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STUDIES OF MYDIDAE (DIPTERA) SYSTEMATICS AND EVOLUTION

I. A PRELIMINARY CLASSIFICATION IN SUBFAMILIES, WITH THE DESCRIPTIONS OF TWO NEW GENERA FROM THE ORIENTAL AND AUSTRALIAN REGIONS

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CONTENTS

ABSTRACT

A preliminary classification of the world Mydidae in 9 subfamilies is proposed:

1. Anomalomydinae, subfam. n. (only genus, Anomalomydas, *gen. n., for* Miltinus mackerrasi *Norris); exclusively Australian;*

2. Apiophorinae, subfam. n. (5 genera); Chile and Australia;

3. Cacatuopyginae. subfam. n. (only genus, Cacatuopyga, *gen. n., for* Mydas fruhstorferi *Wulp); Oriental;*

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1. Museu de Zoologia, Universidade de São Paulo.
2. Mohler Place, Anaheim, California.

4. Diochlistinae Bequaert (3 genera); Chile and Australia;

5. Ectyphinae Wilcox & Papavero (3 genera); South Africa, s. w. United States and Mexico;

6. Leptomydinae, subfam. n. (5 genera); Palearctic, Nearctic, invading n. w. corner of South America;

7. Mydinae Latreille (5 genera); exclusively American;

8. Rhopaliinae, subfam. n. (4 genera); Palearctic (Mediterranean subregion), one genus in n. e. Brazil;

9. Syllegomydinae Bequaert (23 genera); predominantly Ethiopian, a few elements invading the Palearctic and Oriental regions;

10. One unplaced genus, Parectyphus *Hesse (South West Africa, Namib Desert), insufficiently characterized.*

A preliminary key to the subfamilies, a list of their respective genera, their distribution and hypothetical history of phylogeny, are given.

1. INTRODUCTION

The last general classification of the Mydidae on a worldwide basis is over a century old (Gerstaecker, 1868). Since Gerstaecker's Key, genera have been described at a very slow rate, almost one by one, until the present. The group was always so poorly known that tentative keys were not made for the establishment of a general classification. Séguy (1928c) believed in fact that such a thing would be "difficile sinon impossible".

Bequaert (1961a, 1963) proposed the first classification in subfamilies, but his work dealt especially with the Ethiopian and Palearctic faunas.

With the recent contributions to the knowledge of the Mydidae, the family became better structured, and more or less ready for a general classification. Hesse alone (1969, 1972) published 14 new genera, 2 new subgenera, and 124 new species for South Africa and South West Africa; Wilcox & Papavero (1971) revised the American genera of Mydidae, describing a few new ones, and proposed one more subfamily.

The Mydidae have up to now 51 genera accepted as valid, and two "subgenera", that will prove in the future to be either valid genera or synonyms. Several new genera are already known, and will be described by us in the forthcoming papers of this series.

Study of several collections in the Americas and Europe, containing representatives of almost all the known genera, and the examination of types of many authors who have dealt with mydids, enabled the authors to have a general view of the family's structure, and to propose the present classification.

2. MATERIALS AND METHODS

The basic collections used for this series were those of the Museu de Zoologia da Universidade de São Paulo (MZUSP), and that of the junior author (JW). The senior author had the opportunity to visit most of the American and European museums, in 1968, 1970, and

1971-72. A list of all the collections studied has been published elsewhere (Papavero, 1973a).

This preliminary classification is necessarily tentative, and incomplete. In the subsequent papers the several subfamilies will be treated in more detail, better descriptions will be given, and the classification tested. In the end of this series, new keys and diagnoses, and a general interpretation of the evolution of the Mydidae will be published.

The list of intended papers is the following:

1. A preliminary classification in subfamilies, with the descriptions of two new genera from the Oriental and Australian regions;
2. Classification of the Mydinae, with the description of a new genus and a revision of *Ceriomydas* Williston;
3. The genus *Messiasia* d'Andretta (Mydinae) in the Americas;
4. *Mydas* Fabricius and allies (Mydinae) in the Americas;
5. Subfamilies Ectyphinae, Rhopaliinae, and Leptomydinae;
6. Subfamily Diochlistinae;
7. Subfamily Apiophorinae;
8. Subfamily Syllegomydinae;
9. Summary of Mydidae classification and evolution;
10. World catalogue of the Mydidae.

Abbreviations used herein are the following:

A	Australian (region)
An	Anomalomydinae
Ap	Apiophorinae
BMNH	British Museum (Natural History), London
Ca	Cacatuopyginae
Ch	Chilean (subregion)
COPN	Universitetets Zoologiske Museum, Copenhagen
Di	Diochlistinae
E	Ethiopian (region)
Le	Ectyphinae
Le	Leptomydinae
MNHN	Muséum National d'Histoire Naturelle, Paris
My	Mydinae
Nea	Nearctic (region)
Neo	Neotropical (region)
O	Oriental (region)
P	Palearctic (region)
Rh	Rhopaliinae
Sy	Syllegomydinae
ZMA	Zoölogisch Museum, Amsterdam

Drawings were made with the help of a camera lucida; in the genitalia drawings hairs and bristles were not represented and the gonopods (or fused gonopods and hypandrium) were shadowed. Measurements are given in millimeters. Morphological terms follow Wilcox & Papavero (1971).

3. ACKNOWLEDGMENTS

Study of the several collections of mydids was made possible through a Grant of the John Simon Guggenheim Memorial Foundation, which enabled the senior author to visit North American and European museums during 1971-1972.

Previous visits to those museums were undertaken in 1968 (USA and Canada) and in 1970 (France and England), under Grants "Biológicas 68/604" of the Fundação de Amparo à Pesquisa do Estado de São Paulo, and "3289/69" of the Conselho Nacional de Pesquisas do Brasil, respectively. Important Neotropical collections of Mydidae have been acquired by the MZUSP with the help of the Fundação de Amparo à Pesquisa do Estado de São Paulo (Grants "Biológicas 69/882 and 69/883").

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To Dr. D. Colless, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia, our deepest gratitude for important material from Australia.

To the curators of the several collections visited or borrowed, our best thanks.

4. A BRIEF HISTORY OF MYDIDAE CLASSIFICATION

4.1. First period (1773-1831)

The first mydid fly was described and illustrated by Drury, in 1773, and named *Musca clavata.* This species was transferred to *Bibio* by Fabricius (1775), together with *illucens* (now *Hermetia,* Stratiomyidae). The same species was described by De Geer (1776), in his 'Mémoires pour servir à l'Histoire des Insectes', as *Nemotelus asiloides.*

The genus *Midas* was erected by Fabricius (1794) to include the above species. Latreille (1796, 1802) recognized the genus, and in 1810 created the family 'Mydasii' to receive it, designating *Musca clavata* Drury as the type-species of *Midas.*

New species were added by Illiger (1801; North America) and Olivier (1811; South America and Egypt). Olivier had captured his own specimens while travelling in Egypt and published the first biological note:

> "Les Mydas, ainsi que nous l'avons dit, se rapprochent des Asiles par la manière de vivre. Ils vivent de rapine & font une guerre continuelle aux autres insectes, qu'ils atrapent en volant, & dont ils retirent tous les sucs au moyen de leur trompe. On les voit attaquer les Hyménoptères les plus forts & les mieux armés, & les emporter entre leurs longues pattes, sans que l'aiguillon de ceux-ci puisse les atteindre. Leurs larves nous sont inconnues."

Thunberg (1818) described a new species from Brazil. Lamarck (1816), in the 'Histoire Naturelle des Animaux sans vertèbres' also recognized the genus *Midas,* and considered *Thereva* as its synonym.

Wiedemann (1819, 1820, 1821, 1824, 1828, 1830) described many new species from the Cape, Portugal, Brazil, India, Uruguay, Surinam, Cuba, and the United States.

Duméril (1823) placed *Midas* among the genera of his 'family' Aplocera or Simplicicornes, and illustrated *M. filatus.*

Latreille (1829) erected the second genus in the family, *Cephalocera,* for *Midas longirostris* Wiedemann, from the Cape.

Wiedemann (1831) revised the genus *Midas,* including 23 species, most of them illustrated in magnificent colored plates.

4.2. Second period

After Wiedemann's revision, many new species were described by several authors — Perty (1833), Macquart (1834, 1838), Guérin-Méneville (1835), Westwood (1835), and Walker (1837).

Macquart (1834) included the 'Midasiens' as a tribe of his 'family' Tanystoma, together with the 'Asilides, Hybotides, Empides, Vésiculeux, Nemestrinides, Bombyliers and Anthraciens'. The same classification was maintained by him in 1838, when he described a new genus, *Rhopalia,* for *olivieri* Macquart, from Egypt.

In his 'Synopsis of the Dipterous Family Midasidae' (1841) Westwood listed 39 species in *Midas,* 8 in *Cephalocera,* and referred his genus *Apiocera* to this family, based on the complex wing venation. He rejected *Rhopalia* because it differed "only [sic] in the alteration in the veining of the wings and the thickened mass at the extremity of the antennae. If, however, this is admitted", he proceeded, "it will become necessary to form another for my *M. auripennis,* which would, I consider, be unnatural." Westwood also said that the larvae of *M. tricolor* Wiedemann, observed by MacLeay in Cuba, were "parasitic" upon the larvae of the giant Prionidae.

Macquart (1846-1849) added more species, and in 1848 erected *Dolichogaster,* for *Midas brevicornis* Wiedemann, from Brazil.

Dufour (1850), Macquart (1850), Rondani (1850), Blanchard (1852), Bigot (1854, 1856, 1857), Walker (1854, 1858, 1859), Loew (1860, 1866), Bellardi (1861), Bertoloni (1862), and Jaennicke (1867) published several new species or comments, but offered no real contribution to the classification of the family.

Walsh (1864) published the first paper on the biology of the group.

Philippi (1865) erected *Apiophora* for some Chilean species.

Finally, in 1868, Gerstaecker revised the group, and proposed seven new genera (*Leptomydas, Ectyphus, Diochlistus, Mitrodetus, Triclonus, Perissocerus,* and *Miltinus*), rendering the classification of the family more natural. His paper included 89 species, distributed in 11 genera (he did not accept *Apiophora* Philippi), as follows:

1.	*Diochlistus*	1	(Australia)
2.	*Triclonus*	4	(Australia)
3.	*Mitrodetus*	3	(Chile)
4.	*Cephalocera*	11	(Africa)
5.	*Leptomydas*	9	(North America, Europe, Africa)
6.	*Rhopalia*	4	(N. Africa)
7.	*Perissocerus*	1	(N. Africa)
8.	*Miltinus*	10	(Australia)
9.	*Ectyphus*	1	(S. Africa)
10.	*Mydas*	44	(Americas, India, Celebes, ? Australia)
11.	*Dolichogaster*	1	(S. America)

Gerstaecker's key to the genera ran as follows:

1. Zwischen der Gabelzelle und dem Hinterrande des Flügels liegen drei Zellen 2
   Zwischen der Gabelzelle und dem Hinterrande des Flügels liegen zwei zellen 4

2. Gabelzelle lang gestielt; Rüssel sehr lang, ohne Endlippen .... *Mitrodetus*
   Gabelzelle kurz gestielt; Rüssel kürzer, mit Endlippen 3

3. Untergesicht kurz, zurückweichend; Rüssel horizontal hervorstehend .... *Diochlistus*
   Untergesicht lang, senkrecht; Rüssel senkrecht herabsteigend .... *Triclonus*

4. Endkeule der Fühler auffalend gross und monströs gebildet ...... *Perissocerus*
   Endkeule der Fühler von gewöhnlicher Bildung 5

5. Endsegment des weiblichen Hinterleibes ohne Stachelkranz 10
   Endsegment des weiblichen Hinterleibes mit Stachelkranz 6

6. Gabelzelle an der Basis ohne Aderanhang .... *Rhopalia*
   Gabelzelle an der Basis mit Aderanhang 7

7. Rüssel ohne Endlippen .... *Cephalocera*
   Rüssel mit Endlippen 8

8. Beide Aeste der Gabelader in die erste Längsader mündend 9
   Nur der vordere Ast der Gabelader in die erste Längsader mündend .... *Miltinus*

9. Die kleine Querader am Hinterrande des Flügels fehlend; Rüssel lang hervorgestreckt .... *Leptomydas*
   Die kleine Querader am Hinterrande des Flügels vorhanden; Rüssel rudimentär, kaum aus der Mundöffnung hervortretend .... *Ectyphus*

10. Fühler langgestreckt; die Aeste der Gabelader getrennt in die erste Längsader ausmündend .... *Mydas*
    Fühler kurz; die Aeste der Gabelader, zuvor vereinigt, in die erste Längsader ausmündend .... *Dolichogaster*

4.3. Third period (1869-1961)

During the almost hundred years that followed Gerstaecker's revision, and the new classification of the Mydidae proposed by Bequaert in 1961, several new genera were proposed: *Harmophana* Thomson, 1869; *Phyllomydas* Bigot, 1880; *Eremomydas* Semenov Tian-Shanski, 1896; *Ceriomydas* Williston, 1898; *Syllegomydas* Becker, 1906; *Halterorchis, Haplomydas, Mydaselpis,* and *Nomoneura* Bezzi, 1924; *Lampromydas* Séguy, 1928; *Nemomydas* and *Opomydas* Curran, 1934; *Rhopaliana* Séguy, 1934; *Midacritus* Séguy, 1939; *Heteromydas* D. E. Hardy, 1944; *Paramydas* Carrera & d'Andretta, 1948; *Messiasia* d'Andretta, 1951; and *Eremohaplomydas* Bequaert, 1959.

A quantity of papers describing new species, partial revisions, catalogues, faunistic papers, and other notes, were published in several regions:

1. For the Palearctic : Walker (1871), Semenov Tian-Shanski (1896, 1922), Portchinsky (1900), Verrall (1909), Arias (1912, 1914 a-c), Becker & Stein (1913), Hermann (1914), Surcouf (1920), Bezzi (1921, 1924 a-b), Villneuve (1926), Séguy (1927, 1934, 1935, 1941a-b); and Sack (1934);

2. For the Nearctic : Loew (1872), Osten Sacken (1877), Johnson (1912, 1913, 1926, 1933), Cresson (1907), Hine (1903), Adams (1904), Code (1919), Cresson (1919), Curran (1934, 1953 a-b), James (1938), D. E. Hardy (1943, 1944, 1950), and Steyskal (1956);

3. For the Neotropical : Lynch Arribálzaga (1883, 1891 a-b), Roeder (1883), Osten Sacken (1886), Williston (1886, 1898), Austen (1909), Séguy (1939), Reed & Ruiz (1941), Carrera & d'Andretta (1948), Paramonov (1948), d'Andretta (1951), d'Andretta & Carrera (1951), Curran (1951), and Séguy (1951);

4. For the Ethiopian : Bezzi (1924a-b), Brunetti (1929), Séguy (1929, 1931, 1934, 1940, 1960), Sack (1935), Bequaert (1938, 1940, 1951, 1959), and Stuckenberg (1955);

5. For the Australian : G. H. Hardy (1925, 1942, 1949), Mackerras (1928), Norris (1938), and Paramonov (1960, 1955, 1961);

6. For the Oriental : Osten Sacken (1881), Wulp (1881, 1896a-b), and Brunetti (1912, 1913, 1920).

Cockerell described a fossil mydid from Colorado (1913). Jahn (1930) studied the anatomy of *Mydas*. Papers on biology were published by Berg (1899), Greene (1917), Zikán (1942, 1944), and Genung (1959).

No suprageneric classification was proposed, and most of the genera were already needing revisions, since most of the authors had no idea of zoogeography and evolution, and lumped several different genera under the same name.

4.4. Fourth period (1961 to present)

M. Bequaert was the first to employ the male genitalia in the classification of mydids, and proposed a division of the family based mainly on the structure of the aedeagus. The names he proposed in 1961a did not conform to the Code of Zoological Nomenclature and were changed in 1963; his 1961 names are given in parentheses in the key below:

1. Aedeagus with two tubes (Type-genus, *Syllegomydas* Becker) (Heteromydainae) .... *Syllegomydainae*
   Aedeagus with a single tube 2
2. Veins M_1 and M_2 combined (Type-genus, *Mydas* Fabricius) (Orthomydainae Oligoneurinae) .... *Mydainae*
   Veins M_1 and M_2 separated (Type-genus, *Diochlistus* Gerstaecker) (Orthomydainae Polyneurinae) .... Diochlistinae

Bequaert proposed some additional genera : *Pseudonomoneura* (1961), and *Afroleptomydas, Afromydas,* and *Heteromydas* (1963).

In 1969 Hesse described for South Africa 12 new genera, 2 subgenera, and 108 species. The new generic categories created were : *Agarepemius, Arenomydas, Cephalocerodes, Lachnocorynus, Namadytes, Namamydas, Neolaparopsis, Nomoneuroides, Nothomydas, Notobates* (as subgenus), *Notosyllegomydas, Oreomydas,* and *Vespiodes.* He also subdivided the Syllegomydinae in 3 tribes : Cephalocerini, Mydaselpini, and Syllegomydaini. In 1972 the same author synonymized *Namamydas* with *Namadytes,* since both genera were based on sexual differences alone, and erected the new genera *Namibimydas, Mimadelphus,* and *Parectyphus,* and the new tribe Halterorchini.

Catalogues of the Nearctic and Neotropical regions were published by Curran (1965) and Papavero & Wilcox (1968), respectively. New species were described by Cole (1970), and Lyneborg (1970).

Gibson (1965) published some notes on the oviposition of *Mydas.*

Finally, in 1971, Wilcox & Papavero described three new genera for the Americas (*Plyomydas, Pseudorhopalia,* and *Eumydas*), bringing the total number of valid genera up to 51; in the same paper a key to subfamilies was published, and the new subfamily Ectyphinae proposed.

5. KEY TO SUBFAMILIES

This key is still highly tentative, and sometimes includes characters of only one sex; it will be improved, and after the revisions of the several subfamilies, it will be republished into a more complete and adequate form.

1. Hind metatarsus about five times as long as wide 2
   Hind metatarsus shorter, never five times as long as wide 4
2. Veins M_1 and M_2 separated (Australia, Chile, Argentina) .... DIOCHLISTINAE Bequaert
   Veins M_1 and M_2 coalesced, forming a single vein 3
3. Anal cell widely open; relatively small, slender flies; hind trochanters only with bristles; hypandrium fused to gonopods; dististyli absent (Australia) .... ANOMALOMYDINAE, subfam. n.
   Anal cell closed and petiolate; medium-sized, robust flies; hind trochanters with 1-5 spines; hypandrium free, dististyli present (s. w. USA, Mexico; South Africa) .... ECTYPHINAE Wilcox & Papavero

4. Second submarginal cell usually widely open, i. e., R_5 ends in C, far from tip of R_1 5
Second submarginal cell very narrowly open, closed, or closed and petiolate, i. e., R_5 ends either in C very near tip of R_1 or in R_1 6

5. Hind tibiae cylindrical (Mediterranean subregion; N. E. Brazil) .... RHOPALIINAE, subfam. n.
Hind tibiae with ventral keel (carinate) (Chile, Argentina, southern Brazil; Australia). .... APIOPHORINAE, subfam. n.

6. Hind tibiae cylindrical 8
Hind tibiae carinate 7

7. Male aedeagus with a single tube; ♀ terminalia with apical hairs (Americas) .. .. MYDINAE Latreille
Male aedeagus with 3 elements; ♀ terminalia with spines on acanthophorites (Ethiopian; a few elements in the Palearctic and Oriental regions) .... SYLLEGOMYDINAE Bequaert (part)

8. Hypandrium free from the basistyli; ♀ terminalia with apical hairs (Oriental region) .... CACATUOPYGINAE, subfam. n.
Hypandrium coalesced with basistyli 9

9. Aedeagus with 3 elements (Ethiopian; a few elements in the Palearctic and Oriental regions) .... SYLLEGOMYDINAE Bequaert (part)
Aedeagus a single tube (Holarctic; Mexico; Peru) .... LEPTOMYDINAE, subfam. n.

6. DESCRIPTION OF SUBFAMILIES

6.1. Subfamily **ANOMALOMYDINAE,** New

Small, delicate, slender flies; they can be immediately distinguished from all other subfamilies and genera of the family by the widely open anal cell. Additional characters are given in the description of the genus.

Type-genus, *Anomalomydas,* gen. n.

Anomalomydas, gen. n.

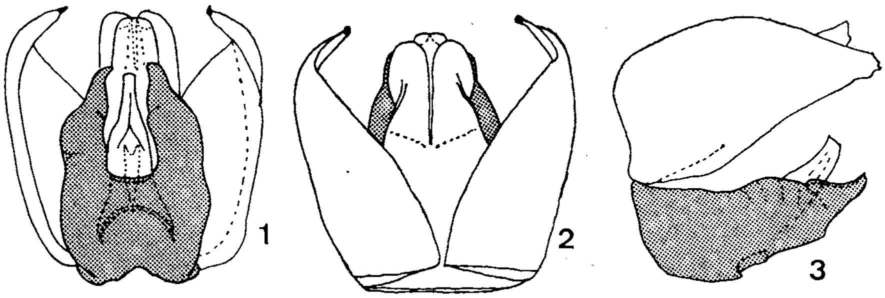
Miltinus Gerstaecker of Norris, 1938 : 46, and of Paramonov, 1950 : 8, 12; 1961 : 103 (part; misident.).

Head in anterior view about one and one-half times as broad as high; face at antennae nearly one-half width of head; facial gibbosity well developed; oral margin about opposite lower eye margin. Stem of proboscis very short; labella oblongate, subequal to length of oral cavity. Lower part of frons noticeably swollen, bare, shining, black. Antennae inserted on the lower edge of the frontal bulge, segment 1 cylindrical and about two times as long as broad; 2 about one-third length of 1 and about one and one-half times as broad as long; 3 cylindrical and more than two times as long as 1; club twice as long as 1-2, about one-half as wide as long.

Mesonotum elongate, with short, semierect hairs on dorsocentral rows, and on anterior and lateral margins, on humeri and postalar calli; central and dorsocentral stripes, anterior and lateral margins, pollinose. Scutellum and arms bare, sparsely pollinose. Postscutellum smooth, bare, pollinose. Pleura bare, except for some very short hairs on supero-posterior part of pteropleura.

Abdomen long and slender, smooth, with only very short and very sparse, recumbent hairs, on all tergites and sternites; in females nearly entirely bare. Bullae (if present) indistinct. Male genitalia as in Figs. 1-3. Female terminalia with a circlet of long and slender spines on the acanthophorites.

Legs very slender. Hind femora about 10 times as long as broad, venter with about 12 spine-like, slender bristles, arranged in two irregular rows. Hind tibiae cylindrical, with several slender bristles on venter and apex. Hind metatarsus about five and one-half times as long as broad and slightly shorter than segments 2-5.



Anomalomydas mackerrasi (Norris), male genitalia : 1, ventral view; 2, dorsal view; 3, lateral view.

Alulae with a sparse fringe of short, fine hairs. Wings about four times as long as broad. Marginal and submarginal cell 1 closed; R_3 present as a stump vein; submarginal cell 2 widely open, i. e., R_5 ends in C, far from tip of R_1; M_1 and M_2 coalesced, forming a single vein; posterior crossvein (M_{3+4}) present; anal cell widely open, 1A ending far from tip of Cu_1; axillary lobe about twice as long as broad. Ambient vein complete.

Length, 10-12.5 mm.

Type-species, *Miltinus mackerrasi* Norris.

The open anal cell separates at once this genus from all other genera in the family. This very primitive character, associated with other primitive conditions, such as the length of the metatarsus, the slender hind femora, the absence of tuberculate spines on the hind femoral venter, and with other derived characters, such as the presence of the frontal bulge, the short proboscis, the wing venation, etc., make *Anomalomydas* a unique genus within the family. We have accordingly segregated it in a special subfamily.

Paramonov (1950, 1961) recognized the open anal cell and the presence of the frontal bulge as characteristics which separated *mackerrasi* and *australicus* from the other *Miltinus*, but did not erect at least a separate genus for them.

As to the biology, ecology, and immature stages of this genus, Norris (1938 : 47-48) published the following notes :

"The species *(mackerrasi)* is common from January to March about the Biology Buildings of the University at Crawley, and odd females have been collected south of Fremantle, and at Applecross, a few miles east of Fremantle.

On hot, still days dozens of specimens may be seen in the grounds of the Biology Buildings, where the males frequent the sunlit walls, tree-trunks, picket fences, and even the top of a packing case standing in the open. Curiously enough the males are seldom seen upon the ground, the usual habitat for Mydaids. Females are evidently much fewer in numbers than males, and usually inhabit the ground.

When the temperature is high the males are very active and may be seen hovering rapidly up and down the surface of tree trunks and walls. Every newcomer to a favourable situation is immediately investigated by the flies already there, and many cases have been observed of males attempting to pair with other males. Pairing takes place readily in captivity.

No evidence has been secured as to feeding habits. The mouth parts are never smeared with pollen as is often the case with Apioceratidae. Dissected specimens have been found with colourless transparent fluid filling the food reservoir.

Occasionally specimens fall victims to the small jumping spiders which frequent the walls.

A curious feature of the external anatomy of this species is that the dorsal surface of the neck-membrane protrudes as a small, reddish vesicle. This can sometimes be seen to pulsate actively when the insect is given warmth and light, and as the movements are synchronised with the respiratory movements of the abdomen, presumably the sac contains a diverticulum of the respiratory system. The pulsation is very rapid but does not occur continuously. Other Mydaid examined have a similar bulge in the dorsal neck membrane."

"*Note on Life History* : Early in February 1936 a male and female were placed together in a glass vessel and were observed to pair several times. After an interval of about two days the female laid three eggs, which were rather football-shaped and dull yellow in colour (1.34 mm X 0.52 mm). A fortnight later these eggs hatched, disclosing three slender shining white larvae, one of which was preserved. The other two were placed in a petri-dish with sand and some wood debris. Some days later one larva could not be recovered, indicating a possible case of cannibalism.

A week after hatching the remaining larva was seen to be undergoing ecdysis, the process taking several days before completion.

The larva was given a broken egg of a phasmid *(Podacanthus sp.)* to feed upon, and was seen to bury its head in the yolk, which was later visible filling the alimentary canal. Unfortunately the larva did not survive until the third instar, the diet provided no doubt proving unsuitable.

First instar larva : Length 2.5 mm. Differs from second instar chiefly in character of head capsule, which is larger in proportion to the body, different in shape and less strongly sclerotised.

Second instar larva : Length 3.3 mm. Shining and creamy white in colour. Body roughly cylindrical, but rather flattened ventrally.

Head capsule with a few weak bristles. Details of mouthparts unfortunately not determinable.

Thoracic segments each bearing a pair of slender bristles ventrally. The abdominal segments bear laterally a slightly projecting flange, which rather breaks the cylindroid contour of the body. This flange is divided up into three slight lobes in each segment.

Body segments 5-9 each have a trasverse row of four small pseudopods near the anterior edge of the ventral surface.

Terminal segment roughly conical, smoothly rounded apically, flattened ventrally. This segment has a very few weak bristles and bears the anus on the ventral surface."

List of species

australicus (Paramonov), 1950 : 12 (*Miltinus*). Type-locality : Australia, South Australia, Leigh Creek. Distr. — Australia (South Australia). Type ♀, South Australian Museum. *N. comb.*

mackerrasi (Norris), 1938 : 46, pl. 1, figs. B (wing), C (head, lateral view), D (apex of male abdomen, lateral view), E (head and first two segments of lst instar larva), F (second instar larva) (*Miltinus*). Type-locality : Australia, Western Australia, Crawley, Fremantle, and Applecross. Distr. Australia (Western Australia). Ref. — Paramonov, 1950 : 14 (additional records). Types ♂ ♀, Perth Museum. *N. comb.*

6.2. Subfamily **APIOPHORINAE**, new

The Apiophorinae may be recognized by the following combination of characters : hind metatarsus never five times as long as broad, veins M_1 and M_2 coalesced, forming a single vein, anal cell closed and petiolate, second submarginal cell usually widely open, and hind tibiae with a ventral keel; male genitalia with hypandrium completely fused to the basistyli, and the dististyli absent; female terminalia with spines on the acanthophorites or sometimes only with hairs.

Type-genus, *Apiophora* Philippi, 1865.

List of genera: 1. *Apiophora* Philippi, 1865 (Ch) ; 2. *Eumydas* Wilcox & Papavero, 1971 (Neo) ; 3. *Midacritus* Séguy, 1939 (Ch) ; 4. *Miltinus* Gerstaecker, 1868 (A) ; 5. *Paramydas* Carrera & d'Andretta, 1948 (Ch).

6.3. Subfamily **CACATUOPYGINAE**, new

Medium-sized flies, characterized by the short, hind metatarsus, the coalesced veins M_1 and M_2, the closed anal cell, the closed second submarginal cell, the hind tibiae cylindrical, the male genitalia with a free hypandrium, only laterally fused to the basistyli, dististyli absent, the aedeagus formed by a single tube, but with a bifid crest on dorsal surface, and the female terminalia only with apical hairs. Other characters will be found in the description of the genus.

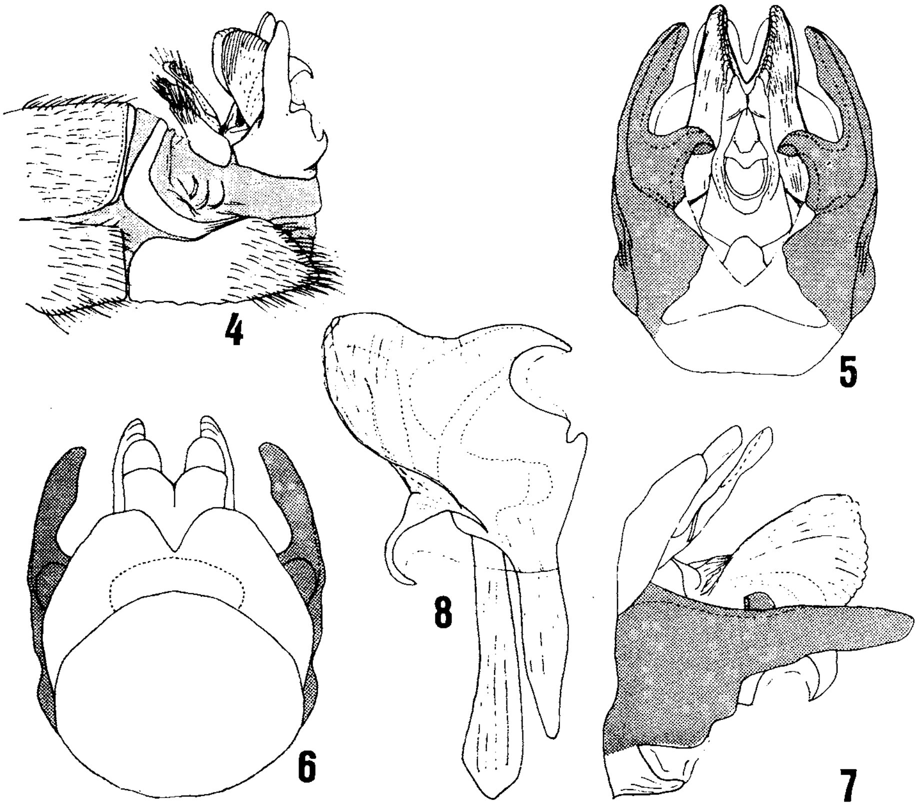
Type-genus, *Cacatuopyga,* gen. n.

Cacatuopyga, gen. n.

Head in anterior view about one and one-half times as broad as high; face at the antennae about two-fifths width of head; oral margin nearly opposite the lower eye margin; facial gibbosity moderately prominent. Stem of proboscis about twice as long as the length of the oral cavity; labella attached to apical one-third and on the same axis of stem; palpi moderately long, about half the length of the stem, and on the same axis of stem; palpi moderately long, about half the length of the stem, and slender. Antennal segment 1 cylindrical and about one and one-half times as long as broad; 2 about one and one-half times as broad as long; 3 slender, slightly widening towards the apex, and five times as long as 1; club about four and one-half times as long as broad, and shorter than 3.

Mesonotum with short recumbent hairs on anterior half (presuturally) and on humeri, and postsuturally along dorsocentral stripes, bare of pollen, except along dorsocentral stripes; polished, and finely striate. Scutellum bare, a few hairs on arms, bare of pollen. Postscutellum weakly rugose, pollinose, bare of hairs. Pleura pilose on episternum-1, pteropleura and metasternum.

Abdominal tergite 1a not tuberculate, bare of hairs, and densely pollinose; 1p moderately long pilose, especially on sides; remaining segments minutely punctate (at the insertion of hairs), with short, recumbent hairs, usually sparse, longer on anterolateral corners of 2; bullae (if present) inconspicuous. Sternites with short, sparse, recumbent hairs. Female terminalia with apical hairs. Male genitalia (Figs. 4-7) : hypandrium transverse, short, free from basistyli, except laterally; basistyli with a long apical digitiform process and a bent



Cacatuopyga sp., male genitalia : 4, tip of ♂ abdomen; 5, male genitalia, ventral view; 6, dorsal view; 7, lateral view; 8, Aedeagus of *Cacatuopyga sp.*, lateral view.

inner process at the base of the digitiform process; epandrial halves short, fused, except apically; cerci fused except apically; anal lamellae long and slender; aedeagus with a very characteristic shaped opening, beak-like, apex bifid, and dorsally with a grooved crest-like process (Fig. 8).

Fore and middle legs moderately robust, the tibiae slightly incrassate and with a dense, bushy covering of hairs. Hind femora six times as long as broad, venter with about 10 tuberculate spines; hairs moderately long and dense. Hind tibiae cylindrical, slightly tapering towards apex, with only a faint basal ventral keel; apical spur absent; venter with some few strong spine-like bristles on distal half. Hind metatarsus about three times as long as broad and subequal in length to 2-4.

Alulae broad, with a dense fringe of squamose hairs. Wings almost three times as long as broad; second submarginal cell closed and short petiolate; first posterior cell broadly open; R_3 present as a stump vein; posterior crossvein present; axillary lobe twice as long as broad; ambient vein complete.

Length, 23-27 mm.

Type-species, *Mydas fruhstorferi* Wulp, 1896.

These flies resemble externally the medium-sized, blackish species of *Mydas*. For that reason, all the species of this genus were placed by the ancient authors in *Mydas*, an exclusively American genus. The different proboscis, the absence of a definite ventral keel on the hind tibiae, the entirely different construction of the male genitalia, among other characters, will immediately differentiate the two genera.

List of species

auriculosa (Séguy), 1934 : 6, figs. 4 (head, lateral view), 5 (pupal skin) (*Mydas*). Type-locality : North Vietnam, Tonkin, near Hoa-Binh (A. de Cooman, 1933). Type ♀, MNHN (seen in 1972). *N. comb.*

basifascia (Walker), 1859 : 104 (*Mydas*). Type-locality : Celebes, Macassar (A. R. Wallace). Ref. — Osten Sacken, 1896 : 75 (cat., comments). Type ♀, BMNH (seen in 1972). *N. comb.*

bifascia Gerstaecker, 1868 : 102, misspell.

carmichaeli (Brunetti), 1913 : 266 (*Mydas*). Type-locality : North India, Darjiling (♂) and Singja (as Singla) (♀). Ref. — Brunetti, 1920 : 318, fig. 23 (whole insect). Types ♂ ♀, Indian Museum. *N. comb.*

fruhstorferi (Wulp), 1896a : 98, pl. 2, figs. (head, lateral view), 4 (female terminalia), 5 (wing) (*Mydas*) : Type-locality : West Java, Sukabumi. Type ♀, ZMA (seen in 1972). *N. comb.*

?*ruficornis* (Wiedemann), 1824 : 20 (*Mydas*). Type-locality : India, Madras, Tranquebar. Refs. — Wiedemann, 1828 : 242, 1831 : 36, 46, pl. 53, fig. 11 (whole insect, color); Westwood, 1841 : 52; Walker, 1854 : 367; Gerstaecker, 1868 : 98; Wulp, 1896b : 75; Brunetti, 1920 : 317 (transl. of orig. descr.). Type ♀, COPN. *N. comb.*

A number of synonyms may exist among the above species. A careful study of the types must be done to clarify the status of the nominal species of *Cacatuopyga;* in special, of *ruficornis* Wiedemann, which differs from all other species by the red anterior half of the mesonotum; it is included here in *Cacatuopyga* with a query.

6.4. Subfamily **DIOCHLISTINAE** Bequaert

Orthomydainae Polyneurinae Bequaert, 1961a.
Diochlistinae Bequaert, 1963.

The Diochlistinae can be at once recognized by the hind metatarsus, which is five times as long as broad, and by the separate veins M_1 and M_2. Additional characters will be furnished in the revision of this subfamily.

Type-genus, *Diochlistus* Gerstaecker, 1868.

List of genera: 1. *Diochlistus* Gerstaecker, 1868 (A); 2. *Mitrodetus* Gerstaecker, 1868 (Ch); 3. *Triclonus* Gerstaecker, 1868 (=*Harmophana* Thomson, 1869) (A).

6.5. Subfamily **ECTYPHINAE** Wilcox & Papavero

Ectyphinae Wilcox & Papavero, 1971 : 66.

The Ectyphinae are very easy to recognize by the following combination of characters : male hypandrium more or less free, only partially fused to the basistyli, but always distinct; hind trochanters with 2-5 short spines; hind metatarsi about five times as long as broad and subequal in length to segments 2-4; ♀ with apical circlet of strong spines on aconthophorites; ♂ genitalia with diststyli.

Type-genus, *Ectyphus* Gerstaecker, 1868.

List of genera: 1. *Ectyphus* Gerstaecker, 1868 (E); 2. *Heteromydas* D. E. Hardy, 1944 (Nea); 3. *Opomydas* Curran, 1934 (Nea).

6.6. Subfamily **LEPTOMYDINAE**, new

Hind metatarsus never five times as long as broad; M_1 and M_2 coalesced, forming a single vein; anal cell closed; second submarginal cell very narrowly open, closed, or closed and petiolate; hind tibiae cylindrical; male hypandrium fused to the basistyli, diststyli absent, aedeagus a single tube; female terminalia with spines on the acanthophorites, or only with hairs.

Type-genus, *Leptomydas* Gerstaecker, 1868.

List of genera: 1. *Eremomydas* Semenov Tian-Shanski (=*Eremomidas*) (P); 2. *Leptomydas* Gerstaecker, 1868 (P); 3. *Nemomydas* Curran, 1934 (Nea); 4. *Plyomydas* Wilcox & Papavero, 1971 (Neo); 5. *Pseudonomoneura* Bequaert, 1961b (Nea).

6.7. Subfamily **MYDINAE** Latreille

Mydasii Latreille, 1810.

Hind metatarsus never five times as long as broad; M_1 and M_2 coalesced, forming a single vein; anal cell closed; second submarginal cell usually closed, sometimes very narrowly open; hind tibiae with ventral keel; male genitalia with hypandrium completely fused to basistyli, dististyli absent; female terminalia always with apical hairs; male aedeagus always simple.

Type-genus, *Mydas* Fabricius, 1794.

List of genera: 1. *Ceriomydas* Williston, 1898 (Neo); 2. *Dolichogaster* Macquart, 1848 (Neo); 3. *Messiasia* d'Andretta, 1951 (Neo, Nea); 4. *Mydas* Fabricius, 1794 (Nea; Neo) (=*Midas*; =*Lampromydas* Séguy, 1928c); 5. *Phyllomydas* Bigot, 1880 (Nea).

6.8. Subfamily **RHOPALIINAE**, new

Hind metatarsus never five times as long as wide; veins M_1 and M_2 coalesced, forming a single vein; anal cell closed; second submarginal cell usually widely open; hind tibiae cylindrical; male hypandrium completely fused to basistyli; dististyli absent; female terminalia with spines on acanthophorites.

Type-genus, *Rhopalia* Macquart, 1838.

List of genera: 1. *Perissocerus* Gerstaecker, 1868 (P); 2. *Pseudorhopalia* Wilcox & Papavero, 1971 (Neo); 3. *Rhopalia* Macquart, 1838 (P); 4. *Rhopaliana* Séguy, 1934 (P).

6.9. Subfamily **SYLLEGOMYDINAE** Bequaert

Heteromydainae Bequaert, 1961a.

Syllegomydainae Bequaert, 1963 (including tribes Cephalocerini and Mydaselpini of Hesse, 1969, and Halterorchini of Hesse, 1972).

Hind metatarsus never five times as long as broad; veins M_1 and M_2 coalesced, forming a single vein; anal cell closed; second submarginal cell usually closed; hind tibiae cylindrical or with a ventral keel; male aedeagus with 3 elements; female terminalia with spines on acanthophorites or only with apical hairs.

Type-genus, *Syllegomydas* Becker, 1906.

List of genera: 1. *Afroleptomydas* Bequaert, 1963 (including "subgenus" *Crossoprosopus* Hesse, 1969) (E); 2. *Afromydas* Bequaert, 1963 (E); 3. *Agarepemius* Hesse, 1969 (E); 4. *Arenomydas* Hesse, 1969 (E); 5. *Cephalocera* Latreille, 1829 (E); 6. *Cephalocérodes* Hesse, 1969 (E); 7. *Eremophaplomydas* Bequaert, 1959 (E); 8. *Halterorchis* Bezzi, 1924 (E); 9. *Haplomydas* Bezzi, 1924b (=*Heleomydas* Séguy, 1929) (E); 10. *Heteroleptomydas* Bequaert, 1963 (E); 11. *Lachnocorynus* Hesse, 1969 (E); 12. *Mimadelphus* Hesse, 1972 (E); 13. *Mydaselpis* Bezzi, 1924b (E); 14. *Namadytes* Hesse (1969) (=*Namamydas* Hesse, 1969) (E); 15. *Namibimydas* Hesse, 1972 (E); 16. *Neolaparopsis* Hesse, 1969 (E); 17. *Nomoneura* Bezzi, 1924b (E); 18. *Nomoneuroides* Hesse, 1969 (E); 19. *Nothomydas* Hesse, 1969 (E); 20. *Notosyllegomydas* Hesse, 1969 (E); 21. *Oreomydas* Hesse, 1969 (E); 22. *Syllegomydas* Becker, 1906 (including "subgenus" *Notobates* Hesse, 1969) (P, O, E); 23. *Vespiodes* Hesse, 1969 (E).

6.10. Unplaced genus

1. *Parectyphus* Hesse, 1972 (E).

7. GEOGRAPHICAL DISTRIBUTION OF THE SUBFAMILIES

Examination of Tables 1-3 and Maps 1-4 shows that :

1. Two subfamilies are endemic to only one zoogeographical region each — the Anomalomydinae in Australia, and the Cacatuopyginae in the Oriental region;

2. Two subfamilies show Trans-Antarctic relationships — the Diochlistinae and Apiophorinae; in the latter subfamily, one genus also occurs in southern Brazil;

3. The Ectyphinae are widely disjunct — *Ectyphus* occurring in South Africa and *Heteromydas* and *Opomydas* in the southwestern United States and Mexico;

4. Also the Rhopaliinae are widely disjunct — 4 genera occur along the Mediterranean subregion, west to Transcaspia, and one single genus in northeastern Brazil;

5. The Leptomydinae are predominantly Holarctic, with one genus occurring in coastal Peru;

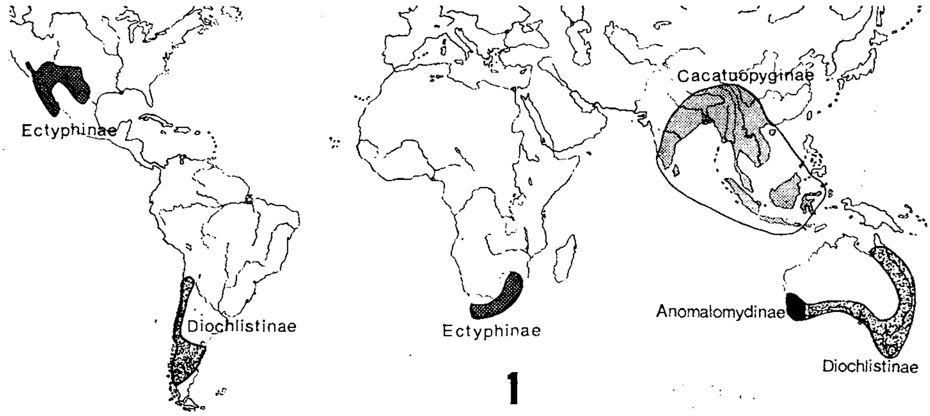
6. The Mydinae are exclusively American;

7. The Syllegomydinae are overwhelmingly Ethiopian, with a great radiation, only one genus being distributed over the Palearctic and Oriental regions.

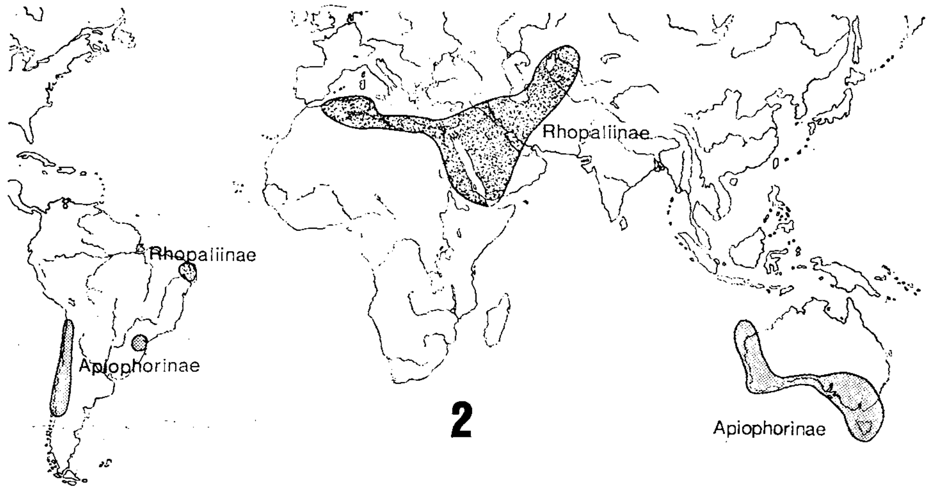
Conversely, examination of each zoogeographical region shows that:

1. The Nearctic has representatives of Ectyphinae (shared with South Africa), Leptomydinae (shared with Eurasia and Peru), and Mydinae (also South American);

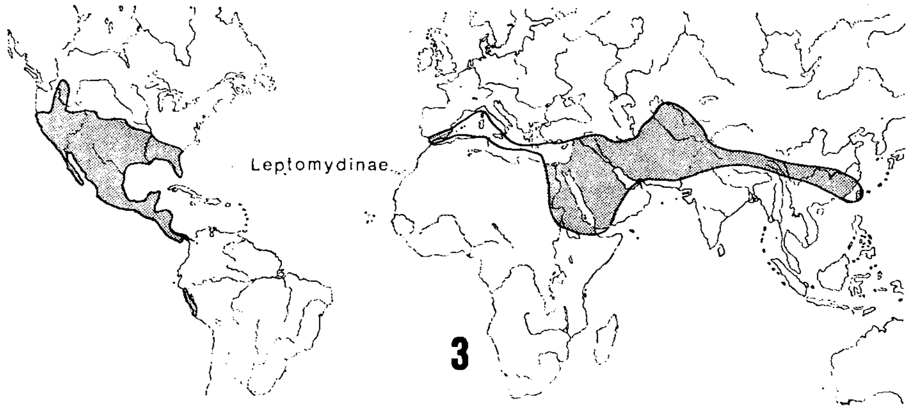
2. The Palearctic has Rhopaliinae (also South American), Leptomydinae (shared with the Nearctic and Peru), and Syllegomydinae (predominantly African);



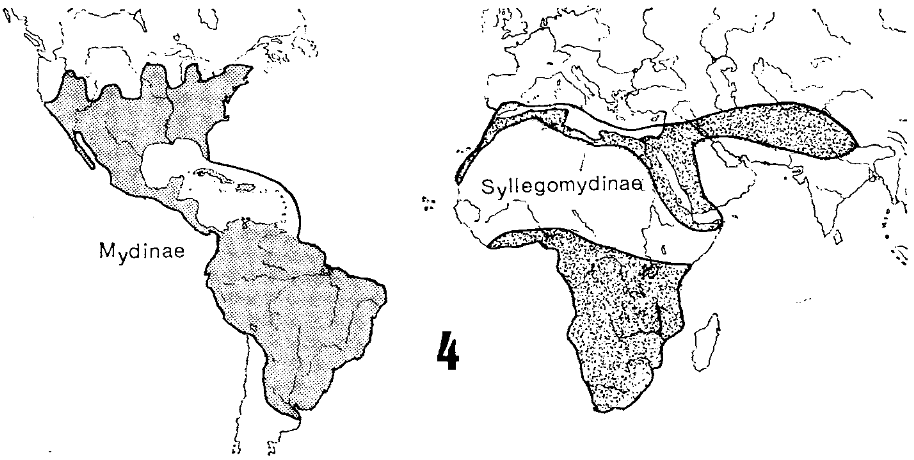
Map 1, Distribution of the Ectyphinae, Cacatuopyginae, Anomalomydinae and Diochlistinae (First radiation of the Mydidae).



Map 2, Distribution of the Rhopaliinae and Apiophorinae (Second radiation of the Mydidae)



Map 3, Distribution of the Leptomydinae (Third radiation of the Mydidae; Laurasian stock).



Map 4, Distribution of the Mydinae and Syllegomydinae (Third radiation of the Mydidae; West Gondwanan stock).

3. The Oriental region has one genus of Cacatuopyginae (so far as known endemic), and one genus of Syllegomydinae (seemingly shared with the Palearctic);

4. The Australian region has Anomalomydinae (one endemic genus), Diochlistinae and Apiophorinae (both also Chilean);

5. Chile shares the Diochlistinae and Apiophorinae with Australia; no Guiano-Brazilian genus enters Chile;

6. The Neotropical region has the largest number of subfamilies: Rhopaliinae (also Palearctic), Apiophorinae (Chile, Australia), Leptomydinae (also Holarctic), and Mydinae (also Nearctic);

7. The Ethiopian region has only one genus of Ectyphinae, and a great wealth of genera and species of Syllegomydinae; *Parectyphus* Hesse is yet unplaced.

8. HYPOTHETICAL PHYLOGENETIC HISTORY OF THE SUBFAMILIES

The apparently complicated geographical patterns formed by the nine subfamilies of Mydidae can be reasonably explained if considered in the light of the modern ideas on continental drift.

Table 1. Number of genera per zoogeographical region.

	An	Ca	Ec	Di	Rh	Ap	Le	My	Sy	Total
No. of nominal genera	1	1	3	3	4*	5*	5	5*	23*	50*
Nea	-	-	2	-	-	-	2	3	-	7
P	-	-	-	-	3*	-	2	-	1	6*
O	-	1	-	-	-	-	-	-	1	2
A	1	-	-	2	-	1*	-	-	-	4*
Ch	-	-	-	1	-	3	-	-	-	4
Neo	-	-	-	-	1	1	1	4*	-	7*
E	-	-	1	-	-	-	-	-	23*	24*

Note: Asterisk (*) indicates that further genera will be added to the total.

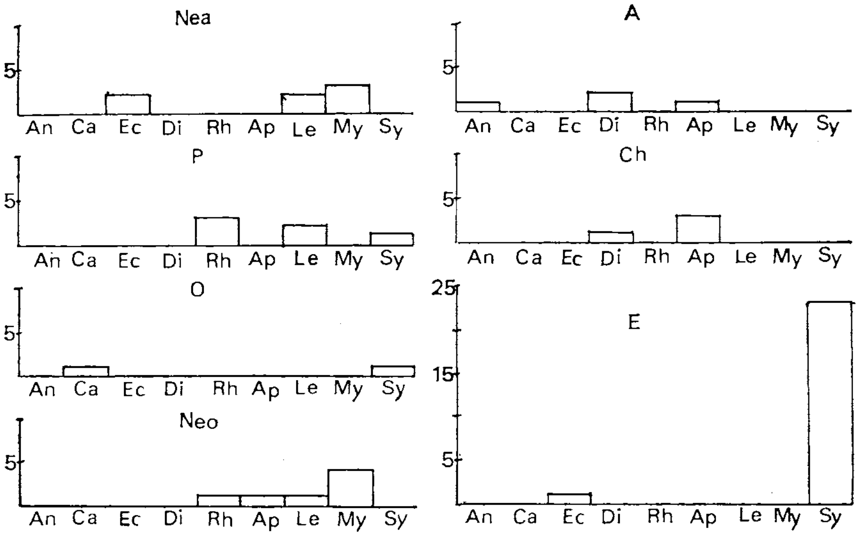


Table 2, Number of genera in each zoogeographical region per subfamily.

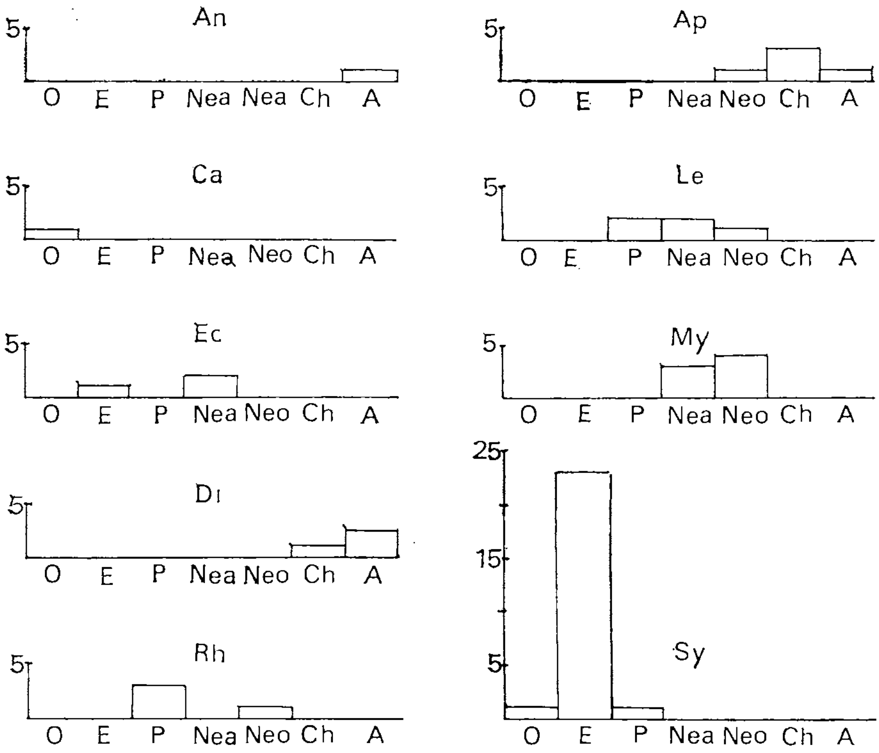


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Table 3, Number of genera in each subfamily per zoogeographical region.

We postulate for the Mydidae, as a working hypothesis to be tested in the forthcoming papers of this series, the following history of evolution. We have employed in Figs. 10 through 14 the Dietz & Holden "reconstructions" of Pangaea and its subsequent breaking into the present continents (1970). We have employed their illustrations only for the sake of convenience; we don't accept 'in totum' neither the reconstructions, nor the datings. For a discussion of the several contradictory reconstructions, datings, and other details, see Keast (1971), Papavero (1973b) and Cracraft (1973).

According to our ideas, therefore, the Mydidae, as many other families of Brachycera, must have appeared during the Mesozoic, between the Jurassic and the Cretaceous.

The Mydidae may be divided in three different groups, representing three different waves of radiation (Fig. 9) :

I. A group characterized by the long hind metatarsus, always five times as long as broad; many of the subdivisions of this group show very primitive characters :

1. The Anomalomydinae — an open anal cell; the posterior femora long and slender; absence of abdominal "bullae", etc.;

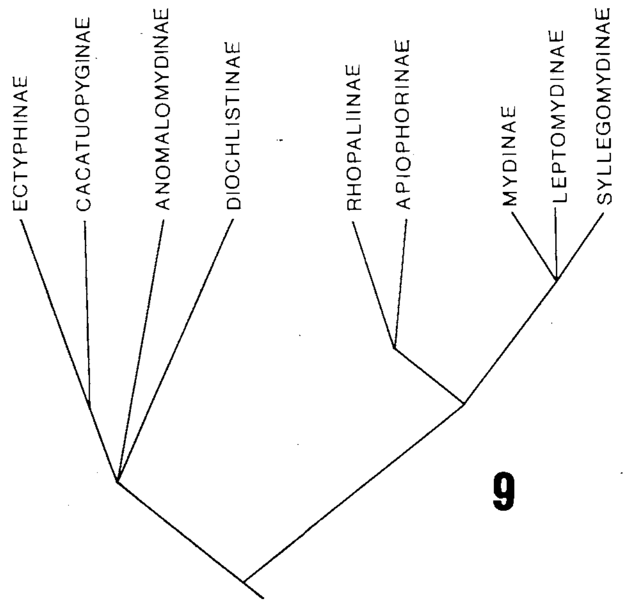


Fig. 9, Hypothetical phylogeny of the subfamilies of Mydidae.

2. The Diochlistinae — veins M_1 and M_2 separate;

3. The Ectyphinae and the Cacatuopyginae — the hypandrium free, only partially fused with the gonopods, but always visible; the former group has even the dististyli present, a unique character in this family; the Cacatuopyginae seem to be related to the Ectyphinae (shown by the male genitalia), but have a short hind metatarsus, and many derived characters.

II. A group characterized by the open second submarginal cell, and the short hind metatarsus — including the Rhopaliinae and the Apiophorinae.

III. A group also with a short hind metatarsus, but with the second submarginal cell normally closed — including Leptomydinae, Mydinae, and Syllegomydinae.

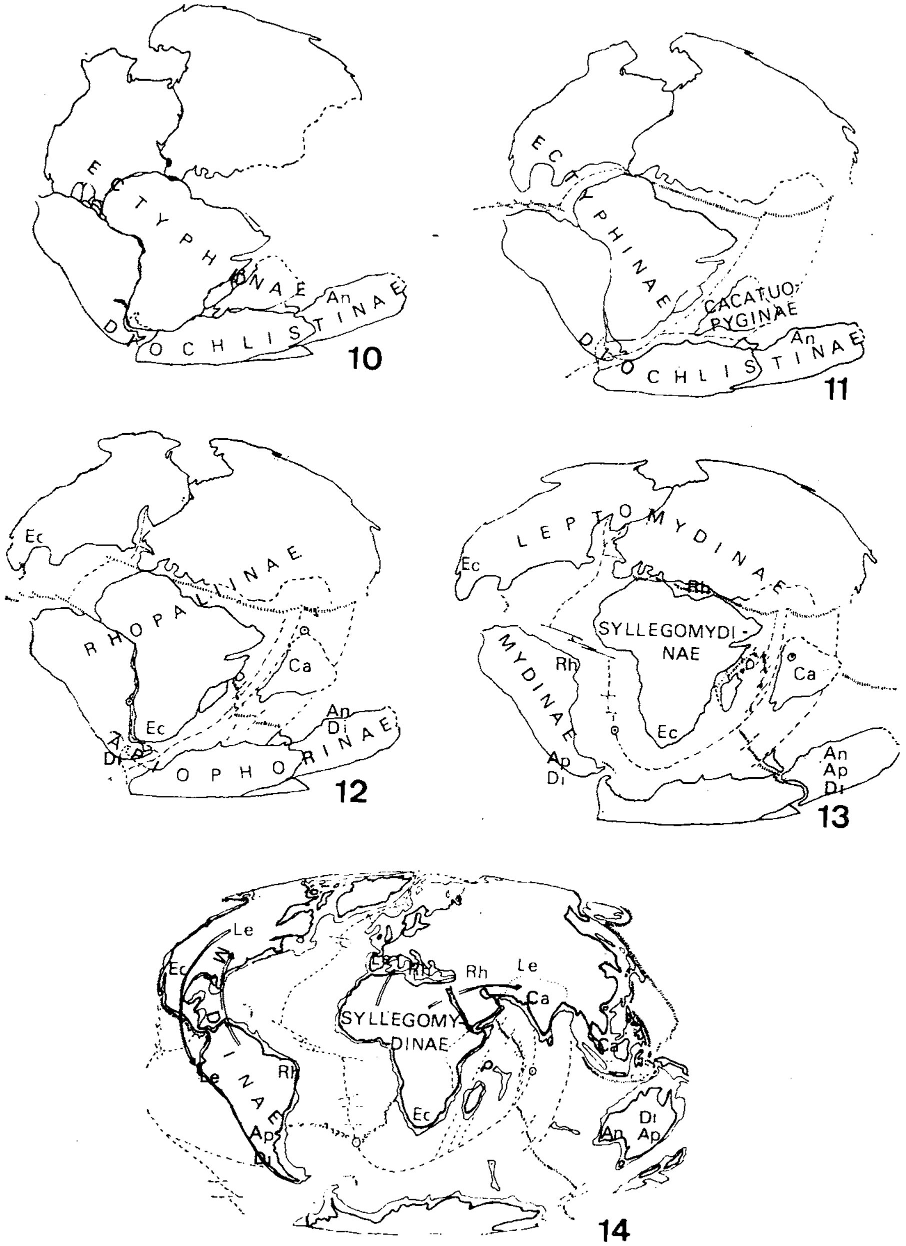
GROUP I. This first wave of radiation has probably occupied the entire supercontinent of Pangaea, prior to the separation of India (? transition Jurassic-Cretaceous). The Ectyphinae have probably occupied all the tropical regions of Pangaea (Laurasia, West Gondwana, and India), while the Diochlistinae were limited to the more temperate southern end of South America, Antarctica, and Australia (Fig. 10). About the Anomalomydinae very little can be said — they are now restricted to Australia, and have no other close relatives in the world. As occurs with the Blepharepiini among the Dasypogoninae (Asilidae; see Papavero & Bernardi, 1973), they represent the "Monotremata" among the Mydidae (see Fooden, 1972).

With the subsequent separation of India (? early Cretaceous), this subcontinent took away with it a primitive stock of Ectyphinae, (Fig. 11), which evolved in isolation, becoming greatly modified during the Tertiary trek of India, giving origin to the highly derived Cacatuopyginae. These have maintained only the primitive male genitalia (with free hypandrium, but with the loss of the dististyli); all other characters show a derived condition. After abutting against Asia (?Eocene), India may have served as a center of dispersal for the Cacatuopynae, which have spread to Southeast Asia and the Malay Archipelago (Map 1; Fig. 14). The Cacatuopyginae do not cross Weber's Line.

GROUP II. The second wave of radiation of the Mydidae has probably occurred after the separation of India. Similarly to the first group, the Rhopaliinae occupied the more tropical parts of Pangaea, and the Apiophorinae the Transantarctic temperate zones. Possibly by climatic changes brought on by the beginning of the fragmentation of Pangaea in the Cretaceous and by competition with Group II, Group I entered in recession, and became restricted to peripheral areas. (Fig. 12).

GROUP III. The third and last radiation of the Mydidae must have occurred immediately prior to the separation of West Gondwana in the present continents of South America and Africa. The Leptomydinae occupied the whole continent of Laurasia; West Gondwana was split in two, and South America was occupied by the Mydinae, while in Africa evolved the Syllegomydinae. These groups have not either occupied the Transantarctic areas, nor given sister-groups there, probably because of geographical, climatic or ecological barriers. Group III probably entered in competition with the previous groups and these also may have suffered from drastic climatic changes occurring with the opening of new oceans, and they became restricted to smaller areas, as relicts (Figs. 13-14).

The highly successful Group III occupied all the possible and ecologically suitable areas. The Mydinae have probably invaded North America in the early Tertiary, as they gave separate tribes and genera there (see Parts II and IV); the Leptomydinae have probably also invaded South America during the early Tertiary, but were forced into the coastal deserts of western South America, as they could not cross the forest barriers of the Amazonian region; the Syllegomydinae also invaded the northern hemisphere, occupying Eurasia, and from there passing to the Oriental region. (Fig. 14).



Hypothetical history of evolution of the subfamilies : 10, first radiation of the Mydidae in the Pangaea; 11, India becomes detached from Pangaea; origin of the Cacatuopyginae; 12, second radiation of the Mydidae; 13, third radiation of the Mydidae; breaking away of Gondwana; 14, Present position of continents, showing recent patterns of Mydidae distribution, and migration of subfamilies during Tertiary and Pleistocene.

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