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STUDIES OF ASILIDAE (DIPTERA) SYSTEMATICS AND EVOLUTION. I. A PRELIMINARY CLASSIFICATION IN SUBFAMILIES

N. PAPAVERO

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CONTENTS

ABSTRACT

A preliminary classification of the Asilidae in 8 subfamilies is proposed: Apocleinae (55 genera), Asilinae (62 genera), Dasypogoninae (70 genera), Laphriinae (69 genera), Laphystiinae (23 genera), Ommatiinae (7 genera), Stenopogoninae (102 genera), and Trigonomiminae (12 genera). A brief diagnosis of the subfamilies, a list of their respective genera, plus their general geographic distribution and hypothetical phylogeny, are given.

1. INTRODUCTION

The family Asilidae contains at present 400 genera considered as valid; some of these should be further divided, some will prove to be synonyms, and many new ones are to be described. Subgenera pro-

Museu de Zoologia, Universidade de São Paulo.

posed up to now will prove in the future, after careful revisions, to be either valid genera or synonyms.

Arrangement of these genera in plausible and natural groupings is still at an initial phase of development, as very rarely evolutionary or phylogenetic factors were taken in consideration by authors working with suprageneric classifications. Added to that, our knowledge of the biology and ecology of this family is remarkably poor. Fossils are fragmentary, few, and in general misidentified and absolutely useless.

In fact, the majority of studies relating to Asilidae classification refer solely to their alpha taxonomy. The high number of genera and species composing this family really demands a previous work of surveying and cataloguing of faunas. Several areas in the world remain to be explored and their faunas studied. The picture is still complicated by the fact that evolution of these flies seems to be processed by different arrangements and combinations of a relatively limited number of characters, the general pattern formed in the family resulting in a series of mosaics. This renders recognition of the several taxonomic categories very difficult, and in a special way the recognition of their phylogenetic relationships.

For these same reasons, a more critical study is imposed, taking in consideration the probable phylogeny, the zoogeography of the taxa, and the morphoclimatic aspects of the areas occupied.

It is possible, even with the present (incomplete) resources of data and collections, to procede with a cataloguing of faunas together with their interpretation, not only to establish the several taxa with a reasonably sounder basis, but also, and especially, to suggest problems and possible tentatives of solution.

I'm proposing here a new arrangement of the world genera in 8 subfamilies. This arrangement is still tentative. The soundness of this classification will be tested in the forthcoming papers of this series, when each subfamily (or tribe) will be treated in more depth, and their systematics and evolution examined in further detail.

2. MATERIALS AND METHODS

I have studied the following collections of robberflies:

AMNH American Museum of Natural History, New York (materials studied by Bromley [part], Curran, and Williston [part])

BMNH British Museum (Natural History), London (materials studied by Oldroyd, Osten Sacken, Ricardo, Walker, and Williston; an extremely good collection for genera)

CAS California Academy of Sciences, San Francisco (North American collection; types of Martin and Wilcox)

CNC Canadian National Collection, Canada Department of Agriculture, Central Experimental Farm, Ottawa (North American collection, plus good material from South America collected by L. Peña)

CSIRO	Australian National Insect Collection, Commonwealth Scientific and Industrial Research Organization, Division of Entomology, Canberra (Australian genera, communicated by Dr. Donald H. Colless)
EF	Collection Eric Fisher, Long Beach (very good representation of Mexican and United States fauna)
FMNH	Field Museum of Natural History, Chicago
FRAN	Natur-Museum und Forschungs-Institut (Senckenberg), Frankfurt a. M. (types of Wiedemann [part] and Jaennicke)
JW	Collection Joseph Wilcox, Anaheim (extremely good for North America)
LACM	Los Angeles County Museum of Natural History, Los Angeles
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge (material and types studied by Banks, Loew, and Osten Sacken)
MNHN	Muséum National d'Histoire Naturelle, Paris (good general collection, plus material and types studied by Bigot, Macquart, and Tsacas)
MIL	Museo Civico di Storia Naturale, Milano (collection Bezzi)
MZUSP	Museu de Zoologia, Universidade de São Paulo (good general collection, excellent for Neotropics, type material of several authors, especially Carrera)
NMW	Naturhistorisches Museum, Wien (material and types studied by Hermann [part], Schiner, and Wiedemann [part])
OXF	Hope Department of Entomology, Oxford University, Oxford (types of Bigot and Hobby)
RNH	Rijksmuseum van Natuurlijke Historie, Leiden (Surinam material, plus general collection; a few types of Wiedemann)
SMN	Staatliches Museum für Naturkunde, Stuttgart-Ludwigsburg (collections of Engel and Lindner)
TORO	Istituto e Museo di Zoologia Sistematica, Università di Torino (collections of Bellardi, Giglio-Tos, and Rondani [small part of Neotropical types])
UCB	University of California, Berkeley
USNM	United States National Museum, Washington, D. C. (very good general collection, including Bromley's collection and types)
ZMA	Zoölogisch Museum, Amsterdam (collections of Meijere and Wulp)
ZSBS	Zoologische Sammlung des Bayerischen Staates, München (excellent collections, including collections of Engel and Hermann, the latter excellent for generic representation)

Specimens were compared with existing descriptions and keys; notes on details were taken, and tentative keys prepared. Drawings of male genitalia and other morphological details will be published in the forthcoming papers of this series.

As for the general methodology, I can here quote Darlington (1971 : 144):

"The methods I use are essentially subjective: comparison of specimens, detection of similarities and differences, and reaching of conclusions based primarily on personal judgement and experience rather than on statistical analyses or other objective tests. I have tried to make my taxonomy conform to phylogeny and reflect the existence of variability as well as the interrelationships of populations in nature. (...) Phylogenies (...) must be deduced and taxonomists are sure to make mistakes about them. Nevertheless, the results of the kind of work I am describing have a gross phylogenetic reality perhaps best demonstrated by its utility: zoogeography based on this kind of taxonomy makes sense, and it would not be expected to make sense if the phylogenetic basis of the taxonomic work were seriously in error."

The following abbreviations were used in the text and in the histograms:

A	Australasian (region)
Ap	Apocleinae
As	Asilinae
Ch	Chilean (subregion)
D	Dasypogoninae
E	Ethiopian (region)
Li	Laphriinae
Ly	Laphystiinae
Nea	Nearctic (region; including Sonoran subregion)
Neo	Neotropical (region; mainly the Guiano-Brazilian subregion)
O	Oriental (region)
Om	Ommatiinae
P	Palearctic (region)
S	Stenopogoninae
T	Trigonomiminae

Because of its present isolation, and of its great number of endemic genera, the Chilean subregion was recognized here as a distinct unit.

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4. A BRIEF HISTORY OF ASILIDAE CLASSIFICATION

4.1. The 19th century

Family status is credited to Leach (1819) (cf. Hull, 1962 : 3).

Macquart (1838 : 14 [1839 : 130]) was the first to subdivide the family, according to the following key:

1. Antennes à style court, tantôt pointu, tantôt obtus, tantôt oblitéré ou nul 2
   Antennes à style allongé, ordinairement sétiforme. Ailes à cellule marginale fermée .... Asilites

2. Ailes à cellule marginale ouverte .... Dasypogonites
   Ailes à cellule marginale fermée. Style nul .... Laphrites

He also called attention to the fact that the then very elastic genus *Dasypogon* Meigen could be separated in species with or without an apical spur on the front tibiae.

Loew (1847-1851) erected a great number of genera, and for the group of *Dasypogon* without tibial spur erected *Stenopogon* and many other "subgenera". Loew has been one of the best authors, having described 69 of the present 400 genera (or almost 20%).

In his "classification générale et synoptique de l'ordre des insectes diptères" (1857), to facilitate the identification of the several genera proposed until then, Bigot divided the "Tribu des Asiliques" in five "curies": Mydasidae, Apioceridae, Laphridae, Asilidae, and Dasypogonidae. The last three groups, now considered as belonging to the same family, were separated as follows:

1. Ailes; cellule marginale fermée près du bord postérieur 2
   Ailes; cellule marginale ouverte au bord postérieur; antennes; troisième article variable .... Dasypogonidae

2. Antennes; troisième article simple; pas de style .... Laphridae
   Antennes; troisième article, tantôt subdivisé vers sons extrémité, tantôt muni d'un style plus ou moins sétiforme ...... Asilidae

Bigot's scheme represented only a minor modification of the one proposed by Macquart, and was equally artificial.

A new tentative was made by Schiner (1862) in his "Fauna Austriaca". There (p. xxxviii) he published a key to the families of Diptera, and in a footnote, in addition to the previously recognized asilid groups, he erected the "Leptogastrinen", which also appeared in his key to the genera of Asilidae (l. cit., p. liv). However, the same author, in his revision of Wiedemann's Asilidae (1866) went back to the original three divisions of the family, synonymizing the "Leptogastrinen" with the "Dasypogoninen".

The division of the family in three groups was maintained by almost all the 19th century authors.

4.2. Williston's classification

In 1908 appeared the "Manual of North American Diptera", by Williston. There the distinguished dipterist gave preference to the palpi to classify the Asilidae. His key was the following:

A. Palpi one-jointed; antennae with a slender terminal arista.
   - B. Marginal cell open; very slender species .... Leptogastrinae
   - BB. Marginal cell closed; less slender or robust species .... Asilinae

AA. Palpi two-jointed; antennae with or without a thickened terminal style; very rarely with a terminal arista.
   - C. Marginal cell open, or rarely closed at extreme tip .... Dasypogoninae
   - CC. Marginal cell closed .... Laphrinae.

Williston's choice of the palpus was an extremely unhappy one, as it is extremely plastic and underwent reduction in several groups, independently. His key also had the shortcoming of being made solely for the North American genera. Many other genera would never fit his key.

4.3. Hermann's classification

Hermann (1912, 1920) tried again to divide the Asilidae. His scheme of classification may be summarized as follows:

1. Leptogastrinae
2. Asilinae
3. Laphriinae
   3.1. Atomosiinae
   3.2. Laphriinae s. s.
4. Dasypogoninae
   4.1. Prytaninae
   4.2. Erecmoneminae
   4.3. Acanthocneminae

Hermann called attention to the fact that Osten Sacken (1884) had discovered that the Laphriinae could be separated from all other Asilidae by the presence of strong bristles on the postero-superior angle of the mesopleura. He was the first to segregate the Dasypogoninae with an apical spur on the front tibiae (Acanthocneminae) from the remaining genera, and to have recognized the Prytaninae (the present Laphystiinae). He introduced a new character in classification: the number of abdominal tergites in the male and female.

His key for subfamilies (1920) ran as follows:

1. Taster 1gliedrig; 3. Fühlerglied fast ausnahmslos mit einer mehr oder minder langen, gegliederten "Endborsten" versehen. Mesopleuralborsten stets fehlend. Segmentzahl der ♂ Abdomen nie unter 8 2

Taster 2gliedrig; 3. Fühlerglied mit oder ohne "Endgriffel", nur ausnahmsweise sich in eine lange, ungegliederte Endborste verjüngend, Mesopleuralborsten vorhanden oder fehlend. Segmentzahl der ♂ Abdomen 8 oder weniger 3

2. Randzelle stets offen. Segmentzahl des Abdomens in beiden Geschlechtern 8; ♀ Genitale, und dessen Aufbau das Sternit des 8. Segments kaum beteiligt ist, stets zum Teil unter dem 8. Tergite verborgen, ohne Kranz von Chitinzähnen und ohne jede auffalende Bedornung. Füsse stets ohne Pulvillen. Auffalend schlanke, wenig behaarte und beborstete Formen .... Leptogastrinae

Randzelle stets geschlossen und gestielt. Segmentzahl des Abdomens in beiden Geschlechtern 8; beim ♀ erweist sich mindestens das 8. Segment (häufig schon das 6. und 7.) durch Skulptur, Behaarung und Färbung als Genitalsegment, Legeröhre stets freistehend, bei einigen Gattungen bedornt. Füsse stets mit Pulvillen. Robustere, häufig dichter behaarte, stets reichlich beborstete Formen .... Asilinae

3. Randzelle durchaus geschlossen und gestielt. Fühler mit oder ohne "Endgriffel"; Spitze des 3. Fühlergliedes bei einigen Formen in eine lange, ungegliederte, eventuell gefiederte "Endborste" verjüngt. Mesopleuralborsten immer vorhanden. Segmentzahl der ♂ 7 (ausnahmsweise nur 6); beim ♀ ist das 8. Segment vor allem mit seinem Sternit beim Aufbau des Genitales stets beteiligt, Legeröhre ohne auffalende Bedornung oder Chitinzähne. Füsse immer mit Pulvillen, Schienenspitze der Vorderbeine stets ohne nagelartigen Enddorn .... Laphrinae

Randzelle vorwiegend offen, nur zuweilen am Flügelrande selbst geschlossen oder gestielt. 3. Fühlerglied mit oder ohne "Endgriffel", ausnahmsweise in eine lange ungegliederte "Endborste" verjüngt. Mesopleuralborsten fehlend. Segmentzahl des Abdomens beim ♂ 8 oder 7 (zuweilen auf 6 reduziert); Segmentzahl der ♀ durchaus 8, Sternit des 8. Segments fast ausnahmslos bei der Bildung des Genitales beteiligt; die meist kurze Legeröhre ist häufig von einem Halbkreis derber Chitinzähne umgeben. Füsse mit oder ohne Pulvillen; Schienenspitze der Vorderbeine mit oder ohne derben nagelartigen Enddorn .. .. Dasypogoninae

The Dasypogoninae were subdivided in three groups:

A. Segmentzahl des Abdomens ♂ 7, ♀ 8

1. Vorderschienen an der Spitze mit einem nagelartigen gekrümmten Fortsatz .... Untergruppe Acanthocneminae

2. Vorderschienen an der Spitze ohne einen nagelartigen gekrümmten Fortsatz .... Untergruppe Erecmoneminae

B. Segmentzahl der ♂ Abdomen nur 6. ..... Untergruppe Prytaninae

Finally, the Laphrinae were separated in two subgroups:

1. Kleine, nur selten mittelgrosse, meist dunkel oder auch metallisch gefärbte, kahle Arten. 3. Fühlerglied stets mit einem Zahngriffel versehen, d. h. einer sift- oder dornartigen Exkreszenz, die sich, meist an der Kante einer ± ausgesprochenen Einkerbung auf der distalen Hälfte des Oberrandes befindet. Seitenhöcker des Metanotums nie kahl, stets entweder behaart oder noch häufiger mit groben und kurzen dorn- oder stiftchen-artigen Borsten besetzt. Die die Discoidal- und die 4. Hinterrandzelle distal abschliessenden Queradern verlaufen nur ausnahmsweise nicht in der gleichen Richtung, meist sogar in der gleichen

Linie. Die relativ kleinen Genitalien sind mit ganz geringen Ausnahmen ventral verlagert und daher von oben nicht sichtbar .... Untergruppe Atomosinae

Mittelgrosse bis sehr grosse, meist lebhafter gefärbte und häufig ausgiebig behaarte Arten. 3. Fühlerglied nie mit einem sog. "Zahngriffel" versehen. Seitenhöcker des Metanotums nackt, nur bei einigen wenigen Formen büschelartig behaart, nie bedornt. Die Discoidal- und die 4. Hinterrandzelle distal abschliessenden Queradern besitzen meist verschiedene Richtung, selten verlaufen sie in der gleichen Richtung, ausnahmsweise auch in der gleichen Linie. Die relativ grossen Genitalien sind nie ventral verlangert und daher ohne weiteres frei sichtbar .... Untergruppe Laphrinae sensu strictiore.

Hermann's classification was followed by Engel (1928-30) and Bromley (1932), among other authors. It was a good tentative, but suffered from the same problems as the other classifications — it was based on the palpal segmentation, on the marginal cell, and some other variable characters; not all the world genera would fit the divisions. Hermann himself could not conveniently place the Megapodini, for instance.

During this period Enderlein (1914b) erected the subfamily Archilaphriinae and the tribe Trigonomimini, taxa that were ignored by most subsequent authors.

4.4. The classifications of Hardy and Carrera

G. H. Hardy, based on the Australian fauna, started a series of works that would modify the suprageneric classification of the Asilidae:

(i) In 1926 he created tribes Brachyrrhopalini, Saropogonini, and Phellini (in the Dasypogoninae);

(ii) In 1927 he reduced the Laphriinae to a tribe of Dasypogoninae, considered the Leptogastrinae as a distinct group, and divided the Asilinae in Asilini and Ommatiini;

(iii) In 1928 he redefined the Atomosiini (a tribe created by Hermann in 1912);

(iv) In 1930a Hardy revised the tribe Brachyrrhopalini, and also in 1930b erected the tribe Stichopogonini;

(v) In 1934a he furnished a key to the subfamilies and tribes of Asilidae, based especially on the structure of the prosternum and pronotum, a very good character first employed by Malloch (1928); in the same paper Hardy revised the concept of Dasypogoninae;

(vi) In that same year (1934) he erected the tribe Chrysopogonini;

(vii) In the following year (1935a, 1935b), he studied the Asilinae;

(viii) Finally, in 1948, he published a general survey of the Asilidae classification, furnishing a complete key to the tribes; at that time he introduced tribes Xenomyzini and Laphystiini, and suggested the creation of the new tribe Isopogonini, to include *Leptarthrus* Stephens (as *Isopogon* Loew); he also remarked that his key was "sufficiently comprehensive to incorporate the world genera and allow further tribes to be formed when the interrelationships become better known".

Hardy's key (1948: 118) ran as follows:

1. Palpi two-segmented. Arista frequently absent, and when present it is short to minute, very rarely long. Subfamily Dasypogoninae 2

   Palpi one-segmented. The arista varies from long to short. Subfamily Asilinae 11

2. Prosternum contiguous with the pronotum and in no way reduced 3

   Prosternum varying from slightly emarginate along the anterior and posterior edges to the emargination meeting so as to form a finger-like process arising from the ventral part, in which latter case the isolated lateral portions of the prosternum become fused to the pronotum. No articulating spines in the female terminalia .... Xenomyzini

   Prosternum completely reduced so as to leave the ventral part isolated broadly by membrane and without the fingerlike projection 6

3. Female with articulating spines in the terminalia .. Stichopogonini

   Female without these spines, the acanthophorites being vestigial or absent 4

4. With the two uppermost radial veins reaching the wing margin independently .... Laphystiini

   With the two uppermost radial veins meeting before the wing margin 5

5. With a minute antennal spine (arista) placed dorsally on the antennae .... Atomosiini

   With the arista placed apically on the antennae or absent .... Laphriini

6. Ninth tergite of the abdomen entire, simple and without articulating spines .... Phellini

Ninth tergite of the female abdomen longitudinally divided, forming normal acanthophorites (these may become vestigial, in which case further tribes are indicated. Possibly the Isopogonini should be placed here) 7

7. Acanthophorites complete with their articulating spines 9

Acanthophorites well formed, but the articulating spines are absent 8

8. Thorax bare, with a spur situated above each wing .... Chrysopogonini

Thorax without such spur .... Dasypogonini

9. Acanthophorites capable of being retracted, owing to the form taken by the median plate, which folds inwards .... Brachyrrhopalini

Acanthophorites with spines permanently exerted and exposed, the median plate being incapable of folding 10

10. Male with the ninth tergite, at most, split along the median line, but otherwise simple. Complete characters not known .... The more primitive genera of Saropogonini

Male with the ninth tergite forming well-developed upper forceps. Complete characters not known .... The more advanced genera of Saropogonini

11. Prosternum incomplete and corresponding to the description under couplet 2, except no case is known where the reduction is sufficient to form the finger-like process. The long arista is provided with filaments on the underside ...... Ommatiini

Prosternum either complete or the ventral area is isolated by membrane 12

12. With the two upper radial veins reaching the wing margin separately .... Leptogastrini

With the two upper radial veins meeting before the wing margin .... Asilini

Hardy has employed in his key highly plastic characters, such as the palpi and the female terminalia. Again, his tentative was not sufficient to include the world genera. Several of his groupings were highly artificial, uniting widely different genera that presented parallel or convergent evolution of some characters. However, if it is considered that Hardy worked with limited resources of material and bibliography, his scheme was relatively good.

Carrera (1949, 1950) applied Hardy's concepts to the neotropical genera. His first tentative was made in 1949, when he revised the neotropical species with an apical spur on the front tibiae (the ancient

"Acanthocneminae" of Hermann, 1912). For the genera *Megapoda, Pronomopsis, Doryclus, Pseudorus* and *Senobasis* the new tribe Megapodini was erected. In 1960 Carrera extended Hardy's classification to the Brazilian genera of robber-flies.

In short, the Hardy-Carrera scheme remained like this:

I. Subfamily Dasypogoninae

1. Xenomyzini
2. Stichopogonini
3. Laphystiini
4. Atomosiini
5. Laphriini
6. Phellini
7. Isopogonini
8. Chrysopogonini
9. Dasypogonini
10. Brachyrrhopalini
11. Saropogonini
12. Megapodini

II. Subfamily Asilinae

1. Leptogasterini
2. Ommatiini
3. Asilini

4.5. Recent contributions

In 1959 Karl published one of the most important contributions to the knowledge of the robber-flies — a comparative study of the male genitalia, stressing the importance of these structures for the establishment of phylogenetic trends within the family. Unfortunately this paper has not had the merited influence among specialists in the group.

Further comments on this subjet and illustrations of the several types of male genitalia and their bearing on evolutionary trends will be presented in the next papers of this series.

In 1962 Hull studied the world genera and proposed a new classification. In spite of several defficiencies, Hull's work had the merit of bringing together all the available information, and especially it tried to include, for the first time in this century, all the genera known. Earlier attempts by Hermann, Hardy and Carrera had the shortcoming of being based on local faunas.

Hull's classification was the following:

I. Subfamily Dasypogoninae

1. Dioctriini (equivalent in concept and artificiality to Hardy's "Dasypogonini"; including several unrelated

genera, based only on the absence of spines on acanthophorites);

2. Phellini
3. Chrysopogonini
4. Damalini (unnecessary change of name; Hull disregarded Enderlein's previous name, Trigonomimini; = Xenomyzini of Hardy and Carrera)
5. Laphystini
6. Stichopogonini
7. Dasypogonini (ex Saropogonini with spur on front tibiae; = Acanthocneminae of Hermann; including "subfamily" Archilaphriinae of Enderlein)
8. Stenopogonini (ex Saroponini without tibial spur)
9. Thereutrini
10. Enigmomorphini

II. Subfamily Leptogastrinae

III. Subfamily Laphrinae

1. Laphrini
2. Andrenosomini
3. Ctenotini
4. Atomosiini

IV. Subfamily Megapodinae (new rank for the Megapodini of Carrera, 1949)

V. Subfamily Asilinae

1. Ommatiini
2. Asilini

Martin (1968) elevated the Leptogastrinae to family rank. The Leptogastridae can be immediately separated from all Asilidae by the presence of fenestrae on sternite 2, and they also differ in the male genitalia. Other distinctive Leptogastridae characters are shared singly and independently by other Asilidae genera. This group seems to be as old as the Asilidae, and to have with them a common ancestor. Both families had afterwards distinct patterns of evolution and radiation. The Leptogastridae will not be discussed in this series any further.

Lehr (1969) proposed for the tribe Asilini (*sensu* Hull, 1962) the "subtribes" Promachina (preocc. Bromley, 1934), Apocleina (as Apocliina, evidently a lapsus), Neomochtherina, and Machimina; he commented upon the general evolutionary trends of the Asilidae and on their probable Mesozoic origin (see specially p. 556, fig. 10).

5. NOTES ON THE CHARACTERS USED IN CLASSIFICATION

For the establishment of the phylogenetic trends of the several groups of Asilidae, the following characters were taken in consideration by past authors, and will be employed here:

1. *Antennal style.* The third antennal segment bears in most genera an apical style, which may be double or single. Primitive condition is represented by a style with 2 microsegments; this style undergoes reduction in many groups, until it becomes totally absent, being represented by only a minute apical spine, normally placed inside a small pit; this spine, as a derived condition, can be displaced to the dorsal surface of the 3rd antennal segment. Several genera present intermediary stages between a one-segmented style and a partially fused style.

As reduction of the antennal style has occurred many times, in many groups, as a notorious tendency, it cannot be used as a diagnostic character for subfamilies, serving merely to show the several trends within the family.

2. *Condition of the prosternum.* The primitive prosternum was complete, fused to the pronotum, forming a complete ring. Later, it became emarginated, and finally separated into a dorsal and a ventral plate, broadly isolated by membrane. Some groups have always maintained the primitive condition, other morphological characters showing the derived conditions; some other groups show all the steps, from complete to dissociated. This character is of tremendous importance to establish the early branchings of a group.

3. *Chaetotaxy.* There is a general tendency among robber-flies to reduce the bristles or hairs, especially the tergal bristles. Of course, many intermediary forms exist. However, within the Asilidae, two tendencies can be noted:

(i) A group that seems to have lost (or reduced) very early in its evolution the tergal bristles;

(ii) A group that primitively kept those bristles, and afterwards had them reduced.

Of great importance is also the chaetotaxy of the pleura, especially of the meso- and metapleura; according to this character, three groups can be more or less segregated:

(i) A group without differentiated meso- and metapleural bristles;

(ii) A group that preserved strongly differentiated mesopleural bristles (secondarily they may be reduced);

(iii) A group that preserved the metapleural bristles (also these may be secondarily reduced).

4. *Pilosity of the post-scutellar ("metanotal") slopes.* Pilosity on the post-scutellar slopes seems to have been acquired (as a derived character) independently by several groups. This is also a good character for the establishment of evolutionary trends.

5. *Pilosity of antennal style.* Several genera show a more or less pilose antennal style. A unique character is shown by a group of genera related to *Ommatius,* where the arista-like style shows a series of filaments on the underside.

6. *Wing venation.* Most authors have relied on wing venation for the classification of Asilidae. The same as other characters, derived conditions appeared several times in several groups, and this character must be used with care.

1. Marginal cell — may be open (primitive condition), closed, or closed and petiolate (derived condition);

2. First and fourth posterior cells, and anal cells same as above;

3. Normally there are 5 posterior cells (primitive condition), which may become reduced to 4 (derived condition);

4. R_3 — present in some genera (primitive condition); normally represented by a mere stump vein (intermediary condition), and in most genera completely absent (derived condition). Sometimes, the field of R_3 is "reactivated" (Hennig, 1954), and a crossvein similar to R_3 appears, forming 3 submarginal cells in the wing (as in certain species of *Pseudorus*); this is also a derived condition, that seldom occurs in the Asilidae; most genera with 3 submarginal cells (R_3 complete) actually show the primitive condition of this character.

7. *Palpus.* The primitively two-segmented palpus becomes reduced to a single segment. This has also occurred several times in the course of evolution.

8. *Apical spur on front tibiae.* This character is very probably derived and monophyletic, as all the steps in its transformation can still be traced. Genera presenting this character were segregated under one subfamily.

9. *Female terminalia.* The primitive female terminalia has spines on the acanthophorites; reduction of spines, fusion of the two halves of the acanthophorites and their subsequent elongation and modification leads to the formation of the several types of ovipositor presented by the different groups. This character, like the prosternum, is extremely important to determine the primitive branchings of the family.

10. *Male genitalia.* The primitive condition is shown in the male genitalia by the free, triangular, hypandrium, the more or less elongate, simple basistylus, and the dististylus placed apically on the basistylus, and the epandrial halves free. The male genitalia seems to evolve more rapidly than the female terminalia, and a wide variety of types exists. These will be discussed in the next papers.

11. *Immature stages and fossils.* Immature stages of a very limited number of genera are known (see Hennig, 1952; a complementary paper on the subject will be published by L. Knutson), and no comprehensive study of the larvae has yet been made, so larval characters can be used in systematics. As to the fossils, a list of papers describing Asilidae (and Leptogastridae) fossils is presented as an Appendix to this paper; fossils described up to the present are, with a few exceptions, few, fragmentary, badly described, and erroneously identified. Therefore, no definite data may be obtained from these sources.

12. *Geography.* This is an extremely important factor in establishing classifications and phylogenies, and one that has been rarely used. I have tried to conform my groupings, as much as possible, to logical geographical (past and present) patterns.

6. KEY TO SUBFAMILIES

1. Anterior tibiae with an apical spur; prosternum complete or dissociated; palpus with 2 or 1 segment; third antennal segment with style double, single, or absent; marginal cell normally open (closed in several genera); female terminalia normally with spines on acanthophorites (spines absent in some genera; in 2 genera female terminalia highly modified) .... Dasypogoninae Macquart

   Anterior tibiae never with an apical spur 2

2. Anterior branch of third vein (R_4) strongly recurrent, sigmoid; mesopleura with or without a strong supero-posterior bristle in front of the wing; palpi usually two segmented; third antennal segment with style double, single, or absent; prosternum complete; marginal cell open or closed; male tergites usually reduced to 6; female with tergites 6 and 8 greatly reduced to linear proportions; female terminalia without spines on acanthophorites .... Laphystiinae Hardy

   Anterior branch of third vein never strongly recurrent 3

3. Supero-posterior angle of mesopleura, in front of wing, with at least one very strong, long bristle; marginal cell always closed; prosternum complete; apical style double, single, or absent; palpus with 1 or 2 segments; female terminalia without spines on acanthoprorites .... Laphriinae Macquart

   Mesopleura without such a bristle 4

4. Marginal cell closed and petiolate and metapleura normally with a vertical row of long bristles or bristly hairs (sometimes reduced to a single bristle); palpi always one-segmented; prosternum variable 5

Marginal cell normally open; if closed (e.g., *Enigmomorphus*), then metapleura bare and palpus with two segments; prosternum variable 7

5. Antennal style feathered; prosternum complete or dissociated; female terminalia without spines on acanthophorites; post-metacoxal area with a complete arch of chitin .... Ommatiinae Hardy

Antennal style bare 6

6. Post-scutellar slopes bare; prosternum complete or dissociated; 3 or 2 submarginal cells and usually R_3 present as a stump vein; apical microsegment double or single; female terminalia with or without spines on acanthophorites, highly variable .... Apocleinae Lehr

Post-scutellar slopes pilose; prosternum complete or dissociated; always with only 2 submarginal cells and R_3 always absent; apical microsegment double or single, or absent; female terminalia with or without spines on acanthophorites, also highly variable .... Asilinae Leach

7. Head exceptionally wide and short, vertex low, leaving a goggle-eyed appearance; deep, mediogenal grooves present, corresponding to anterior arms of tentorium; female terminalia simple, tubular and not spiny; prosternum usually complete .. .. Trigonomiminae Enderlein

Head variable, but never as above and never with mediogenal grooves; female terminalia normally with spines on acanthophorites (many genera without); prosternum complete or dissociated .... Stenopogoninae Hull

7. HYPOTHETICAL PHYLOGENETIC HISTORY OF SUBFAMILIES

(Fig. 1)

I believe that the Asilidae, like most other families of Diptera, had their origin during the Mesozoic, in the supercontinent of Pangaea.

The ancestral Asilidae stock should have the following primitive characters:

i. Two-segmented palpus;

ii. Two-segmented antennal style;

iii. Prosternum complete, fused to pronotum, forming a complete ring;

iv. Fore tibiae without apical spur;
v. Wings with 3 submarginal cells (i.e., R_3 complete), and all cells (marginal, posterior and anal) widely open;
vi. Tergal bristles present on all tergites;
vii. Mesopleura and metapleura with several strong bristles;
viii. Female terminalia with spines on acanthophorites;
ix. Male genitalia with free hypandrium, free epandrial halves, and dististylus apically set on basistylus.

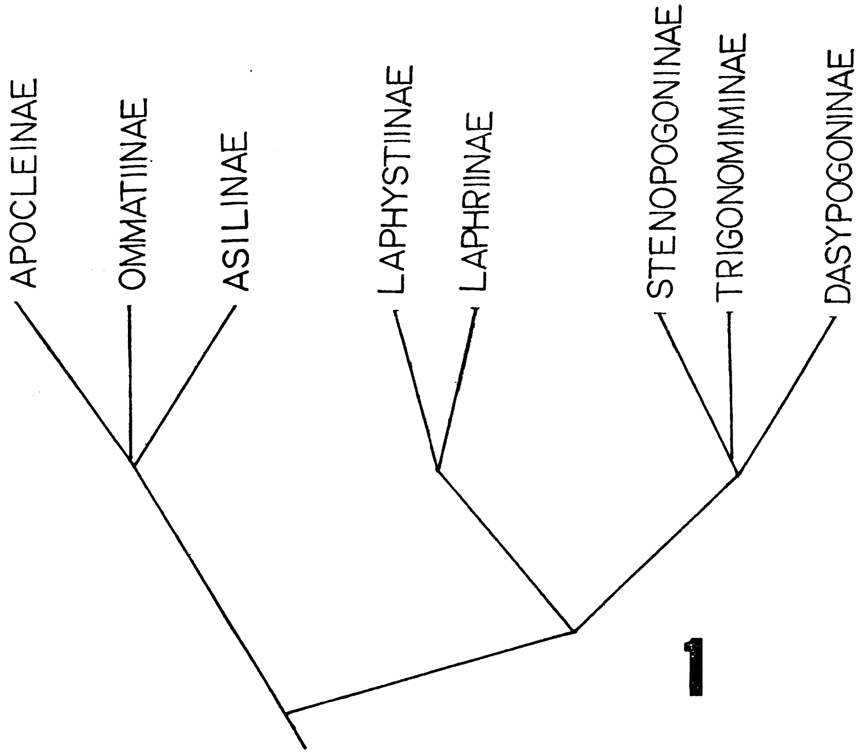

Fig. 1, Hypothetical phylogeny of the subfamilies of Asilidae.

The ancestral stock has probably occupied all the available ecological areas and radiated rapidly, soon becoming differentiated in several branches, which originated the present subfamilies.

In this initial differentiation, two trends may be discerned:

I. One group characterized primitively by the open wing cells, the almost complete loss of pleural and tergal bristles, by the spinous acanthophorites, but which very soon had the prosternum dissociated (while in some other genera the prosternum retained the primitive condition);

II. One group that kept most of the primitive characters; meso- and metapleural bristles, complete prosternum, wing venation.

The first group originated three other branches:

1. One that acquired a twisted spine or spur on the fore tibiae — the Dasypogoninae;

2. A branch where the head underwent strong modifications; the females lost the spines on the acanthophorites; deep mediogenal grooves on the face were developed; in most genera the prosternum remained with the primitive condition — the Trigonomiminae;

3. The third branch remained relatively unchanged, and did not originally acquire derived characters, as the two groups above; the prosternum remained complete in a limited number of genera (the Stichopogonini), but became dissociated in many others; similarly to the Dasypogoninae, most forms kept the original spinous acanthophorites — this branch originated the Stenopogoninae.

Group II became differentiated in two subgroups and several branches:

A. One which primarily kept the mesopleural bristles, and where females soon lost the spinous condition of the acanthophorites; this branch originated:

1. The Laphriinae, with closed marginal cell and always with mesopleural bristles;

2. The Laphystiinae, with originally a mesopleural bristle, that later became absent, and with R_4 strongly recurrent and sigmoid; the marginal cell remained open in some genera, closed in others.

B. A subgroup without differentiated mesopleural bristles, but with a row of bristles on the metapleura, always with closed marginal cell and a single-segmented palpus; the greatest mosaic of characters is obtained in this subgroup, which became modified in 3 branches:

1. One where the antennal style became feathered, and where females lost the spinous acanthophorites — Ommatiinae;

2. A branch with bare post-scutellar slopes; the most primitive genera have maintained the spinous acanthophorites, or wings with 3 submarginal cells; in other genera, the female terminalia became modified and the wings had their submarginal cells reduced to 2, R_3 represented by a stump vein, or absent; the prosternum remained complete or was dissociated — the Apocleinae;

3. Finally, in the third branch, the post-scutellar slopes became pilose, the wings had their submarginal cells reduced to 2, and R_3 disappeared completely; the most primitive genera maintained the spinous acanthophorites, and the other developed different types of ovipositor — this group originated the Asilinae.

8. SUBFAMILY APOCLEINAE LEHR, *STATUS N.*

(Subtribe Apocleina Lehr, 1969; including "subtribe" Promachina Lehr, 1969)

Diagnosis : Marginal cell closed and petiolate; palpus one-segmented; mesopleural bristle absent; metapleura usually with vertical row of bristles; post-scutellar slopes bare (sometimes, as in *Porasilus* and *Diplosynapsis*, with hairs placed on inner margin of callosities, but never *on top* of them, and then R_3 present as a stump vein); prosternum complete or dissociated; 3 or 2 submarginal cells; R_3 present, reduced to a stump vein, or absent; female terminalia with or without spinous acanthophorites; male genitalia variable.

I have preferred to maintain Lehr's name (although proposed for a small group of genera with similar biology, originally), as *Apoclea* Macquart is one of the most primitive genera of this group.

List of genera:

1. *Alcimus* Loew, 1848 (E)
2. *Amblyonychus* Hermann, 1921 (= *Promachina* Bromley, 1934) (Neo)
3. *Anacinaces* Enderlein, 1914a (O)
4. *Antilophonotus* Lindner, 1955 (E)
5. *Apoclea* Macquart, 1838 (= *Bisapoclea* Becker, 1925) (P, E, O)
6. *Apotinocerus* Hull, 1962 (Neo)
7. *Atractocoma* Artigas, 1970 (Ch)
8. *Blepharotes* Westwood, 1840 (= *Blepharis* Macquart, 1838; = *Craspedia* Macquart, 1838; = *Psecas* Jaennicke, 1867) (A)
9. *Carreraomyia* Cole, 1969 (= *Carreraia* Cole & Pritchard, 1964) (Nea)
10. *Cerozodus* Bigot, 1857 (Neo)
11. *Cratolestes* Hull, 1962 (Ch)
12. *Ctenodontina* Enderlein, 1914a (= *Catostola* Hull, 1958c) (Neo)
13. *Dasophrys* Loew, 1858 (E)
14. *Diplosynapsis* Enderlein, 1914a (Neo)
15. *Dysclytus* Loew, 1858 (E)
16. *Eccritosia* Schiner, 1866 (Neo, Nea)
17. *Efferia* Coquillet, 1893 (= *Nerax* Hull, 1962) (Neo, Nea)
18. *Eicherax* Bigot, 1857 (= *Eristicus* Loew, 1848; = *Neoeristicus* Osten Sacken, 1878) (Neo)
19. *Eichoichemus* Bigot, 1857 (= *Proctophorus* Schiner, 1866) (Neo)
20. *Epitriptus* Loew, 1849 (= *Epitreptus* Walker, 1855) (P)
21. *Eraxasilus* Carrera, 1959 (Neo)
22. *Eretomyia* Artigas, 1971 (= *Eremomyia* Artigas, 1970) (Ch)
23. *Glaphyropyga* Schiner, 1866 (= *Tapinostylus* Enderlein, 1914a; = *Opopotes* Hull, 1957) (Neo)
24. *Hippomachus* Engel, 1927b (= *Trichonotus* Loew, 1858) (E)
25. *Hobbyus* Bromley, 1952 (= *Merogymnus* Hobby, 1933) (E)

26. *Labromyia* Hull, 1962 (Neo)
27. *Lecania* Macquart, 1838 (Neo)
28. *Leptoharpacticus* Lynch Arribálzaga, 1880b (= *Rhadinosoma* Artigas, 1970) (Neo, Ch)
29. *Lochmorhynchus* Engel, 1930a (Neo)
30. *Lonchodogonus* Hull, 1962 (Neo)
31. *Lycoprosopa* Hull, 1962 (E)
32. *Mallophora* Macquart, 1834 (Neo, Nea)
33. *Megadrillus* Bigot, 1857 (E)
34. *Megametopon* Artigas, 1970 (Ch)
35. *Megaphorus* Bigot, 1857 (= *Mallophorina* Curran, 1934b) (Nea)
36. *Myaptex* Hull, 1962 (Ch)
37. *Neodasophrys* Ricardo, 1962 (E)
38. *Neolophonotus* Engel, 1925b (= *Lophonotus* Macquart, 1838; including "subgenera" *Lophopeltis* Engel, 1925b, and *Lophybus* Engel, 1925b) (E)
39. *Nesiotes* Artigas, 1970 (Ch)
40. *Nomomyia* Artigas, 1970 (Ch)
41. *Nyssoprosopa* Hull, 1962 (Neo)
42. *Pachychaeta* Bigot, 1857 (Neo)
43. *Pararatus* Ricardo, 1913 (A)
44. *Philodicus* Loew, 1847 (= *Teretromyia* Bigot, 1859) (P, E, O)
45. *Philonerax* Bromley, 1932 (Ch)
46. *Polyphonius* Loew, 1848 (P)
47. *Porasilus* Curran, 1934a (Neo)
48. *Proctacanthella* Bromley, 1934 (Nea)
49. *Proctacanthus* Macquart, 1838 (= *Acanthodelphia* Bigot, 1857) (Nea, Neo)
50. *Promachella* Cole & Pritchard, 1964 (Nea)
51. *Promachus* Loew, 1848 (= *Bactria* Meigen, 1820; = *Trupanea* Macquart, 1838; = *Telejoneura* Rondani, 1863; including "subgenera" *Enagaedium* Engel, 1930a, *Parapromachus* Hull, 1962, *Philomachus* Karsch, 1887, and *Trypanoides* Becker, 1925d) (Nea, Neo, P, E, O, A)
52. *Regasilus* Curran, 1931 (Nea, Neo)
53. *Synolcus* Loew, 1858 (E)
54. *Triorla* Parks, 1968 (Nea, Neo)
55. *Zoticus* Artigas, 1970 (Ch)

9. SUBFAMILY ASILINAE LEACH

(Leach, 1819; including "subtribes" Neomochtherina and Machimina of Lehr, 1969)

Diagnosis : Marginal cell closed and petiolate; palpus one-segmented; mesopleural bristle absent; metapleura usually with a vertical row of bristles; post-scutellar slopes pilose; prosternum complete or dissociated; only 2 submarginal cells; R_3 normally absent; female terminalia with or without spinous acanthophorites, or strongly modified; male genitalia variable.

Most characters in this subfamily are derived, which could mean that this group is derived from the Apocleinae; however, the primitive condition of the prosternum and of the acanthophorites, found in some genera, point to a contemporary origin with the Apocleinae. The two subfamilies have a strong complementary distribution, and possibly different geographic origins.

List of genera:

1. *Acanthopleura* Engel, 1927a (P)
2. *Amphiscolops* Hull, 1962 (O, A)
3. *Anarmostus* Loew, 1860 (Neo)
4. *Antipalus* Loew, 1849 (P, O)
5. *Antiphrisson* Loew, 1849 (P)
6. *Argillemisca* Lehr, 1967 (P)
7. *Asilella* Lehr, 1970 (P)
8. *Asilus* Linnaeus, 1758 (P, Nea; very few species; species from other areas included or "abandoned" here belong to other genera, known or new)
9. *Astochia* Becker, 1913 (P,O)
10. *Cerdistus* Loew, 1849 (= *Rhabdoitamus* White, 1917a; including "subgenus" *Neocerdistus* G. H. Hardy, 1926) (P, O, ?A)
11. *Chilesus* Bromley, 1932 (Ch)
12. *Clephydroneura* Becker, 1925 (O)
13. *Cnodalomyia* Hull, 1962 (Neo)
14. *Cobalomyia* Hull, 1962 (E)
15. *Congomochtherus* Oldroyd, 1970 (E)
16. *Cratopoda* Hull, 1962 (Ch)
17. *Dinozabrus* Hull, 1962 (E)
18. *Dysmachus* Loew, 1860 (P)
19. *Eccoptopus* Loew, 1860 (= *Coelopus* Becker, 1907) (P)
20. *Echthistus* Loew, 1849 (P)
21. *Epiklisis* Becker, 1925 (O)
22. *Epipamponeurus* Becker, 1919 (Neo)
23. *Erax* Scopoli, 1763 (= ? *Protophanes* Loew, 1860) (P, ?E, ?A)
24. *Erebunus* Richter, 1966 (P)
25. *Eremisca* Zinovieva, 1956 (P)
26. *Eutolmus* Loew, 1848 (P)
27. *Filiolus* Lehr, 1967 (P)
28. *Heligmoneura* Bigot, 1858 (= ? *Cinadus* Wulp, 1898a; = *Chaetogonophora* Hull, 1962; = *Haplonota* Frey, 1934)
29. *Hoplopheromerus* Becker, 1925 (O)
30. *Ktyr* Lehr, 1967 (P)
31. *Ktyrimisca* Lehr, 1967 (P)
32. *Leinendera* Carrera, 1945 (Neo)

33. *Lestophonax* Hull, 1962 (Neo)
34. *Lochyrus* Artigas, 1970 (Ch)
35. *Lycomya* Bigot, 1857 (= *Lycomyia* Kertész, 1909) (Ch)
36. *Machimus* Loew, 1849 (= *Tolmerus* Loew, 1849; including "subgenus" *Conosiphon* Becker, 1923) (Nea, P, E, O, A)
37. *Menexenus* Artigas, 1970 (Ch)
38. *Negasilus* Curran, 1934b (Nea)
39. *Neoaratus* Ricardo, 1913 (= *Aratus* Wulp, 1898b) (A)
40. *Neoitamus* Osten Sacken, 1878 (= *Itamus* Loew, 1849; = ?*Trichoitamus* White, 1917a) (Nea, P, E, O, A)
41. *Neomochtherus* Osten Sacken, 1878 (= *Mochtherus* Loew, 1849) (P, E, O, A)
42. *Nigrasilus* Hine, 1908 (Nea)
43. *Nyssomyia* Hull, 1962 (O)
44. *Oligoschema* Becker, 1926 (O)
45. *Orophotus* Becker, 1925 (P, O)
46. *Pamponerus* Loew, 1849 (P)
47. *Paritamus* Verrall, 1909 (= *Marikowskia* Lehr, 1964) (P)
48. *Pediophoneus* Lynch Arribálzaga, 1883 (Neo)
49. *Philonicus* Loew, 1849 (= *Philonotus* Neuhaus, 1886) (Nea, P, O, A)
50. *Polysarca* Schiner, 1866 (P)
51. *Polysarcodes* Paramonov, 1937 (P)
52. *Rhadiurgus* Loew, 1849 (P, ?E, ?O)
53. *Satanas* Jacobson, 1908 (P)
54. *Senoprosopis* Macquart, 1838 (= *Stenoprosopis* Kertész, 1909) (O, ?E, ?A)
55. *Stenasilus* Carrera, 1960 (Neo)
56. *Stilpnogaster* Loew, 1849 (P)
57. *Stizolestes* Hull, 1962 (Ch)
58. *Strophipogon* Hull, 1958e (O)
59. *Templasilus* Peris, 1957 (P)
60. *Threnia* Schiner, 1866 (Neo)
61. *Trichomachimus* Engel, 1934 (P, O)
62. *Ujguricola* Lehr, 1970 (P)

10. SUBFAMILY DASYPOGONINAE MACQUART

(Dasypogonitae Macquart, 1838; including "subfamily" Archilaphriinae Enderlein, 1914b, and "tribes" Brachyrrhopalini G. H. Hardy, 1926, Saropogonini G. H. Hardy, 1926 [part], Chrysopogonini G. H. Hardy, 1934b, Isopogonini G. H. Hardy, 1948, and Thereutrini Hull, 1962)

Marginal cell normally open (closed in some genera); palpus one- or two-segmented; differentiated mesopleural and metapleural bristles absent; 2 submarginal cells; prosternum complete in only 1 genus, dissociated in all others; anterior tibiae always with an apical spur; female terminalia with or without spines on acanthophorites; male genitalia variable.

List of genera:

1. *Aczelia* Carrera, 1955b (Neo)
2. *Allopogon* Schiner, 1866 (Neo)
3. *Alvarenga* Carrera, 1960 (Neo)
4. *Annamyia* Pritchard, 1941 (Neo)
5. *Aphamartania* Schiner, 1866 (Neo)
6. *Apotechyla* Hull, 1962 (A)
7. *Araiopogon* Carrera, 1949 (Neo)
8. *Archilaphria* Enderlein, 1914b (P)
9. *Aspidopyga* Carrera, 1949 (Neo)
10. *Aterpogon* G. H. Hardy, 1930b (A)
11. *Austenmyia* Carrera, 1955a (Neo)
12. *Austrosaropogon* G. H. Hardy, 1934 (A)
13. *Blepharepium* Rondani, 1848 (= *Planetolestes* Lynch Arribálzaga, 1879) (Neo, Nea)
14. *Brachyrrhopala* Macquart, 1847 (A)
15. *Cabaza* Walker, 1851 (A)
16. *Caenarolia* Thomson, 1869 (= *Caenorolia* Williston, 1891) (Neo)
17. *Chryseutria* G. H. Hardy, 1928 (A)
18. *Chrysopogon* Roeder, 1881 (A)
19. *Chylophaga* Hull, 1962 (A)
20. *Cleptomyia* Carrera, 1949 (Neo)
21. *Comantella* Curran, 1923 (Nea)
22. *Cophura* Osten Sacken, 1887 (= *Blax* Loew, 1871; = *Blacodes* Loew, 1874; = *Loewiella* Williston, 1896; = *Buckellia* Curran, 1925) (Nea, Neo)
23. *Cyrtophrys* Loew, 1851 (= *Myolestes* Brèthes, 1904; = *Myiolestes* Kertész, 1909; = *Mirolestes* Curran, 1935) (Neo)
24. *Dakinomyia* G. H. Hardy, 1934 (A)
25. *Daptolestes* Hull, 1962 (A)
26. *Dasypogon* Meigen, 1803 (= *Cheilopogon* Rondani, 1856; = *Seilopogon* Rondani, 1861; = *Chilopogon* Bigot, 1878; = *Ceilopogon* Bigot, 1878; = *Selidopogon* Bezzi, 1902)
27. *Deromyia* Philippi, 1865 (Ch)
28. *Diogmites* Loew, 1866 (Nea, Neo)
29. *Erythropogon* White, 1914 (A)
30. *Hodophylax* James, 1933 (Nea)
31. *Lagodias* Loew, 1858 (= *Laparus* Loew, 1861; = *Neolaparus* Williston, 1889; = *Cenopogon* Wulp, 1898a) (E, P, O)
32. *Lastaurax* Carrera, 1949 (Neo)
33. *Lastaurina* Curran, 1935 (Neo)
34. *Lastauroides* Carrera, 1949 (Neo)
35. *Lastauronia* Carrera, 1949 (Neo)
36. *Lastauropsis* Carrera, 1949 (Neo)

37. *Lastaurus* Loew, 1851 (= *Morimna* Walker, 1851) (Neo)
38. *Leptarthrus* Stephens, 1829 (= *Isopogon,* 1847) (P, E)
39. *Lestomyia* Williston, 1883 (Nea)
40. *Lycomax* Hull, 1962 (?)
41. *Macrocolus* Engel, 1930a (Neo)
42. *Megapoda* Macquart, 1834 (Neo)
43. *Metalaphria* Ricardo, 1912b (A)
44. *Molobratia* Hull, 1958b (P, O)
45. *Neocyrtopogon* Ricardo, 1912a (A)
46. *Neoderomyia* Artigas, 1971 (Ch)
47. *Neodiogmites* Carrera, 1949 (Neo)
48. *Neosaropogon* Ricardo, 1912a (including "subgenus" *Lycotherates* Hull, 1962) (A)
49. *Nerterhaptomenus* G. H. Hardy, 1934 (A)
50. *Nicocles* Jaennicke, 1867 (= *Pygostylus* Loew, 1866) (Nea)
51. *Oberon* Carrera & Papavero, 1962 (Ch)
52. *Omninablautus* Pritchard, 1935 (Nea)
53. *Opseostlengis* White, 1914 (A)
54. *Paraphamartania* Engel, 1930b (P)
55. *Parataracticus* Cole, 1924 (Nea)
56. *Paraterpogon* Hull, 1962 (A)
57. *Pegesimallus* Loew, 1858 (= *Pagesimallus* Verrall, 1882) (E)
58. *Phonicocleptes* Lynch Arribálzaga, 1881 (Neo)
59. *Pronomopsis* Hermann, 1912 (Ch)
60. *Pseudorus* Walker, 1851 (= *Ampyx* Walker, 1855; = *Doryclus* Jaennicke, 1867; = *Pseudoryclus* Carrera, 1952) (Neo)
61. *Questopogon* Dakin & Fordham, 1922 (A)
62. *Rachiopogon* Ricardo, 1912a (A)
63. *Saropogon* Loew, 1847 (= *Sarapogon* Williston, 1891) (Nea, P, O)
64. *Senobasis* Macquart, 1838 (= *Stenobasis* Agassiz, 1846; = *Astylium* Rondani, 1848; = *Lochites* Schiner, 1866; = *Astylum* Kertész, 1909; = *Lochitomyia* Brèthes, 1925) (Neo)
65. *Stizochymus* Hull, 1962 (A)
66. *Taracticus* Loew, 1872 (= *Dioctrodes* Coquillett, 1904) (Nea)
67. *Thereutria* Loew, 1851 (= *Scandon* Walker, 1851) (A)
68. *Theromyia* Williston, 1891 (= *Cylindrophora* Philippi, 1865; = *Lynchia* Williston, 1889; = *Myiothera* Williston, 1889) (Ch)
69. *Theurgus* Richter, 1966 (P)
70. *Tocantinia* Carrera, 1955a (Neo)

11. SUBFAMILY LAPHRIINAE MACQUART

(Laphritae Macquart, 1838; including tribes Atomosiini Hermann, 1920, and Andrenosomini and Ctenotini of Hull, 1962)

Marginal cell closed and petiolate; mesopleura with at least one differentiated, strong, long bristle on postero superior angle, in front of wing (except in *Dasylechia*) ; palpi one- or two-segmented; antennal style with two or one microsegments, or absent; 2 submarginal cells; post-scutellar slopes bare or pilose; prosternum always complete; female terminalia always without spines; male genitalia characteristic (see Karl, 1959).

List of genera:

1. *Adelodus* Hermann, 1912 (A)
2. *Afromelittodes* Oldroyd & Bruggen, 1963 (E)
3. *Amathomyia* Hermann, 1912 (P)
4. *Andrenosoma* Rondani, 1856 (= *Elaeotoma* A. Costa, 1863) (Nea, Neo, P, E, O, A, Ch)
5. *Anoplothyrea* Meijere, 1914 (O)
6. *Aphestia* Schiner, 1866 (Neo)
7. *Aphistina* Oldroyd, 1972 (O)
8. *Atomosia* Macquart, 1838 (Neo, Nea)
9. *Atomosiella* Wilcox, 1937 (Nea)
10. *Atoniomyia* Hermann, 1912 (= *Atonia* Williston, 1889) (Neo, Nea)
11. *Atractia* Macquart, 1838 (Neo)
12. *Automolina* Hermann, 1912 (Ch)
13. *Bathropsis* Hermann, 1912 (Neo)
14. *Borapisma* Hull, 1957 (O)
15. *Bromotheres* Hull, 1962 (A)
16. *Cenochromyia* Hermann, 1912 (A)
17. *Cerotainia* Schiner, 1866 (= *Ceratotaenia* Lynch Arribálzaga, 1880a; = *Cyphotomyia* Williston, 1889) (Neo, Nea)
18. *Cerotainiops* Curran, 1930a (Nea)
19. *Chymedax* Hull, 1958a (A)
20. *Clariola* Kertész, 1901 (A)
21. *Cryptomerinx* Enderlein, 1914a (= *Alipiolaphria* Carrera, 1951) (Neo)
22. *Ctenota* Loew, 1873 (= *Epilamyra* Becker, 1913; = *Paractenota* Engel, 1925c) (P, O)
23. *Cyanonedys* Hermann, 1912 (A)
24. *Dassylina* Bromley, 1935 (E)
25. *Dasylechia* Williston, 1907 (?) (Nea)
26. *Dasyllis* Loew, 1851 (Neo)
27. *Dasythrix* Loew, 1851 (= *Nusa* Walker, 1851; = *Halictosoma* Rondani, 1873) (P, E, O, A)
28. *Despoticus* Bezzi, 1928 (A)
29. *Dichaetothyrea* Meijere, 1914 (O)
30. *Epaphroditus* Hermann, 1912 (= *Eopaphroditus* Hull, 1962) (O)
31. *Eumecosoma* Schiner, 1866 (Neo)
32. *Goneccalypsis* Hermann, 1912 (E, O)
33. *Hodites* Hull, 1962 (= *Holites*, Zool. Rec.) (Neo)
34. *Hybozelodes* Hermann, 1912 (Neo)
35. *Hyperechia* Schiner, 1866 (E, O)

36. *Ichneumolaphria* Carrera, 1951 (Neo)
37. *Katharma* Oldroyd, 1959 (E)
38. *Laloides* Oldroyd, 1972 (= *Anisosis* Hermann, 1914) (O)
39. *Lampria* Macquart, 1838 (= *Bruchomyia* Hull, 1962) (Neo)
40. *Lamprozona* Loew, 1851 (Ch)
41. *Lamyra* Loew, 1851 (E, P)
42. *Laphria* Meigen. 1803 (= *Lapria* Meigen. 1800; = *Rhopalocera* Meigen, 1820; = *Laphyra* Billberg, 1820; = *Choerades* Walker, 1851; = *Epholkiolaphria* Hermann, 1914; = *Sullaphria* Hennig, 1941; including "subgenus" *Bombomima* Enderlein, 1914a) (Nea, P, E, O, A)
43. *Laxenecera* Macquart, 1838 (= *Acurana* Walker, 1851; = *Dyseris* Loew, 1858) (E, O)
44. *Loewinella* Hermann, 1912 (P, E)
45. *Lophoceraea* Hermann, 1912 (Neo)
46. *Lycosimyia* Hull, 1958a (= *Catonomyia* Hull, 1962) (Neo)
47. *Maira* Schiner, 1866 (O, A)
48. *Neophoneus* Williston, 1889 (= *Phoneus* Macquart, 1838) (Neo)
49. *Oidardis* Hermann, 1912 (Neo)
50. *Opeatocerus* Hermann, 1912 (O)
51. *Opocapsis* Hull, 1958b (A, O)
52. *Orthogonis* Hermann, 1914 (? Nea, E, O)
53. *Othoniomya* Hermann, 1912 (= *Sphagolestes* Hull, 1962) (Neo)
54. *Pagidolaphria* Hermann, 1914 (= *Saliomima* Enderlein, 1914a (O)
55. *Paratractia* Hull, 1962 (Neo)
56. *Phellopteron* Hull, 1962 (Neo)
57. *Pholidotus* Hermann, 1912 (preocc.) (Neo)
58. *Pilica* Curran, 1931 (Neo)
59. *Pogonosoma* Rondani, 1856 (Nea, P, O)
60. *Proagonistes* Loew, 1858 (E)
61. *Protichisma* Hermann, 1912 (Neo)
62. *Rhatimomyia* Lynch Arribálzaga, 1882b (= *Rhatitomyia* Williston, 1891; = *Dissmeryngodes* Hermann, 1912; = *Centrolaphria* Enderlein, 1914a) (Neo)
63. *Rhopalogaster* Macquart, 1834 (Neo)
64. *?Senoxericera* Macquart, 1850 (= *Stenoxericera* Kertész, 1909) (E)
65. *Smeryngolaphria* Hermann, 1912 (= *Panamasilus* Curran, 1930b) (Neo)
66. *Stiphrolamyra* Engel, 1928 (P, E)
67. *Storthyngomerus* Hermann, 1919 (= *Nusina* Curran, 1927) (E)
68. *Strombocodia* Hermann, 1912 (Neo)
69. *Systropalpus* Hull, 1962 (E)

12. SUBFAMILY LAPHYSTIINAE G. H. HARDY, *STATUS N.*

(Laphystiini G. H. Hardy, 1948; = Hoplistomerini Karl, 1959)

Marginal cell open or closed; anterior branch of 3rd vein (R_4) strongly sigmoid and recurrent; mesopleural bristle present or absent;

antennal style one- or two-segmented or entirely absent; prosternum always complete; 2 submarginal cells; female terminalia always without spines; male genitalia variable.

List of genera:

1. *Acrochordomerus* Hermann, 1920 (P)
2. *Anypodetus* Hermann, 1907 (= ? *Sporadothrix* Hermann, 1908) (E)
3. *Apoxyria* Schiner, 1866 (= *Helolaphyctis* Hermann, 1920) (Neo)
4. *Asicya* Lynch Arribálzaga, 1880a (= ? *Zabrops* Hull, 1957) (Neo, Nea)
5. *Cormansis* Walker, 1851 (O)
6. *Gerrolasius* Hermann, 1920 (E)
7. *Glyphotriclis* Hermann, 1920 (P)
8. *Hexameritia* Speiser, 1920 (= *Eutrichodes* Hermann, 1920) (Ch)
9. *Hoplistomerus* Macquart, 1838 (= *Hoplistomera* Walker, 1855) (E, O)
10. *Hoplotriclis* Hermann, 1920 (P)
11. *Laphygmolestes* Hull, 1962 (Neo)
12. *Laphystia* Loew, 1847 (= *Laphyctis* Loew, 1859; including "subgenus" *Laphystiella* Hull, 1962) (Nea, P, E, O)
13. *Macahyba* Carrera, 1947 (= *Martinia* Hull, 1962) (Neo)
14. *Nyximyia* Hull, 1962 (A)
15. *Perasis* Hermann, 1905 (P)
16. *Psilocurus* Loew, 1874 (= *Orthoneuromyia* Williston, 1893) (Nea, Neo)
17. *Saucropogon* Hull, 1962 (E)
18. *Scytomedes* Hermann, 1920 (P) (= *Scytemedes* Stein, 1881)
19. *Torebroma* Hull, 1957 (P)
20. *Trichardis* Hermann, 1906 (= *Strobilothrix* Becker, 1907) (P, E)
21. *Triclioscelis* Roeder, 1900 (Neo)
22. *Triclis* Loew, 1851 (= *Gastrichelius* Rondani, 1856; = *Gastricheilus* Bigot, 1857) (P)
23. *Udenopogon* Becker, 1913a (= ? *Trichardopsis* Oldroyd, 1958) (P)

13. SUBFAMILY OMMATIINAE G. H. HARDY, *STATUS N.*

(Ommatiini G. H. Hardy, 1927)

Marginal cell closed; palpus one-segmented; antennal style feathered; 2 submarginal cells; prosternum complete or dissociated; mesopleural bristle absent; female terminalia never with spines; post-scutellar slopes bare; male genitalia variable.

List of genera:

1. *Cophinopoda* Hull, 1958b (O)
2. *Emphysomera* Schiner, 1866 (O, E)

3. *Merodontina* Enderlein, 1914a (P, O)
4. *Michotamia* Macquart, 1838 (= *Allocotosia* Schiner, 1866; = *Allocotasia* Wulp, 1872) (O, A)
5. *Ommatius* Wiedemann, 1821 (= *Ommatinus* Becker, 1925; including "subgenus" *Metommatius* Hull, 1962; possibly several different genera are mixed up here) (Nea, Neo, P, E, O, A)
6. *Stenommatius* Matsumura, 1916 (O)
7. *Thallosia* Oldroyd, 1970 (E)

14. SUBFAMILY STENOPOGONINAE HULL, *STATUS N.*

(Stenopogonini Hull, 1962; including tribes Phelini G. H. Hardy, 1926, Stichopogonini G. H. Hardy, 1930b, Dioctrini Hull, 1962 [part], and Enigmomorphini Hull, 1962).

Marginal cell open (rarely closed); no spur on anterior tibial apex; prosternum complete or dissociated; head variable; mediogenal grooves absent; mesopleural bristles absent; female terminalia with or without spines on acanthophorites; male genitalia variable.

List of genera:

1. *Ablautus* Loew, 1866 (= *Ablautatus* Loew, 1874) (Nea)
2. *Acnephalum* Macquart, 1838 (E, P, ?A)
3. *Acronyches* Williston, 1908 (= *Megonyx* Hull, 1962) (Neo)
4. *Afganopogon* Hradsky, 1962 (P)
5. *Alyssomyia* Hull, 1962 (Ch)
6. *Amphisbetetus* Hermann, 1906 (P)
7. *Anarolius* Loew, 1844 (P)
8. *Ancylorrhynchus* Berthold in Latreille, 1827 (= *Xiphocera* Macquart, 1834; = *Enchocera* Blanchard, 1840; = *Elasmocera* Rondani, 1845; = *Opegiocera* Rondani, 1845; = *Xiphocerus* Loew, 1847) (P, E, O, ?A)
9. *Aplestobroma* Hull, 1957 (A)
10. *Archilestris* Loew, 1874 (= *Archilestes* Schiner, 1866; *Pseudarchilestes* Bigot, 1889; = *Pseudoarchilestes* Bigot, 1890) (Neo, Nea)
11. *Astylopogon* Meijere, 1913 (A)
12. *Backomyia* Wilcox & Martin, 1957 (Nea)
13. *Bathypogon* Loew, 1851 (A)
14. *Broticosia* Hull, 1957 (A) (= *Pegolabrus* Hull, 1962)
15. *Callinicus* Loew, 1872 (= *Chrysoceria* Williston, 1907) (Nea)
16. *Ceraturgus* Wiedemann, 1824 (= *Ceraturgopsis* Johnson, 1903) (Nea, P)
17. *Clinopogon* Bezzi, 1910b (A, O)
18. *Codula* Macquart, 1850 (A)
19. *Coleomyia* Wilcox & Martin, 1935 (Nea)
20. *Creolestes* Hull, 1962 (Ch)
21. *Crobilocerus* Loew, 1847 (P)

22. *Cyclosocerus* Bezzi, 1926 (= *Cycloscerus* Hull, 1962) (P)
23. *Cylicomera* Lynch Arribálzaga, 1881 (Neo)
24. *Cyrtopogon* Loew, 1947 (= *Euarmostus* Walker, 1854; = *Enarmostus* Walker, 1854; = *Philammosius* Rondani, 1856; including "subgenus" *Palamopogon* Bezzi, 1927 [= *Eupalamus* Jaennicke, 1867]) (Nea, P.O)
25. *Daspletis* Loew, 1859 (E)
26. *Dasycyrton* Philippi, 1865 (Ch)
27. *Dasypecus* Philippi, 1865 (Ch)
28. *Dicolonus* Loew, 1866 (P, Nea)
29. *Dicranus* Loew, 1851 (= *Macronix* Bigot, 1857) (Neo)
30. *Dioctobroma* Hull, 1962 (E)
31. *Dioctria* Meigen, 1803 (= *Methylla* Hansen, 1833; including "subgenera" *Bohartia* Hull, 1958c, *Eudioctria* Wilcox & Martins, 1941, *Metadioctria* Wilcox & Martin, 1941, *Nannodioctria* Wilcox & Martin, 1942 [= *Neodioctria* Wilcox & Martin, 1941]) (Nea, P, ?E, ?A)
32. *Dogonia* Oldroyd, 1970 (E)
33. *Echtodopa* Loew, 1866 (= *Echtopoda* Loew, 1871) (Nea)
34. *Enigmomorphus* Hermann, 1912 (= *Enigmomorpheus* Hull, 1962) (Neo)
35. *Eremodromus* Zimin, 1928 (P)
36. *Eriopogon* Loew, 1847 (P)
37. *Eucyrtopogon* Curran, 1923 (Nea)
38. *Euthrixius* Artigas, 1971 (Ch)
39. *Galactopogon* Engel, 1929 (P)
40. *Gonioscelis* Schiner, 1866 (E)
41. *Graptostylus* Hull, 1962 (Neo)
42. *Grypoctonus* Speiser, 1928 (P, O)
43. *Habropogon* Loew, 1847 (= *Dactiliscus* Rondani, 1856; = *Dactyliscus* Marschall, 1873) (P, ?E)
44. *Hadrokolos* Martin, 1959 (Nea)
45. *Harpagobroma* Hull, 1962 (A)
46. *Hermanella* Hull, 1962 (E)
47. *Heteropogon* Loew, 1847 (Nea, P, ?E) (= *Anisopogon* Loew, 1874)
48. *Holopogon* Loew, 1847 (= *Podoctria* Meigen, 1820; including "subgenus" *Dasyholopogon* Martin, 1959) (Nea, P, ?E)
49. *Hullia* Paramonov, 1964 (A)
50. *Hynirhynchus* Lindner, 1955 (E)
51. *Hypenetes* Loew, 1858 (= *Clavator* Philippi, 1865; = *Tillobroma* Hull, 1962) (Neo, E)
52. *Hystrichopogon* Hermann, 1905 (P)
53. *Illudium* Richter, 1962 (P)
54. *Iranopogon* Timon-David, 1955 (P)
55. *Itolia* Willcox, 1936 (Nea)
56. *Jothopogon* Becker, 1913a (P)

57. *Lasiopogon* Loew, 1847 (= *Daulopogon* Loew, 1874; = *Alexiopogon* Curran, 1934b) (Nea, P, O)
58. *Leptochelina* Artigas, 1970 (Ch)
59. *Lissoteles* Bezzi, 1910a (Neo)
60. *Lithoeciscus* Bezzi, 1927 (P)
61. *Lycostomus* Hermann, 1907 (E)
62. *Mecynopus* Engel, 1925a (P)
63. *Metapogon* Coquillett, 1904 (Nea)
64. *Microstylum* Macquart, 1838 (= *Megapollyon* Walker, 1851; = *Megapollion* Bigot, 1857; = *Mimoscolia* Enderlein, 1914b; including "subgenera" *Epiblepharis* Bezzi, 1908, and *Eclipsis* Bezzi, 1908) (Nea, P, E, O, A)
65. *Myelaphus* Bigot, 1882 (= *Myielaphus* Kertész, 1909) (Nea, P)
66. *Nannocyrtopogon* Wilcox & Martin, 1936 (Nea)
67. *Neodioctria* Ricardo, 1918 (A)
68. *Neodysmachus* Ricardo, 1925 (E)
69. *Neopogon* Bezzi, 1910b (Neo, Nea)
70. *Neoscleropogon* Malloch, 1928 (A)
71. *Obelophorus* Schiner, 1866 (Ch)
72. *Oldroydia* Hull, 1956b (= *Toremyia* Hull, 1958d) (O)
73. *Oratostylum* Ricardo, 1925 (E)
74. *Ospriocerus* Loew, 1866 (Nea)
75. *Parastenopogon* Paramonov, 1964 (A)
76. *Phellus* Walker, 1851 (A)
77. *Plesiomma* Macquart, 1838 (= *Dolichodes* Macquart, 1838; = *Plesioma* Schiner, 1866; = *Boropis* Hull, 1962; = *Dapsilochaetus* Hull, 1962; = *Cyrtoprosopa* Hull, 1962) (Neo, Nea)
78. *Pritchardia* Stuardo, 1946 (= *Strobilopygius* Hull, 1956a) (Ch)
79. *Pritchardomyia* Wilcox, 1965 (Nea)
80. *Prolepsis* Walker, 1851 (= *Dizonias* Loew, 1866; = *Sphageus* Loew, 1866; = *Cacodaemon* Schiner, 1866; = *Tolmerolestes* Lynch Arribálzaga, 1881; = *Cacodaemonides* Strand, 1928) (Neo, Nea)
81. *Pseudoholopogon* Strobl, 1898 (P)
82. *Psilinus* Wulp, 1899 (E)
83. *Psilozona* Ricardo, 1912b (A)
84. *Pycnomerinx* Hull, 1962 (E)
85. *Pycnopogon* Loew, 1847 (P)
86. *Rhabdogaster* Loew, 1858 (E)
87. *Rhacolaemus* Hermann, 1907 (E)
88. *Rhadinus* Loew, 1856 (P)
89. *Scleropogon* Loew, 1858 (Nea)
90. *Scylaticus* Loew, 1858 (E, O, ?Neo) (= ? *Euthrix* Philippi, 1865)
91. *Sintoria* Hull, 1962 (Nea)
92. *Sisyrnodytes* Loew, 1856 (E, P)
93. *Spanurus* Loew, 1858 (E)
94. *Stackelberginia* Lehr, 1964 (P)

95. *Stenopogon* Loew, 1847 (Nea, P, ?E, O)
96. *Stichopogon* Loew, 1847 (= *Stilopogon* Costa, 1883; = *Dichropogon* Bezzi, 1910b; = *Echinopogon* Bezzi, 1910b; = *Cryptopogon* White, 1917a) (Nea, P, E, O, A).
97. *Teratopus* Loew, 1858 (E)
98. *Townsendia* Williston, 1895 (Nea, Neo)
99. *Turkmenomyia* Paramonov, 1930 (P)
100. *Wilcoxia* James, 1941 (Nea)
101. *Willistonina* Back, 1909 (Nea)
102. *Zabrotica* Hull, 1958b (Neo)

15. SUBFAMILY TRIGONOMIMINAE ENDERLEIN, *STATUS N.*

(Trigonomimini Enderlein, 1914b; = Xenomyzini G. H. Hardy, 1948; = Damalini Hull, 1962)

Small flies with open marginal cell, prosternum normally complete, no spur on apex of fore tibiae, strongly modified antennal style, without mesopleural or metapleural bristles, head exceptionally wide and short, vertex low, leaving a goggle-eyed appearance, and with deep, mediogenal grooves; female terminalia simple, tubular and not spiny; male genitalia variable.

I have preferred to maintain Enderlein's name for the subfamily, as (i) it has priority, and (ii) the type-genus of the other proposed names (Xenomyzini, Damalini) are based on a nomenclaturally unstable name (*Damalis* or *Xenomyza*).

List of genera:

1. *Bromleyus* D. E. Hardy, 1944 (Nea)
2. *Damalina* Doleschall, 1858 (O)
3. *Damalis* Fabricius, 1805 (= *Xenomyza* Wiedemann, 1817; = *Chalcidimorpha* Westwood, 1835; = *Discodamalis* Karsch, 1887; = *Lasiodamalis* Hermann, 1926; = *Lophurodamalis* Hermann, 1926; = *Aireina* Frey, 1934; = *Protodamalis* Hull, 1962; = *Zygocolon* Hull, 1962) (E, O)
4. *Haplopogon* Engel, 1930b (Nea, P)
5. *Holcocephala* Jaennicke, 1867 (= *Discocephala* Macquart, 1838; = *Helcocephala* Loew, 1874; = *Holocephala* Williston, 1891; = *Arthriticopus* Enderlein, 1914b) (Neo, Nea)
6. *Icariomima* Enderlein, 1914b (E)
7. *Oligopogon* Loew, 1847 (E)
8. *Orrhodops* Hull, 1958c (Nea)
9. *Oxynoton* Janssens, 1951 (E)
10. *Rhipidocephala* Hermann, 1926 (= *Paroxynoton* Janssens, 1953; = *Margaritola* Hull, 1958b) (E)

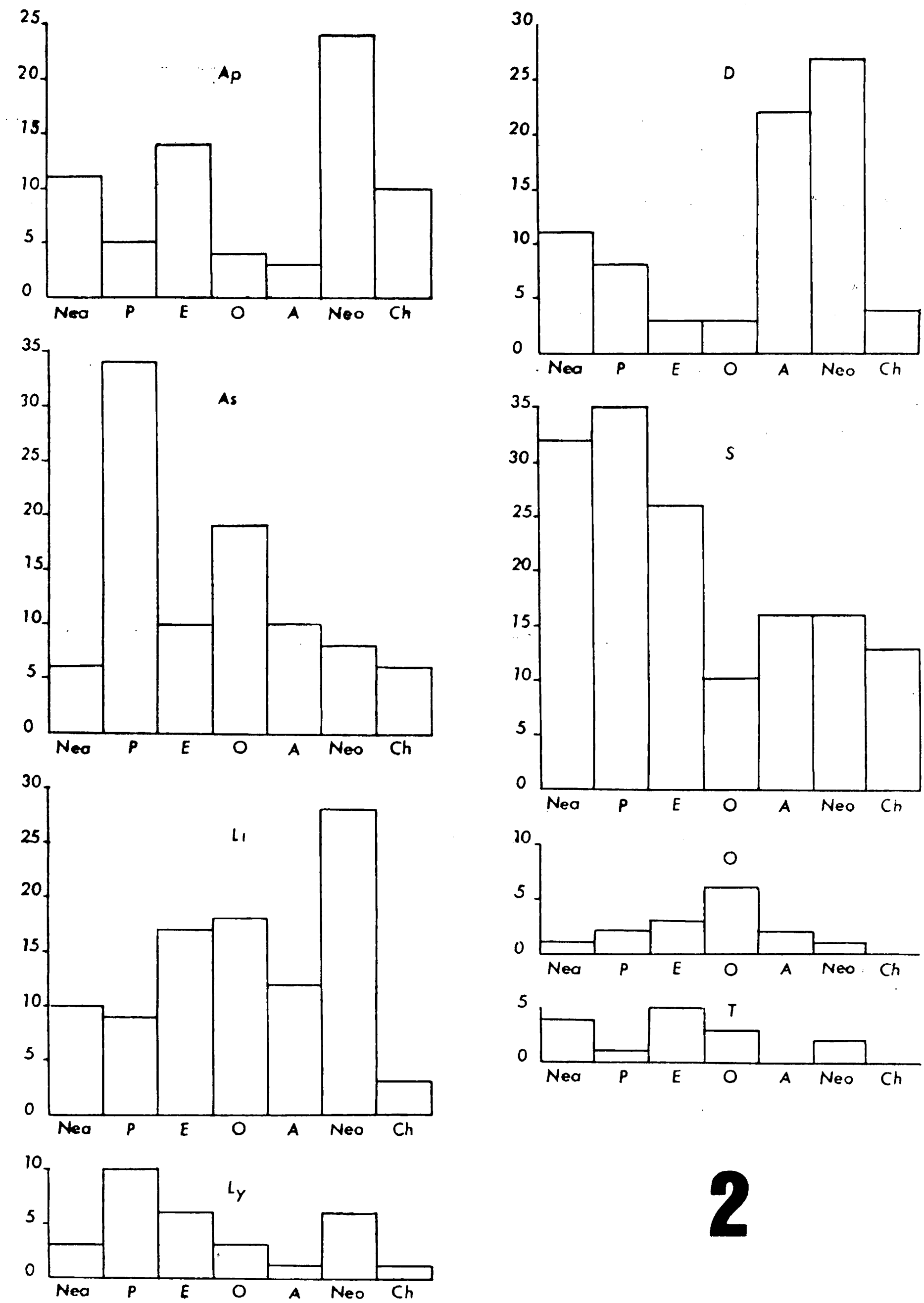

Fig. 2, Geographical distribution of subfamilies (number of genera in each subfamily per zoogeographical region).

11. *Seabramyia* Carrera, 1960 (Neo)
12. *Trigonomima* Enderlein, 1914b (O)

16. GEOGRAPHIC DISTRIBUTION OF SUBFAMILIES

Examination of the histograms (Figs. 2-3) and table discloses the following facts:

1. The Apocleinae are predominantly Neotropical (and Chilean) and Ethiopian. The Nearctic region also has a significant fauna, but it must be considered that most Nearctic genera are really neotropic invaders. The Asilinae, on the contrary, are overwhelmingly Palearctic (also Oriental and Ethiopian, but these regions share many of the Palearctic genera).

The two subfamilies are therefore strongly complementary. Is this a result of competition between two groups with simultaneous, but different origins, one in Laurasia, and the other in Gondwana?

Table

Number of genera per zoogeographical region

	Ap	As	Om	Li	Ly	S	D	T	Total
Nº of nominal genera	55	62	7	68	23	102	69	12	398
Nea	11	6	1	10	3	32	11	4	78
P	5	34	2	9	10	35	8	1	104
E	14	10	3	17	6	26	3	5	84
O	4	19	6	18	3	10	3	3	66
A	3	10	2	12	1	16	22	-	66
Neo	24	8	1	28	6	16	27	2	112
Ch	10	6	-	3	1	13	4	-	37

2. The same result is obtained for the subfamilies Dasypogoninae and Stenopogoninae. The former is extremely abundant in South America and Australia, while the latter is undoubtedly Holarctic, colonizing also the Ethiopian and Oriental regions, as well as the other regions of the world.

3. The Laphriinae are more or less evenly distributed throughout the world, but commoner in the Neotropical and Oriental regions.

4. The Ommatiinae are worldwide (they do not enter Chile, however), and are predominantly Oriental.

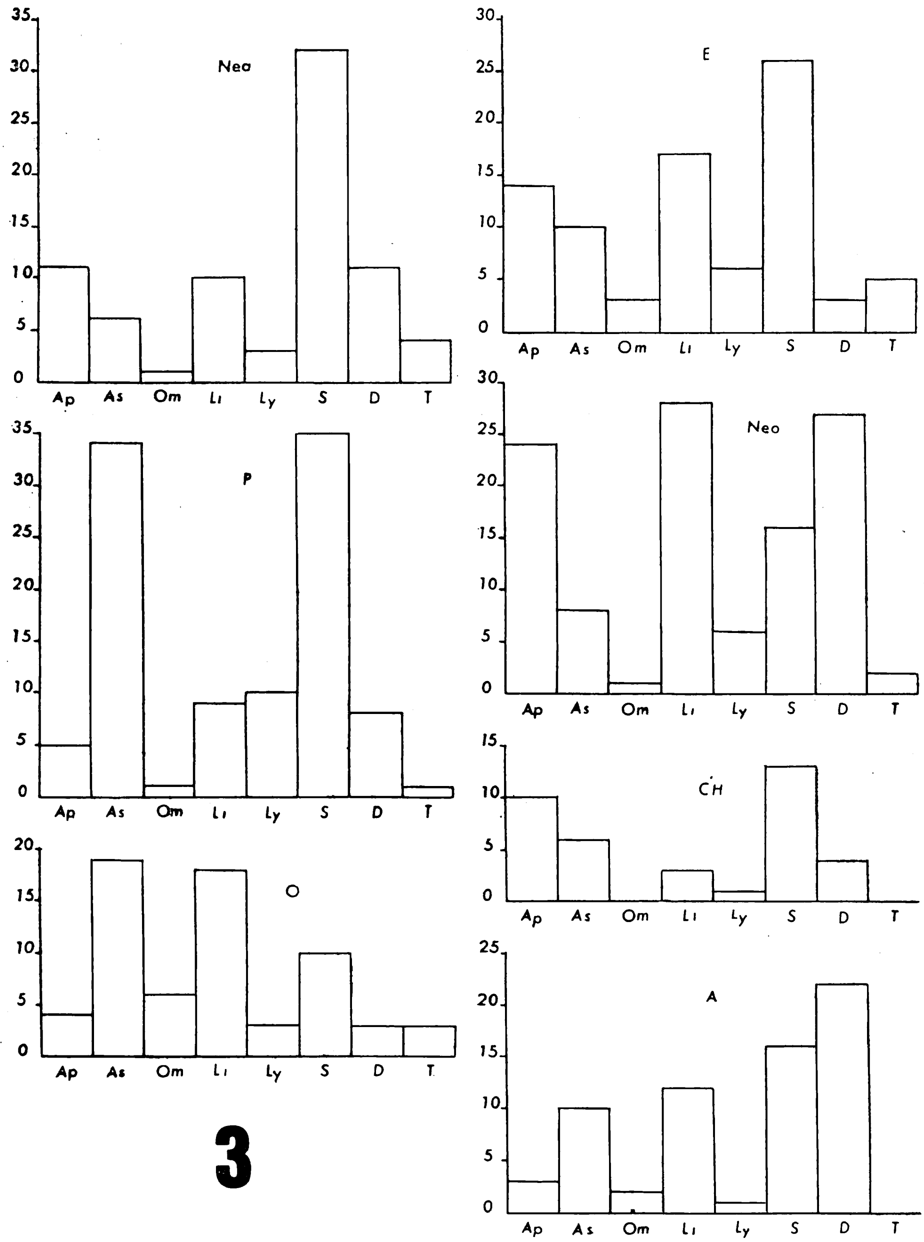

Fig. 3, Faunistic composition of the zoogeographical regions (number of genera of the different subfamilies in each zoogeographical region).

5. The Laphystiinae are common in the Palearctic, Ethiopian and Neotropical regions.

6. The Trigonomiminae are commoner in the Ethiopian and Nearctic regions, and absent in Chile and Australia.

Conversely, examination of the composition of the world's faunal regions shows:

1. The Nearctic Region has representatives of all the subfamilies, relatively few genera of all of them, but a wealth of Stenopogoninae;

2. The same occurs with the Palearctic, but both the Asilinae and Stenopogoninae are very rich in genera;

3. The Oriental Region also has representatives of all the subfamilies, and is very rich in Asilinae and Laphriinae; the Ommatiinae have here their richest domain;

4. The Ethiopian region has a more or less balanced fauna, but Apocleinae, Laphriinae and Stenopogoninae are dominant;

5. The Neotropical Region is very rich in genera of Apocleinae, Laphriinae, and Dasypogoninae;

6. Chile is rich in Apocleinae (also Asilinae) and Stenopogoninae genera, but lacks Ommatiinae and Trigonomiminae;

7. Finally, the Australian region has a relatively good number of genera of Asilinae (very poor in Apocleinae), Laphriinae, Stenopogoninae, and a very rich fauna of Dasypogoninae; it lacks Trigonomiminae.

This is, of course, a very gross analysis of the distribution of the subfamilies. In the forthcoming papers a better study of each one of them will be presented, and the zoogeographic patterns analyzed, taking in consideration all the factors that have influenced the distribution of the several groups — continental drift, migration, competition, dominance, substitution, radiation, ecological adaptations to forested or desert areas, etc.

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1883. On the North American Asilidae (Dasypogoninae, Laphrinae), with a new genus of Syrphidae. *Trans. Amer. Ent. Soc. and Proc. Acad. Nat. Sci. Philad., Ent. Sect.* (1884) *11*: 1-35, 2 pls.

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1893. New or little-known Diptera. *Kansas Univ. Quart. 2*: 59-78.

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1898b. *Asilus hercules* Wied. *Természetrajzi Füzetek 21*: 235-237.

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APPENDIX

LITERATURE ON FOSSIL ASILIDAE (AND LEPTOGASTRIDAE)

BODE, A.

1953. Die Insektenfauna des Ostniedersächsichen Oberen Lias. *Paleontographica.* Stuttgart, (*A*) *103*: 1-375, 15 pls., 1 map. (*Eosilidea fragmentosa*).

COCKERELL, T. D. A.

1908. Two fossil Diptera. *Canadian Ent.* *40*: 173-175, pl. 4. (*Microstylum wheeleri;* Florissant shales).

1909a. New fossil insects from Florissant, Colorado. *Ann. Ent. Soc. Amer.* *2*: 251-256, pl. 28. (*Dioctria? florissantina, Microstylum? destructum, Nicocles miocenicus*).

1909b. Fossil insects from Florissant, Colorado. *Bull. Amer. Mus. Nat. Hist.* *26*: 67-76, pl. 16. (*Asilus peritulus*).

1910. Fossil insects and a crustacean from Florissant, Colorado. *Ibidem* *28*: 275--288. (*Taracticus contusus*).

1911. Fossil insects from Florissant, Colorado. *Ibidem* *30*: 71-82, 3 figs., pl. 3, figs. 1-5. (*Taracticus renovatus, Asilus amelanchieris*).

1913. A fossil asilid fly from Colorado. *Entomologist* *46*: 213-214. (*Cophura antiquella*).

1914. Miocene fossil insects. *Proc. Acad. Nat. Sci. Philad.* *66*: 634-648. (*Saropogon oblitescens, Asilus wickhami;* Florissant shales).

1917. Some fossil insects from Florissant, Colorado. *Proc. U. S. Nat. Mus.* *53* (2210): 239-392. (*Dioctria? pulveris*).

1920. Eocene insects from the Rocky Mountains. *Ibidem* *57* (2313): 233-260, pls. 32-36. (*Asilopsis fusculus;* Green River shales).

1921a. Fossil arthropods in the British Museum. VI. Oligocene insects from Gurnet Bay, Isle of Wight. *Ann. & Mag. Nat. Hist.* *7*: 453-480, 50 figs. (*Proctacanthus fractus, Asilus gurnetensis*).

1921b. Some Eocene insects from Colorado and Wyoming. *Proc. U. S. Nat. Mus.* *59* (2358): 29-39. (*Asilus paleolestes*).

HEER, O.

1847-1849. *Die Insektenfauna der Tertiärgebirge von Oeningen und Radoboj in Croatien* *2*: 1-4 + 269 pp., 17 pls. (*Asilus antiquus, A. deperditus, A. bicolor*).

HELM, O.

1896. Beiträge zur Kenntniss der Insecten des Bernsteins. *Schrift. naturf. Ges.,* Danzig, *9*: 220-231. ("Asilidae").

HEYDEN, C. H. G. VON

1870. Fossilien Diptera aus der Brauenkohle von Rott im Siebengebirge. *Paleontographica,* Stuttgart, *17*: 259. ("*Asilus* sp.").

HULL, F. M.

1957. Tertiary flies from Colorado and the Baltic amber. *Psyche* *64* (2): 37-45, pls. 2-4. (*Eosenoprosopis romeri*).

1960. A new genus and four new species of fossil Diptera from Montana and Colorado. *Contr. Mus. Pal. Univ. Michigan 15* (11): 269-279, 4 pls. (*Holopogon archilestes;* Ruby Basin, Montana).

162. (See General references). (Genus *Palaeomolobra,* for *Senoprosopis antiquus* James).

JAMES, M. T.

1939. A preliminary review of certain families of Diptera from the Florissant Miocene beds. *Jour. Pal. 13*: 42-48, 5 figs. (*Lestomyia miocenica, Caturgopsis praecursor, Senobasis borealis, Asilus florissantinus, Philonicus saxorum, Senoprosopis antiquus*).

LEWIS, S. E.

1972. Two new species of fossil robber-flies (Diptera: Asilidae) from the Ruby River Basin (Oligocene) of Southwestern Montana. *Ann. Ent. Soc. Amer. 65* (1): 275-277, fig. 1 A-B. (*Dioctria? jamesi, Senoprosopis beckeri*).

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1850. Ueber den Bernstein und die Bernsteinfauna. *Progr. Realschule zu Meseritz 1850*: 1-4, 1-44. (*Holopogon pilipes, Asilus angustifrons, A. trichurus*).

MELANDER, A. L.

1946. Some fossil Diptera from Florissant, Colorado. *Psyche 53* (3-4): 43-48. (*Leptogaster prior, Asilus curculionis*).

1949. A report on some Miocene Diptera from Florissant, Colorado. *Amer. Mus. Nov. 1407*: 1-63. (*Senoprosopis eureka*).

MEUNIER, F. A.

1906. Sur deux insectes (hyménoptère et diptère) du copal fossile de Zanzibar, et sur un "asilide" (diptère) du copal récent de Zanzibar. *Rev. Sci. Bourbonnais,* Moulins, *1906*: 59-62, 1 pl. (*Leptogaster erecta*).

1908. Les Asilidae de l'ambre de la Baltique. *Bull. Soc. ent. France 1908*: 18-20 (*Asilus klebsii*).

1915. Nouvelles recherches sur quelques insectes des plâtrières d'Aix en Prevence *Verh. Koningl. Akad. Wetenschappen te Amsterdam* (2) *18* (5): 1-17, 5 pls. (*Asilus snnoisiensis*).

SCUDDER, S. H.

1878. The fossil insects of the Green River shales. *Bull. U. S. Geol Surv. Terr. 4*: 747-776. (Asilidae, p. 751).

1881. The Tertiary lake-basin of Florissant, Colorado, between Sauth and Hayden Parks. *Ibidem 6* (2; art. 11): 279-300. ("Asilidae", p. 291).

1890a. The Tertiary insects of North America. *Rep. U. S. Geol. Surv. Terr. 13*: 1-734, 28 pls. (*Stenocinclis anomala;* Green River shales).

1890b. A classed and annotated bibliography of fossil insects. *Bull. U. S. Geol. Surv. Terr. 69*: 1-101.

SERRES, P. M. T. DE

1829. *Géognosie des terrains tertiaires, ou tableau des principaux invertébrés des terrains marins tertiaires du midi de La France,* xcil + 276 pp., 6 pls., 3 tables. Montpellier. (*Asilus* sp., Aix en Provence).

Théobald, N.

1937. *Les insectes fossiles des terrains oligocènes de France,* 473 pp., 7 maps, 29 pls. Nancy. (*Leptogaster falloti;* Camoins, France).

Timon-David, J.

1944. Insectes fossiles de l'Oligocène inférieur de Camoins (Bassin de Marseille). Pt. 1. Diptères, Brachycères. *Bull. Soc. ent. France 48* (1943): 128-134, 1 pl., 1 fig. (*Machimus kollmani*).

Unger, F.

1841. Fossilen Insecten Radoboj. *Nova Acta Acad. Caes.-Leopold.-Carol. Natur. Cur. 19*: 412-428, 2 pls. (*Leptogaster hellii*).