., Texas, Dallas. Distr.: Canada (British Columbia, Manitoba), U. S. A. (Washington, Montana and California to Florida). Refs.: Bequaert, 1934: 182, 1950c: 104; Prescott, 1955: 392, figs. 1-3, 1961: 566; York, 1955: 328; York & Prescott, 1952: 5, fig. 1.

**costata* (Loew), 1858: 113, pl. 1, figs. 26-30 (*Symmictus*). Type-locality: South Africa, Cape. Neotype: Somaliland, near Marsham (Greathead, 1960: 104). Distr.: Spain, France, Caucasus, Algier, Ethiopia, Somaliland, Kenya, Mozambique, Botswana, South Africa. Refs.: Arias, 1911: 561, figs. 1-9 (*Symmictus*); Frisch, 1965: 368, figs. 1-3 (*Symmictus costatus* ssp. *frischi*); Greathead, 1958: 107, text-figs. 1-11, pl. 1 (*Symmictus flavopilosus*), 1960: 103, fig. 1 (*Symmictus*), 1963: 461, figs. 38-44 (*Symmictus*), 1967: 308, fig. 3; Léonide, 1962a: 104 (*Symmictus*), 1962b: 550, text-figs. 1-2, pls. 1-2 (*Symmictus*), 1963: 7, pl. 1 (*Symmictus*), 1964a: 135, pls. 1-3 (*Symmictus*), 1968: 65 (*Symmictus*), 1969: 139, figs. 39-47 (*Symmictus*); Sack, 1933: 38, text-figs. 26-27, pl. 1, fig. 9, pl. 3, fig. 39 (*Symmictus flavopilosus*); Séguy, 1926: 174, figs. 423, 441 (*Symmictus*).

flavopilosa Bigot, 1879: LXVII. Type-locality: "Southern Europe?".

frischi Teschner, 1965: 366, fig. 1. Type-locality: France, Crau.

**oestracea* Westwood, 1839: 151, pl. 14, fig. 9. Type-locality: Australia. Distr.: New Guinea, Australia (West Australia, Queensland, New South Wales, Victoria, Tasmania). Refs.: Fuller, 1938: 95, figs. 1-9; Greathead, 1967: 307, figs. 1-2; Hardy, 1924: 457, figs. 3, 9; Mackerras, 1925: 550, figs. 12-13; Paramonov, 1953: 255.

ostracea Greathead, 1958: 107, 1967: 307 (error).

9. Súbfamily Atriadopsinae, new subfam.

Definition: head flattened, with a strong depression below the antennae; face convex; proboscis vestigial; 3rd antennal segment completely fused with style, forming a single, elongate piece. Thorax normal in relation to the insect's size; scutellum normal. Ist segment of hind tarsus clearly shorter than the last four together, the fifth longer than each one of the three intermediary. Wings opaque, sometimes with hyaline areas. Alula narrow or absent. Venation complete or more commonly strongly reduced; M1 and M2 running towards the apical margin. Hypandrium absent; gonopods fused, forming a single ventral piece. Ovipositor type 2.

Genus **Ceyloniola** Strand

(Fig. 35, map 4)

Ceylonia Lichtwardt, 1909c: 646 (preocc. Buckton, 1891). Type-species, *magnifica* Lichtwardt (orig. des.).

Ceyloniola Strand, 1928: 49 (new name for *Ceylonia* Lichtwardt). Type-species, *Ceylonia magnifica* Lichtwardt.

Ref.: Bequaert, 1935a: 140.

Definition: 1st antennal segment cylindrical, 2nd spherical, half of the length of the 1st, 3rd spherical and pointed (there seems to be an indication of suture between the 3rd segment and the style, but this is not certain); style longer than remainder of antenna. Wings opaque, with large hyaline areas. Alula developed. R3 present as a stump projecting from the base of R4, interrupted midway between R4 and R2; R4 and R5 free (3rd submarginal cell open; R4+5 and M1+2 fused; M1 and M2 free (2nd posterior cell open); m-cu present; Cu1 and 1A free (anal cell open); axillary cell very enlarged. Male genitalia not dissected. Ovipositor presumably type 2 (female unknown).

Distribution: Ceylon.

Catalog:

**magnifica* (Lichtwardt), 1909c: 646, fig. 5 (*Ceylonia*). Type-locality: Ceylon, Pundaluoya. Distr.: Ceylon. Refs.: Bequaert, 1935a: 140; Brunetti, 1920: 156, pl. 2, fig. 23.

nivea Brunetti, 1912: 477, pl. 37, fig. 11. Type-locality: Ceylon, Haldumulla.

Genus **Atriadops** Wandolleck

(Figs. 11, 36, 69-71, map 4)

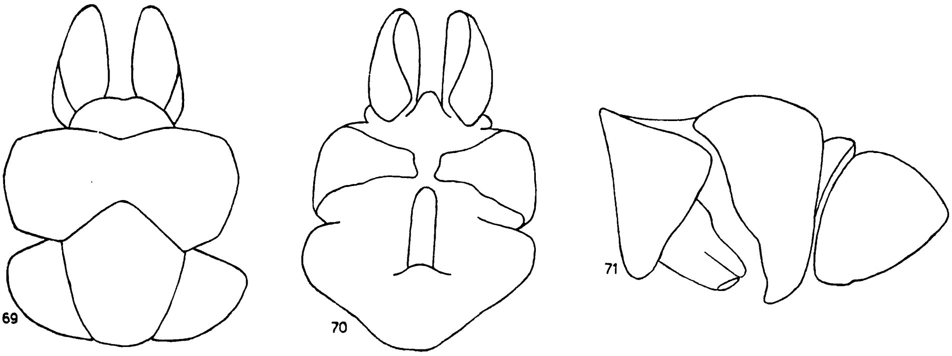
Colax Wiedemann, 1824: 18 (preocc. Hübner, 1816). Type-species, *macula* Wiedemann (Blanchard, 1840: 608).

Atriadops Wandolleck, 1897a: 246 (new name for *Colax* Wiedemann). Type-species, *Colax macula* Wiedemann (aut.).

Atriatops Hardy, 1924: 456 (error).

Refs.: Bequaert, 1937: 206; Hardy, 1924: 456; Lopes, 1936: 883; Mackerras, 1925: 551; Paramonov, 1953: 252.

Definition: ocelli absent; mouthparts extremely reduced; antennae very small, the first two segments short and wide, the 3rd much smaller in volume, globate-elongate, continuous with the long and tapering style. Wings opaque, leathery. Alula vestigial. R3 absent; R4 and R5 totally fused (3rd submarginal cell absent); R4+5 and M1+2 fused; M1 and M2 free (2nd posterior cell open); M2 may be lacking beyond the diagonal vein (this is due to reduction, not to fusion with M1, as it may be proved by the presence of traces of M2 in some specimens, the presence or absence of the vein in *A. macula* and the presence of a free portion of M2 in the diagonal vein, between the point where M1 leaves the diagonal and the point where M3 enters it); M3 free in the diagonal vein because M2 leaves the diagonal before M4 entering it (this character may be obscured when M2 disappears); m-cu present; Cu1 and 1A free (anal cell open); axillary cell greatly enlarged, especially in the males; 2A present in the axillary cell. Male genitalia: figs. 69-71. Ovipositor type 2.



Male genitalia of *Atriadops macula*. 69, dorsal view; 70, ventral view; 71, lateral view.

Distribution:

1) Brazil (Mato Grosso, Bahia, Rio de Janeiro).

2) Ghana, Togo, Uganda, Ethiopia, Sokotra, Kenya, Congo, Tanzania, Malawi, Botswana, Mozambique, South Africa.

3) India, Ceylon, China (Foo-Chow), Japan, Formosa, Laos, Sumatra, Java, Aru Is., Bismarck Arch., New Guinea, Australia (Northern Territory, Queensland, New South Wales).

Catalog:

amamioshimensis Ouchi, 1939: 241, fig. 2. Type-locality: Southern Japan, Sumiyogusuku, Amami-Oshima. Distr.: Japan.

aruanus Paramonov, 1953: 253. Type-locality: Indonesia, Aru I. Distr.: Indonesia, Aru Is.

**javanus* (Wiedemann), 1824: 18, pl. 8 (*Colax*). Type-locality: Java. Distr.: India, Ceylon, China (Foo-Chow), Formosa, Laos, Singapore, Sumatra, Java, Bismarck Arch., Australia (Northern Territory, New South Wales). Refs.: Bequaert, 1935a: 137; Hardy, 1924: 456, figs. 2, 8; Mackerras, 1925: 552, fig. 14a-d; Paramonov, 1953: 253; Sack, 1933: 41, text-fig. 29, pl. 1, fig. 11, pl. 3, fig. 40.

iavanus, error.

variegatus Westwood, 1848: 38, pl. 18, figs. 5, 5a. Type-locality: China, Foo-Chow.

**macula* (Wiedemann), 1824: 18, fig. 8 (*Colax*). Type-locality: Brazil. Distr.: Brazil (Bahia, Mato Grosso, Rio de Janeiro). Refs.: Bequaert, 1937: 206; Lopes, 1936: 886, pl. 1. figs. 1-5.

maculata Ouchi, 1939: 241 (error).

**vespertilio* (Loew), 1858: 340 (*Colax*). Type-locality: Botswana, Ngami. Distr.: Ghana, Togo, Uganda, Ethiopia, Sokotra, Kenya, Congo, Tanzania, Malawi, Botswana, Mozambique, South Africa. Ref.: Bequaert, 1937: 207; Greathead, 1967: fig. 9 (*cinnamomea*).

africana Wandolleck, 1897a: 248, figs 4-5. Type-locality: Togo (Misahöhe), Angola (Chinchoxo).

cinnamomea Brunetti, 1929: 5. Type-locality: Malawi, Mt. Mlanje.

cinnamonea Greathead, 1967: 309, fig. 9 (error).

**westwoodi* Lichtwardt, 1909c: 650. Type-locality: New Guinea. Distr.: New Guinea, Australia (Queensland). Ref.: Paramonov, 1953: 254.

Genus **Nycterimyia** Lichtwardt

(Figs. 12, 37, 72-74, map 4)

Nycterimyia Lichtwardt, 1909c: 648. Type-species, *Trichopsidea dohrni* Wandolleck (orig. des.).

Refs.: Bequaert, 1925a: 18, 1935a: 138; Hardy, 1924: 459; Mackerras, 1925: 553; Paramonov, 1953: 244.

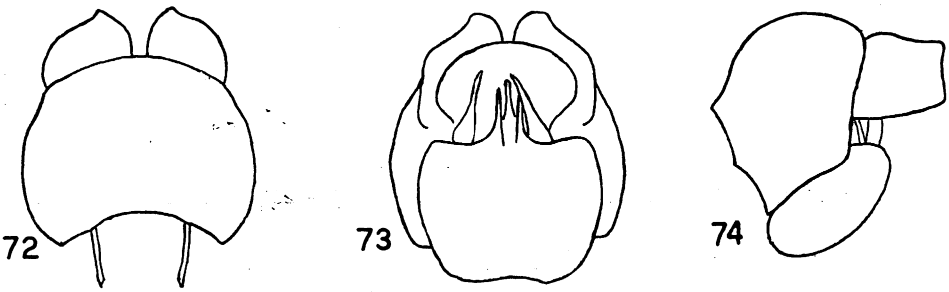
Definition: 1st and 2nd antennal segments short and wide, the 3rd plus style forming a long piece of approximately uniform width, a little narrower at tip. Femora swollen distally. Wings characteristic in shape, with posterior margin wavy, projecting in the regions of the diagonal vein and the anal cell, opaque, with hyaline areas; alula narrow. R3 absent; R4 and R5 free (3rd submarginal cell open); R2 fused with R4 for a short distance, then separating from it and fusing with R1, resembling a cross-vein between R1 and R4; R4+5 and M1+2 fused for a long distance (much longer than the width of the discal cell); M1 and M2 totally fused (2nd posterior cell absent); M4 and Cu1 fused: Cu1 and 1A free (anal cell open). Male genitalia; figs. 72-74. Ovipositor type 2.

Distribution:

1) Kenya, Malawi, South Africa, Madagascar.

2) Formosa, Andaman Is., Rhio Arch., Sumatra, Philippines, Bismarck Arch., New Guinea, Australia (Queensland).

Comments: the venation of this genus is the most difficult to interpret. I am following Hennig's (1954) interpretation, that seems to be the best as to the complexities of the radial field. As to M1 and M2, I agree that it is impossible to know which type of fusion has occurred, as Hennig remarks, but I prefer to think that it was M1+M2; it is the only fusion well proven in this area.



Male genitalia of *Nycterimyia dohrni*. 72, dorsal view; 73, ventral view 74, lateral view.

Catalog:

bezzii Lichtwardt, 1925: 393, fig. 2. Type-locality: Malawi. Distr.: Malawi.

capensis Bezzi, 1924: 168. Type-locality: South Africa, Natal, Durban, Stella Bush. Distr.: South Africa (Natal).

commoni Paramonov, 1953: 246, fig. 2. Type-locality: Australia, Queensland, Yeppoon. Distr.: Australia (Queensland).

**dohrni* (Wandolleck), 1897a: 251, figs. 7-8 (*Trichopsidea*). Type-locality: Sumatra. Distr.: Andaman Is., Rhio Arch., Sumatra, Philippines (Mindanao). Refs. Bequaert, 1935a: 139; Greathead, 1967: fig. 8.

fenestroclathrata Lichtwardt, 1912a: 28, pl. 2, fig. 3. Type-locality: Formosa, Fuhosho. Distr.: Formosa. Ref.: Bequaert, 1935a: 140.
fenestroclatrata, error.

fenestroinornata Lichtwardt, 1912a: 28, pl. 2, fig. 4. Type-locality: Formosa, Fuhosho. Distr.: Formosa. Ref.: Bequaert, 1935a: 140.

**horni* Lichtwardt, 1912a: 27, pl. 2, fig. 1. Type-locality: Australia, Queensland, Kuranda. Distr.: Australia (Queensland). Refs.: Hardy, 1924: 459; Mackerras, 1925: 554, fig. 15b; Paramonov, 1953: 245, fig. 1.

kerteszi Lichtwardt, 1912a: 27, pl. 2, fig. 2. Type-locality: Formosa, Fuhosho. Distr.: Formosa. Ref.: Bequaert, 1935a: 140.

nairobensis Bequaert, 1935b: 499, fig. 3. Type-locality: Kenya, Nairobi. Distr.: Kenya.

papuana Bequaert, 1925a: 18, fig. 2a-b. Type-locality: New Guinea, Geelvink Bay. Distr.: New Guinea.

septempunctata Lyneborg, 1967: 215, fig. 1. Type-locality: Bismarck Arch., New Britain I., Yalom, 1000 m. Distr.: Bismarck Arch.

seyrigi Ségui, 1951: 55, unnumbered text-fig. Type-locality: Madagascar, Fort Dauphin. Distr.: Madagascar.

Genus **Nycterimorpha** Lichtwardt

(Figs. 13, 38, map 4)

Nycterimorpha Lichtwardt, 1909c: 648. Type-species, *speiseri* Lichtwardt (mon.).

Refs.: Edwards, 1932: 137; Hardy, 1924: 459; Mackerras, 1925: 556; Paramonov, 1953: 247.

Definition: ocellar triangle prominent; 1st and 2nd antennal segments cylindrical, approximately as wide as high, the 3rd continuous with style. Hind tibiae club-shaped. Wings elongate, characteristic in shape, extremely narrowed at base, without posterior angle and without alula; opaque, with hyaline areas. R3 absent. R2 and R4+R5 fused, forming R2+R4+5 which runs to the margin; R4+5 R5 and M1+2 fused for a long distance (longer than width of discal cell); M1 and M2 totally fused (2nd posterior cell absent); M4 and Cu1 fused for a long distance; M3 and M4 fuse before reaching the diagonal vein, shortening the 4th posterior and placing the discal and the 5th posterior cells in contact; Cu1 and 1A free (anal cell open). Abdomen narrow and elongate, completely different from any other in the family. Male genitalia not dissected. Ovipositor presumably type 2 (female unknown).

Distribution: Malay Peninsula, Australia (Queensland, New South Wales).

Catalog:

**pyralina* Edwards, 1932: 138, figs. 1, 1b, 1c, 2a. Type-locality: Malay Peninsula, Fraser's Hill, Pahang, 4000 ft. Distr.: Malay Peninsula.

**speiseri* Lichtwardt, 1909c: 648, fig. 6. Type-locality: Australia, Queensland, Cairns. Distr.: Australia (Queensland, New South Wales). Refs.: Edwards, 1932: 137, figs. 1a, 2b; Hardy, 1924: 459, figs. 5, 11; Mackerras, 1925: 557, fig. 16a-d; Paramonov, 1953: 247, figs. 3b, 4a.

10. Genus "incertae sedis"

Genus †**Prohirmoneura** Handlirsch

(Fig. 17)

†*Prohirmoneura* Handlirsch, 1908: 633. Type-species, †*jurassica* Handlirsch (mon.).

Definition: "Eine hochinteressante Form mit grossem Kopf, dessen mächtig entwickelte Facettenaugen auf der Stirne zusammenstossen, mit einem kurzen nach oben gerichteten Rüssel, etwas gedrungenem Körper und kräftigen Beinen. Die schlanken Flügel lassen das Geäder wohl nur undeutlich erkennen doch sieht man aus den wenigen Aderresten ganz deutlich, dass es jenem der rezenten Nemestriniden ähnlich war. Der Anallapen ist gross" (Handlirsch, 1908: 633).

Distribution: Jurassic of Eichstätt (Germany).

Comments: this fossil is very badly preserved and its position in the family is impossible to assess. It may be more probably a Hirmoneurinae, but there is no sound basis for this placement.

Catalog:

†*jurassica* Handlirsch, 1908: 633, pl. 51, figs. 11-12. Type-locality: Germany, Bavaria, Blumenberg, near Eichstätt (Jurassic).

PART III: EVOLUTION AND ZOOGEOGRAPHY

This section is divided in two parts. The first part deals with the evolution of the Nemestrinidae; it is an explanation of the phylogeny of the family. The second part contains some zoogeographical considerations, as well as some inferences about the ages of certain groups. Fig. 75 shows the phylogeny of the nemestrinids. Tables 4 through 7 present the main characters used in establishing the phylogeny, considering their primitive or specialized condition. These tables must be compared with Table 2, where each character is analysed. Maps 1 through 4 give the geographical distribution of Recent genera, excluding *Cyclopsidea,* restricted to Australia.

1. Evolution of the Nemestrinidae

The six subfamilies of Nemestrinidae (Table 4) may be divided in three groups:

Group 1: †Archinemestriinae
Group 2: Hirmoneurinae, Nemestrininae and Cyclopsideinae
Group 3: Trichopsideinae and Atriadopsinae

Group 1, consisting of the subfamily †Archinesmestriinae, is characterized by the poorly individualized radial phragma of the basial and backwardly bent extremities of R5, M1 and M2, reaching the hind margin. Groups 2 and 3 have the radial phragma distinctly individualized, forming a strong oblique vein, and R5, M1 and M2 are directed towards the apical margin. Group 2 possesses ovipositor type 1 and Group 3 has ovipositor type 2.

For the placement of the †Archinemestriinae in the system of the family the two characters mentioned above have especial importance, because they distinguish the subfamily from all others. The radial phragma of the basial is primitive, characterized only by a darkening of the wing membrane, without traces of venation. In the other subfamilies there is a strong and robust oblique vein (Rohdendorf, 1968: 189).

The bend of the branches of R and M is phylogenetically important because it relates the Nemestrinidae to other Brachycera (especially Tabanoidea) which possess these branches backwardly bent. The †Archinemestriinae have this same character, while the other subfamilies have the mentioned veins running to the apical margin. Among the †Archinemestriinae, †*Archinemestrius* may be considered more primitive than †*Protonemestrius,* because it has R5, M1 and M2 directed backwards, while the last genus has only M1 and M2 with this characteristic.

The †Archinemestriinae are also important in another connection. According to Rohdendorf (op. cit.), comparing the †Archinemestriinae with Jurassic Hirmoneurinae, it is easy to find the primary stage of the diagonal vein, presenting a pronouced zig-zag pattern in its posterior part. Among Recent species the zig-zag pattern of the final section of the diagonal vein is also found, so that this pattern is not to be considered a distinctive feature of the †Archinemestriinae, but it is useful in understanding the origin of the diagonal vein. Likewise, other Brachycera are important in the same way. An example is *Rhaphiomidas acton* (Apioceridae), figured and discussed by Cazier (1941: 595 ff., fig. 5).

The wing venation pattern of the subfamily is complete. R3 is absent, but the difficulty that exists in the interpretation of this vein has already been mentioned. Absence of R3 may be either explained by Hennig's (1954) idea that it might be a "reactivation" of the course of the primitive R3 or by assuming that the †Archinemestriinae really lost the vein, while other groups kept it. I prefer the last hypothesis. In other Nemestrinidae, as we shall see, R3 was paralelly lost in different lineages.

Table 4. Nemestrinid subfamilies

	22	33	14	7	2	9	8	11	19	4
†*Archinemestriinae*	-	-	?	-	-	?	?	?	?	?
Hirmoneurinae	+	+	-	-	-	-	-	-	-	-
Nemestrininae	+	+	-	-	-	-	-	-	-	-
Cyclopsideinae	+	+	-	+	+	+	-	-	-	-
Trichopsideinae	+	+	+	∓	-	-	-	-	-	-
Atriadopsinae	+	+	+	+	-	-	+	+	+	+

Table 5. Nemestrininae

	5	23	39	27	34	38	16	Shape of	
								wing	hypandrium
Trichophthalma	-	+	-	-	-	-	-	/	/
Prosoeca	+	+	-	-	-	-	-	-	-
Stenobasipteron	+	+	-	-	-	-	-	+	+
†*Palembolus*	+	+	-	-	-	-	-	/	/
Nemestrinus	+	-	∓	-	-	-	-	/	/
Stenopteromyia	+	+	-	+	+	+	-	/	/
Moegistorhynchus	+	-	+	-	-	-	-	/	/

Table 6. Trichopsideinae

	7	17	21	24	27	34	37	30
Neorhynchocephalus	-	+	∓	-	-	∓	-	-
Fallenia	-	-	-	+	-	-	+	+
Trichopsidea	+	-	+	∓	∓	+	∓	-

Table 7. Atriadopsinae

	40	23	20	24	6	34	31	10	28	26	36	35
Ceyloniola	+	∓	-	-	-	-	-	-	-	-	-	-
Atriadops	+	+	∓	+	+	-	-	-	-	-	-	-
Nycterimyia	-	+	∓	-	-	+	+	+	-	+	-	-
Nycterimorpha	-	+	+	+	-	+	+	+	+	-	+	+

Distribution of the main characters among the Nemestrinidae. The numbers correspond to those used in Table 2; - primitive, + specialized.

The Hirmoneurinae, Nemestrininae and Cyclopsideinae form Group 2 which has, as already seen, ovipositor type 1 as distinctive feature. The three subfamilies represent different evolutionary trends of the same basic stock. The Hirmoneurinae are the most primitive. An important evolutionary tendency is the reduction and loss of the hypandrium, leaving a free space between the gonopods. This tendency is well observed in the genus *Hirmoneura,* in which most species have lost the hypandrium, but this structure is present, although reduced, in *H. obscura.* Obviously, it is impossible to say anything about the genitalia of †*Eohirmoneura,* although it is considered a Hirmoneurinae.

The venation pattern of the Hirmoneurinae is complete, but there are some specializations that need to be mentioned. Several species of *Hirmoneura* have supernumerary cross-veins on the apical third of the wing, but this tendency is never so highly pronounced as in *Nemestrinus* and *Moegistorhynchus.* In the same genus there are species with and without R3. In †*Eohirmoneura* there is a supernumerary cross-vein beween M1 and M2, dividing the 2nd posterior cell, and R3 is a stump attached to R4. The proboscis, short in the †Archinemestriinae, more rarely equal to the length of the head (Rohdendorf, 1968: 181), in the Hirmoneurinae is extremely shortened and always inconspicuous (in †*Eohirmoneura* the region is not preserved). *Hirmoneura* has species with densely pilose eyes, others with bare or sparsely pilose eyes. In †*Eohirmoneura* there are no traces of pilosity. Considering all these facts one cannot say which genus is more primitive. Besides that, there is the possibility that *Hirmoneura* is a polyphyletic group. This would make it more difficult to understand the genus, but as this is at present only a suspicion, the best that can be done is to consider it as a single genus.

†*Prohirmoneura,* as mentioned in the systematic section, is a very badly preserved fossil and it is impossible to know its true relationships. Perhaps the best place for it is near the Hirmoneurinae.

The Nemestrininae come from the same stock as the previous subfamily but, although also very primitive, show many specializations (Table 5). The hypandrium is always developed, free, almost always elongate and longer than the gonopods. The proboscis is always well developed, long, sometimes longer than the whole insect. The genera fall into three groups:

(1) *Trichophthalma* group, with one genus.
(2) *Prosoeca* group, including *Stenobasipteron.*
(3) *Nemestrinus* group, including *Stenopteromyia, Moegistorhynchus* and, probably, †*Palembolus.*

The *Trichophthalma* group is characterized by the loss of R3 and preservation of the abundant pilosity of the eyes. In the *Prosoeca* group R3 is absent, but eyes are bare. Both genera of the group are morphologically very similar, but *Stenobasipteron* may be considered more specialized in the shape of the wings and of the hypandrium.

The three Recent genera placed in the *Nemestrinus* group are clearly related, although it is difficult to unite them by a clear-cut character. All have approximately the same habitus. All have bare eyes. *Nemestrinus* and *Moegistorhynchus* have R3, but *Stenopteromyia* has lost this vein. *Nemestrinus* has a strong tendency to the appearance of supernumerary cross-veins on the apical third of the wing (character 39 of Table 5); there is a perfect gradation from complete absence to a strong reticulation. A tendency to the projection of the face is also observed. *Stenopteromyia* and *Moegistorhynchus* are extremely similar to *Nemestrinus* and may be easily derived from the same stock. *Stenopteromyia* has retained the same habitus of *Nemestrinus,* including the same type of male genitalia (character 16), but greatly modified the wing venation: there is no reticulation (character 39), R3 is absent (character 23) and two important fusions have occurred: R2 and R4, closing the 2nd submarginal cell (character 27), and M1 and M2, closing the 2nd posterior cell (character 34). Also, the diagonal vein is incomplete (character 38). This pattern represents the most specialized wing venation among the Nemestrininae. *Moegistorhynchus* has retained the wing reticulation and specialized in the form of the hypandrium, which is characteristically sub-quadrate, approximately half as long as the gonopods, high in lateral view and with a ventral tuft of hairs.

It is not easy to ascertain the position of †*Palembolus.* On the basis of wing characters, it would be close to *Prosoeca,* but this is not very sound basis. In the absence of firmer criteria I prefer to keep it in a separate taxon.

Cyclopsidea has developed characters that give it an isolated position within the family. In habitus it is completely different from any other known nemestrinid, because of the peculiar shape of the abdomen, the great development of the head in relation to the thorax, the enlarged size of the post-scutellum and the characteristic shape of the wings. The hypandrium is fused with the gonopods (see comments in the systematic section) and the wing venation is reduced because of a fusion of R4 and R5, thus eliminating the 3rd submarginal cell (see comments in the systematic section). The proboscis is atrophied.

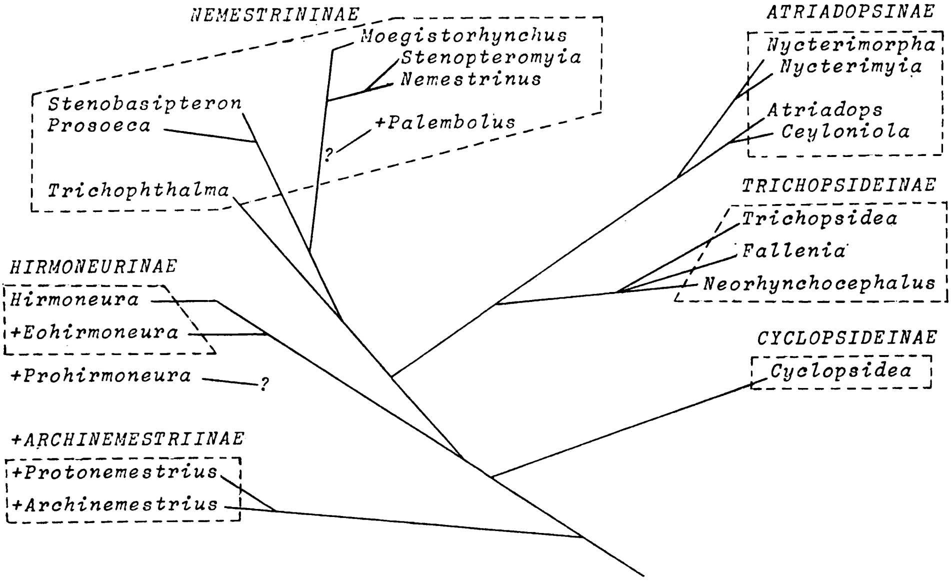


Fig. 75, Phylogeny of the Nemestrinidae.

The position of the subfamilies of Group 3, Trichopsideinae and Atriadopsinae, characterized by ovipositor type 2, is not easily decided. The most probable situation is that the group had its origin from the same stock that gave rise to the Nemestrininae. The Trichopsideinae, especially *Neorhynchocephalus* and *Fallenia,* are very similar to *Nemestrinus* in aspect and in all these genera the proboscis is well developed. I believe that these resemblances are more than superficial.

The three genera of Trichopsideinae are clearly related, but each has distinct morphological specializations (Table 6). *Neorhynchocephalus* and *Fallenia* have the proboscis well developed, whereas this organ is atrophied in *Trichopsidea* (character 7). All three genera have lost the hypandrium. In four species of *Neorhynchocephalus* the gonopods have fused, forming a single ventral piece, but in *Fallenia* and *Trichopsidea* they remained free (character 17). In *Fallenia* the costa encircles the whole wing; this is also the usual situation in *Neorhynchocephalus,* but there are some species which have only traces of the costa on the hind margin. In *Trichopsidea* the costa reaches the apical margin (character 21). *Neorhynchocephalus* is the most primitive in respect to its wing venation; the 3rd submarginal and the anal cells are open and there is a tendency to close the 2nd posterior cell (open in some species, closed in others). The diagonal vein is generally complete, but in some species it is incomplete. In *Trichopsidea* there is a tendency toward closure of the 2nd and 3rd submarginal and anal cells, and the 2nd posterior cell is closed. *Fallenia* has the most specialized venation in the subfamily, with the 3rd submarginal cell closed and strongly reduced, the 1st posterior and anal cells closed and the 2nd posterior cell open (rarely closed). As can be seen from the above presentation all characters are not equally distributed among the genera.

The Atriadopsinae (Table 7) constitute the most specialized subfamily. Besides the strong tendency toward reduction of wing venation, they show some peculiar modifications. The 3rd antennal segment has fused with the style, resulting in a single piece (character 8). The proportions of the segments of hind tarsus are modified: the 1st segment is clearly shorter than the last four together, the 5th being longer than each one of the three intermediary (character 11). The wings are opaque, frequently leathery in aspect, sometimes with hyaline areas (character 19). The face, below the antennae, has developed a strong transversal depression (character 4). The male genitalia has lost the hypandrium and gonopods have fused.

Two groups may be easily distinguished: 1) *Atriadops* group, including *Ceyloniola;* 2) *Nycterimyia* group, including *Nycterimorpha.*

Ceyloniola and *Atriadops* greatly developed the axillary cell (Table 7, character 40). *Ceyloniola* unlike the other genera of the subfamily, has a primitive wing venation, without reduction: all veins are present and no cells are closed. R3 exists as a stump attached to R4 (character 23). *Atriadops* has lost the ocelli (character 6), R3 has been eliminated, the 3rd submarginal cell is absent (character 24) and there is a tendency towards the atrophy of M2 (in some species). The specialization of the ventral structure of the male genitalia, formed by the fusion of the gonopods, has gone very far, including a fusion of part of the aedeagus.

Nycterimyia and *Nycterimorpha* have the wings emarginate at the hind margin and with distinct hyaline areas. The alula is reduced in the first genus and absent in the second (character 20). Wing venation is highly specialized. R3 is absent (character 23), R4+5 and M1+2 are fused for a long distance (character 31) and the 2nd posterior cell has been eliminated (character 34). In *Nycterimyia* the femora are swollen (character 10), the 3rd submarginal cell remained open (character 24) and R2 is present in a very peculiar way: it fuses with R4 for a short distance, separates from it and fuses with R1, resembling a cross-vein (character 26). In *Nycterimorpha* the hind tibiae are club-shaped (character 10), the alula has been eliminated (character 20) and the wings are even more emarginate at the hind margin. R2 has fused with R4+R5, so that R2+R4+R5 reaches the apical margin (character 28). M4 and Cu1 are united for a long distance (character 36) and M3 and M4 are fused before entering the diagonal vein, shortening the 4th posterior cell and putting the discal and the 5th posterior cells in contact (character 35). Another interesting and unique specialization is the shape of the abdomen, which is narrow and elongate, completely different from any other in the family.

2. Zoogeography of the Nemestrinidae

On account of the considerable geological age and poor fossil record of the Nemestrinidae, it is practically impossible to choose one among the alternative hypotheses that can be proposed to explain their present distribution. Notwithstanding, the geographical problems presented by the Nemestrinidae are extremely interesting and it is worthwhile to examine them in some detail. First, we will see what conclusions are permitted by the paleontological evidence. Then follows a brief summary of the basic ideas concerning continental drift, because these ideas will be referred to several times in the following discussion. Finally, I will try to interpret the distribution of the various groups of nemestrinids.

The Jurassic fauna of Karatau, as we have already seen, consisted of at least two subfamilies, three genera and six species. These data yield three important conclusions:

1) The family Nemestrinidae was already in existence in the Jurassic. Just when the family originated is impossible to say, but Jurassic is a long period and it is not necessary to postulate an origin before that period.

2) In the Jurassic the family was already diversified into two distinct lineages, according to the patterns of wing venation. These are considered subfamilies.

3) The family must have been very abundant in the area where it existed. Six species in one locality represent a relatively large number.

The Oligocene fauna of Florissant presents a similar picture. Five species are known, in three genera and three subfamilies. Today, in North America, only two subfamilies, three genera and six species occur. The following conclusions are thus possible:

1) In the Oligocene of Florissant the Nemestrinidae were more abundant than now, in the same area.

2) They were possibly also more varied as to subfamilies. I say possibly because the placement of †*Palembolus* among the Nemestrininae is not assured.

The above conclusions allow us to make the following statements:

1) The subfamilies †Archinemestriinae (genera †*Archinemestrius* and †*Protonemestrius*) and Hirmoneurinae (genus †*Eohirmoneura*) have been in existence at least since the Jurassic of Karatau.

2) The subfamilies Hirmoneurinae (genus *Hirmoneura*), Trichopsideinae (genus *Neorhynchocephalus*) and, possibly, Nemestrininae (genus †*Palembolus*) were in existence by the times of the Oligocene of Florissant.

Let us turn our attention now to a consideration of the fascinating problem of continental drift. Until some time ago, zoogeographers looked for interpretation beginning with the supposition that the present day continents have been in relatively stable position for a very long time. Their explanations did not take into account the movements of the continents or, at most, accepted only a very limited displacement (Darlington, 1965). The evidence provided by geologists, however, particularly during the last ten years, have shown that continental drift is perfectly acceptable on a sound basis provided by the modern theory of plate tectonics. See, for instance, the papers of Dietz & Holden (1970), Dewey & Horsfield (1970), McKenzie (1970), Maxwell at al. (1970), Helwig (1971) and Jardine & McKenzie (1972).

Today it is accepted that a single original continent, the Pangaea, fragmented during the Mesozoic and that the resulting fragments moved in different directions. The present forms and positions of the continents are the result of this process. By the end of the Paleozoic only the Pangaea existed (fig. 76). By the end of the Triassic Pangaea underwent the initial steps of its fragmentation. Two major parts were formed: a) Laurasia-West Gondwana, including the Americas, Africas and Eurasia (except India); b) East Gondwana, including Antarctica, India, Australia, New Guinea and New Zealand. At about the same time the separation of India from East Gondwana began, and North America lost its connections with South America and Africa, remaining united to Eurasia. Approximately between Upper Jurassic and Lower Cretaceous South America detached from Africa. During the Cretaceous Madagascar detached from the African continent and by the end of that period Australia began to move away from Antarctica. During the Tertiary, North America (including

Greenland) separated from Eurasia, uniting posteriorly with South America. India united with Eurasia and Australia got closer to southeastern Asia. During the whole process of fragmentation, Africa kept a more or less continuous connection with Eurasia: Gondwana as a whole never existed apart from Laurasia. Fig. 76 shows the main steps of the fragmentation of Pangaea. A thorough discussion may be found in Dietz & Holden (1970).

As far as these ideas are based on good geophysical data, zoologists must have them in mind as they try to explain the distributions of the groups in which they are interested (Jardine & McKenzie, 1972). It is not a matter of assuming that animal distribution is more permanent than land distribution or that ancient geography is the only important factor influencing animal distribution, or even that land animals never or rarely cross even narrow water barriers between continents (Darlington, 1965: 184). Instead, it is a matter of conscientiously taking into account an important scientific hypothesis, which has, time and again, received the support of evidences from many sources. Recently, this line of work was followed, for instance, by Myers (1966) in interpreting the origin of the fish fauna of Central America; by Papavero (1971) in the interpretation of the history of the Megapodini (Diptera, Asilidae); by Lynch (1971) (Anura, Leptodactylidae); by Leme (1971) (Gastropoda, Pulmonata, Strophocheiloidea); by Jardine & McKenzie (1972) (Marsupials); by Fooden (1972), studying the autochtonous faunas of land mammals of Australia, South America and Madagascar. Without judging individually each one of these papers, I believe that the ways chose by their

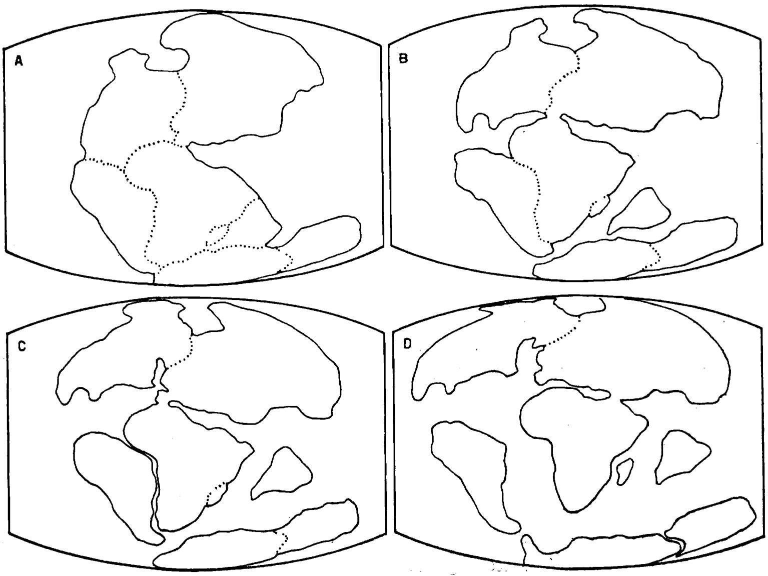


Fig. 76, Breakup of Pangaea. A, End of Permian; B, End of Triassic; C, End of Jurassic; D, End of Cretaceous. (Adapted from Dietz & Holden 1970: figs. 2-5).

authors are rich in possibilities. The last mentioned paper (Fooden, 1972) deserves some comments in view of the importance of the conclusions it contains. Fooden studied the autochtonous faunas of land mammals of Australia-New Guinea (formed by Prototheria and Metatheria), South America (formed by Metatheria and Eutheria), and Madagascar (formed by Eutheria), relating them with the most recent ideas on continental drift. As a result of this comparison he proposed the hypothesis that the three faunas represent successive samples of an evolving world fauna, isolated at the moment in which these areas separated from the rest of the world as a result of the progressive fragmentation of Pangaea. Thus, the Australian fauna would have been isolated since the Upper Jurassic-Lower Cretaceous, the South America fauna since the Middle Cretaceous-Upper Cretaceous, and the Madagascan fauna since the Paleocene-Eocene. The basic point of this hypothesis is that a relationship exists between relict animal groups in different evolutionary stages and the time the areas they inhabit were isolated. This scheme may be usefully applied to other groups, besides mammals.

Now I shall try to explain the history of the Nemestrinidae. First, as to the subfamily †Archinemestriinae, it is only possible to say that they existed in the Palearctic Region (then Laurasia) in the Jurassic. When did they originate? Where? How long lasted their existence? All these questions must remain without answer, at present.

The three subfamilies of Group 2, Hirmoneurinae, Nemestrininae and Cyclopsideinae, phylogenetically, must be placed in this order, but as to their time of origin, perhaps they may be considered simultaneous, with origin in different areas, from a widely distributed ancestral stock. The Hirmoneurinae have a northern origin. They were already in the Paleartic Region (Laurasia) in the Jurassic. The Nemestrininae and Cyclopsideinae may be considered Gondwanian. In the history of both groups Africa must have had a very important role. I think the basic nemestrinine stock was African, as we shall see later. The original stock of the Cyclopsideinae must have been in Africa, reaching Australia through Antarctica or India. During the Jurassic, the proximity of the continents permitted this passage; at the end of the period South Africa was still very near Antarctica and during this period India was also very near Africa, Antarctica and Australia (fig. 76). This would explain the position of *Cyclopsidea*, a Recent genus that, phylogenetically and geographically, is a completely isolated group. The isolation of the Cyclopsideinae can, thus, date from the Upper Jurassic-Lower Cretaceous.

The Mesozoic Hirmoneurinae are known only by the genus †*Eohirmoneura*. The Recent genus *Hirmoneura* was already in existence in the Oligocene of Colorado and may represent a presently restricted remainder of a once abundant lineage. This does not mean that *Hirmoneura* is a badly succeeded group, as it is well shown by its wide distribution, its high number of species (46) and, judging from the latitude and longitude of its distribution, its ability to occupy different environments. The disjunct distribution (map 1) suggests a wider distribution in the past and, perhaps, a greater number of species. The explanation of the present distribution presents some problems. The genus occupies a large portion of the Mediterranean area, extending throughout the whole Oriental Region, and penetrating into the south of the Palearctic Region. In the New World it occurs in southern United States, Mexico, Central America, western South America, including Chile and Argentina. The internal structure of the genus, as explained in the systematic section, is poorly worked out and it is possible that it is poliphyletic, but probable component groups are not geographically segregated, so that if these groups are to be trusted, the history of *Hirmoneura* will be much more complex than it seems at first sight. There is no doubt as to the old age of the genus and it is difficult to say if it had a New World or an Old World origin. In view of our present knowledge, it is not wise to say anything more about *Hirmoneura*.

For the Nemestrininae (map 2) it is better to postulate a great expansion in the Upper Jurassic, with differentiation in three main groups. The *Trichophthalma* group differentiated in South America, the *Prosoeca* group in Africa, giving rise to *Prosoeca* and *Stenobasipteron*, and the *Nemestrinus* group in the Palearctic Region. This last group gave *Nemestrinus* and *Stenopteromyia* in the Palearctic Region, with a branch that reached Africa, giving rise to *Moegistorhynchus*. The phylogenetic position of †*Palembolus* is doubtful, but it seems better from the zoogeographical standpoint to put it in the *Nemestrinus* group; this procedure is permitted by our ignorance of what the genus really was rather than assured by positive knowledge.

Trichophthalma deserves a more detailed discussion. It is the only case in the family of a genus occurring in Australia and South America. Hennig (1960) called groups with this type of distribution AS groups. These cases have always caused problems to zoogeographers. Two basic opinions have been held. The first postulates the origin of the AS groups in the northern hemisphere, with migration to the south and extinction in the north. The alternative opinion which, as reminded by Vockeroth (1969), has been the one preferred by dipterists, condiders Antarctica as a dispersion route or an evolutionary center.

Hennig (1960), studying the AS groups among Diptera, concluded that there were no groups sufficiently well known to provide definite evidence for the second hypothesis just mentioned, although he believed this alternative to be possible. Based on the supposition that each group of animals occurring in southern continents must have a "sister group" (the phylogenetically most closely related group) in the north, Hennig tried to estimate the minimum age of an AS group and, very carefully, proposed an origin between Oligocene and Miocene.

Darlington (1965) also studied the subject extensively, basing his work especially on *Nothofagus* and some insect groups. The basic opinion held by Darlington is the northern origin of AS groups followed by dispersion to Australia and South America and subsequent extinction in northern continents. However, he does admit some exceptions. Based on the mentioned groups, he concludes that there is evidence that the Antarctic continent served as a migration route for a few groups of plants and invertebrates, between Australia and New Zealand on the one hand, and South America on the other. However, in the few cases in which he leaves room for a southern migration, he does not believe it to have occurred by land connection, but by the crossing of water gaps. According to his estimates, based on paleontological data, the possibility of such dispersion lasted from the end of the Cretaceous until, probably, the Miocene.

In his revision of the genera of Syrphini (Diptera, Syrphidae), Vockeroth (1969) considering the almost complete absence of higher Diptera (Cyclorrhapha) among the AS groups, proposed a well-balanced hypothesis to explain this fact, concluding that transantarctic dispersions ended, at most, at the beginning of Tertiary, well before the time proposed by Darlington and Hennig. Vockeroth starts from the following observations:

a) There are evidences that at least the margins of Antarctica served as a migration route between Australia and or New Zealand and South America, during Cretaceous times and, probably, during the Lower Tertiary.

b) Many groups of Diptera suggest AS relations.

c) Those groups are almost exclusively Nematocera and Brachycera (Orthorrhapha).

d) The generic pattern of groups such as the Syrphini suggests that one or a few ancestor species entered South America at the very beginning of the Tertiary, finding an area where the group was absent before.

Vockeroth thinks that the absence of AS groups among the Cyclorrhapha is not because they might not have been in existence during the time of faunistic interchange between South America and Australia/New Zealand, but because, although abundant and highly diversified in North America and most of the Old World, they where prevented from entering South America and Australia by the isolation of these continents until the disappearance of conditions that made transantarctic dispersion possible. Vockeroth believes that his hypothesis is supported by being in accordance with the possible evolutionary rates of the groups involved. To him, instead of many pairs of species in South America and Australia/New Zealand remaining almost unchanged, while such families as Syrphidae, Muscidae and Tachinidae developed and produced hundreds of genera and thousands of species, it is probable that these same species groups have remained unchanged only while the genus *Allograpta* (Syrphidae) and a species group of *Fannia* (Muscidae) entered South America and radiated. It is necessary to point out that Vockeroth's hypothesis, although having in its favor some facts and being extremely stimulating, depends on a high degree on his assumption that the ancestor of South American Syrphini entered the continent at the beginning of the Tertiary.

My own line of thought is different. The most recent researches on continental drift, already mentioned, show clearly that Australia and Antarctica were united until the Tertiary. According to Dietz & Holden (1970) the separation began by the end of the Cretaceous (fig. 76). The reconstruction of Jardine & McKenzie (1972: fig. 3) presented Australia and Antarctica still united 45 million years ago, during the Eocene. During the Cretaceous and still into the Tertiary, South America was much closer to Antarctica than it is now. My explanation of the history of *Trichophthalma,* then, is as follows: a group of Gondwanian Nemestrininae differentiated in South America, moved through Antarctica and reached Australia. The beginning of the separation of Africa and South America occurred, according to Dietz & Holden (1970), between the ends of Jurassic and the beginnings of Cretaceous times (fig. 76). Maxwell et al. (1970) estimated this separation as occurring at beginning of the Cretaceous. Therefore, during the Cretaceous, the differentiation of the South American stock occurred. The age of the genus *Trichophthalma,* however, is not necessarily so old, since transantarctic connections lasted for a great part of the Tertiary and there was sufficient time, during this period, for the appearance and dispersion of the genus.

We now come to Group 3, which includes the two most highly evolved subfamilies, Trichopsideinae and Atriadopsinae. The distribution of the Recent genera of both subfamilies shows that the genera may be considered Tertiary. The morphological specialization of both subfamilies in relation to the previous ones, plus the fact that both show signs of being in expansion, indicates that they may be considered posterior to the subfamilies of Group 2. They have widely distributed genera, while most of the genera of Group 2 are geographically segregated. I think it is reasonable to suppose that both subfamilies are Cretaceous in origin; the original stock of Group 3 must be even older. The most probable origin for the Trichopsideinae is Palearctic, and for the Atriadopsinae, Oriental.

The three trichopsideine genera occur in the Palearctic Region. *Fallenia* (map 2) is restricted to that region, but *Neorhynchocephalus* and *Trichopsidea* (map 3) occur also in other areas. *Neorhynchocephalus* was present in North America in the Oligocene, with at least three species. From there, undoubtedly, it reached South America. There is one species in Europe, from the Mediterranean to southwestern Siberia. This disjunct distribution may indicate a wide expansion in the Tertiary, with posterior retraction; this is consistent with the existence of the genus in the Oligocene. Where to locate the place of origin, whether in North America or Eurasia, is difficult to decide. With *Trichopsidea* something very similar must have occurred, with the difference that this genus reached Africa and Australia, but not the Neotropical Region. A Palearctic origin for *Trichopsidea,* with expansion at the end of the Tertiary, explains the present distribution. The strong disjunction of the Recent species did not result in pronounced differences; the species are extremely similar. This picture is in contrast with the disjunction at the generic level in the Nemestrininae. It must be remembered that the differentiation is not a perfect index of the time of isolation, but presently it is the only available resource.

The Atriadopsinae constitute the most specialized subfamily and are now restricted to the Ethiopian, Australian and Oriental regions, with penetration in the south of the Palearctic Region and one species in Brazil (map 4). This pattern indicates a group in expansion. I think the subfamily to have originated in the Oriental Region. *Ceyloniola* is restricted to Ceylon. *Nycterimyia* may have reached Africa from the Oriental Region and Madagascar from Africa. In addition, the genus extends from southeastern Asia to Australia. With *Nycterimorpha* something similar occurs but it did not reach Africa.

Atriadops has the widest distribution in the subfamily. Its presence in the Oriental Region, Africa and Australia may be explained by expansion from the first, but the fact that one species lives in Brazil needs some comments. In cases with this type of distribution, we usually think of something related to the drift of the two continents. As we have seen, the separation started by the beginning of the Cretaceous. Since then, the distance between Africa and South America continued to grow. In the Tertiary, both were much closer to each other than now. The Brazilian species, *A. macula,* and the African, *A. vespertilio,* are extremely similar. Besides *Atriadops,* four more genera of Nemestrinidae occur in Africa, none of which is represented in South America. If past faunistic exchanges had been common, traces of African elements in Brazil would be expected, although negative evidence is not conclusive proof. It is interesting to point out that, so far as is known, *Atriadops* is the only African genus represented in the western half of the African continent; all others are southern and eastern. From the above mentioned remarks, I conclude that the presence of *Atriadops* in Brazil must be explained by accidental crossing of the ocean during the Tertiary, when distance was much shorter than now.

Summing up my zoogeographical conclusions, the following points can be made:

1) The †Archinemestriinae were in existence in the Jurassic in the Palearctic Region (then Laurasia). For how long, we do not know.

2) The subfamilies of Group 2, Hirmoneurinae, Nemestrininae and Cyclopsideinae, represent different lines of the same basic stock that differentiated in different areas. The Hirmoneurinae differentiated in Laurasia, the Nemestrininae in Africa and South America and the Cyclopsideinae in Australia. The three groups may have arisen simultaneously in the Jurassic.

3) The Hirmoneurinae have existed at least since the Jurassic. †*Eohirmoneura* is known only from the Jurassic. *Hirmoneura* was in

existence in the Oligocene, in North America, and today it has a wide and disjunct distribution, indicating antiquity. The structure of the genus, however, is poorly known and does not allow detailed discussion.

4) The Nemestrininae are a stock which may have expanded widely in the Upper Jurassic, giving rise to three main groups. *Trichophthalma* originated in South America, from where it reached Australia, through Antarctica. *Prosoeca* and *Stenobasipteron* are African. A third group gave rise to *Nemestrinus* and *Stenopteromyia* in the Palearctic Region, with a branch that, later, reached Africa, giving rise to *Moegistorhynchus*. †*Palembolus,* of North America, is provisionally related to this third group.

5) The subfamilies of Group 3, Trichopsideinae and Atriadopsinae, are later than those of Group 2. The origin of Trichopsideinae is suggested to be Palearctic and that of Atriadopsinae, Oriental.

6) *Neorhynchocephalus* occurs in America and Europe, and it is difficult to say where it originated. *Fallenia* is exclusively Paleartic and *Trichopsidea* is Palearctic in origin, having reached North America, Africa and Australia.

7) The genera of Atriadopsinae may be considered Tertiary, with Oriental origin. *Ceyloniola* became restricted to Ceylon. *Atriadops* reached Australia and Africa, passing from this latter continent to Brazil in the Tertiary. *Nycterimyia* and *Nycterimorpha* occur from southeastern Asia to Australia, the first genus also reaching Africa and Madagascar.

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