STUDIES OF MYDIDAE (DIPTERA). V. PHYLOGENETIC AND BIOGEOGRAPHIC NOTES, KEY TO THE AMERICAN GENERA AND ILLUSTRATIONS OF SPERMATHECAE*

ESTUDIOS DE MYDIDAE (DIPTERA). V. NOTAS FILOGENETICAS Y BIOGEOGRAFICAS, CLAVE PARA LOS GENEROS AMERICANOS E ILUSTRACIONES DE LA ESPERMATECA

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ABSTRACT

The Diochlistinae (comprising the genera Mitrodetus Gerstaecker, from Chile, and Diochlistus Gerstaecker and Triclonus Gerstaecker, from Australia) are considered the sister-group of all the remaining Mydidae. The Diochlistinae present as symplesiomorphy separate veins M1 and M2, and as synapomorphies an elongated scape and the gonostyli internally fused to the hypandrium. The remaining Mydidae have as synapomorphy the fusion of veins M₁ and M₂. A phylogeny of the three genera of Diochlistinae is presented, with Mitrodetus as the sister-group of the genera Diochlistus and Triclonus. It is postulated that the Diochlistinae and their sistergroup were sympatrically distributed all over Pangaea, and that the Diochlistinae were extinct all over that supercontinent, except in Southern South America and Australia. A key to the American genera of Mydidae is presented, and illustrations furnished of the spermathecae of Mitrodetus, Triclonus, Anomalomydas, Opomydas, Heteromydas,

*This research was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Grants 85/1772-5, 86/3327-1 and 87/3170-8)

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KEYWORDS: Diptera, Mydidae, America, Taxonomy, Phylogeny, Biogeography, Morphology, Spermatheca.

RESUMEN

Los Diochlistinae (con los géneros Mitrodetus Gerstaecker, de Chile, y Diochlistus Gerstaecker y Triclonus Gerstaecker, de Australia) son considerados el grupo-hermano de todo el resto de los Mydidae. Los Diochlistinae presentan, simplesiomórficamente, las venas M1 y M2 separadas y como sinapomorfías el escapo alargado y los gonóstilos internamente hundidos con el hipandrio. Los restantes Mydidae presentan como sinapomorfía la fusión completa de las venas M1 y M2. Se presenta también una filogenia de los tres géneros de Diochlistinae, siendo Mitrodetus el grupo-hermano de Diochlistus y Triclonus. Se postula que los Diochlistinae y su grupo-hermano (el resto de los Mydidae) se hallaban simpátricamente distribuidos por toda la Pangaea, y que los Diochlistinae se han extinguido en casi todo ese supercontinente, excepto en el Cono Sur de América del Sur y Australia. Se presenta una clave para la identificación de los géneros americanos de Mydidae e ilustraciones de las espermatecas de los géneros Mitrodetus, Triclonus, Anomalomydas, Opomydas, Heteromydas, Pseudorhopalia, Miltinus, Dolichogaster, Messiasia, Phyllomydas, Protomydas, Gauromydas, Mydas, Ceriomydas, Mapinguari, Nemomydas y Pseudonomoneura.

PALABRAS CLAVES: Diptera, Mydidae, América, Taxonomía, Filogenia, Biogeografía, Morfología, Espermateca.

Gayana Zool. 54(3-4), 1990

INTRODUCTION

Previous parts of this series of papers have dealt with the following subjects: part I with the classification of the Mydidae in subfamilies (Papavero & Wilcox, 1974a); part II with the classification of the Mydinae (Papavero & Wilcox, 1974b); part III with the revision of *Messiasia* d'Andretta (Wilcox & Papavero, 1975); part IVa with the revision of *Phyllomydas* Bigot (Wilcox, 1978), and part IVb with the revision of *Mydas* Fabricius and allied genera (Wilcox, Papavero & Pimentel, 1989).

In this paper we present the basic phylogenetic dichotomy of the Mydidae, a phylogeny of the genera of Diochlistinae, plus a brief biogeographic hypothesis of this group. A key tho the identification of the American genera of Mydidae is given, with illustrations of the female spermathecae of some genera.

The material used here belongs to the Museu de Zoologia da Universidade de Sao Paulo, Brazil and Museo de Zoología de la Universidad de Concepción (MZUC), Chile. The methodology employed in the dissection and preservation of the male terminalia, female spermathecae and other morphological details is the same employed by Artigas (1971).

1. THE BASIC DICHOTOMY OF THE MYDIDAE AND THE PHYLOGENY OF THE GENERA OF DIOCHLISTINAE

We hypothesize that the Diochlistinae (comprising the genera *Mitrodetus* Gerstaecker, from Chile and Argentina, and *Diochlistus* Gerstaecker and *Triclonus* Gerstaecker, from Australia) are the sister-group of all the remaining Mydidae. The heterobathmy between these two groups is obtained in the following manner:

1) The Diochlistinae have, symplesiomorphically, separate veins M_1 and M_2 , i.e., they enter the Costa, or the apex of R_1 and the Costa, independently, at or above the wing apex (Figs. 1-2). As synapomorphies they present an elongated scape —the scape is about three times as long as the pe-

dicel (Figs. 4-7)— and the male terminalia shows the gonostyli internally fused to the hipandrium (Figs. 10-12; see also Artigas & Palma, 1979: Figs. 108-125). The wing venation of the Diochlistinae ressembles more that of the Apioceridae (see, for instance, the figure of the wing of *Rhaphiomidas acteon* in Peterson, 1981) than that of the Mydidae.

2) The remaining Mydidae show as synapomorphy the complete fusion of veins M_1 and M_2 , i.e., vein M_{1+2} is the only vein that enter C between the apex of the wing and the apex of R_1 ; they show, symplesiomorphically, a short scape (at most twice as long as the pedicel) and the gonostyli are not internally fused to the hypandrium (Textfig. 1):



MYDIDAE

TEXTFIG. 1: Basic dicotomy of the Mydidae. List of apomorphic characters (in parentheses the plesiomorphic state): 1. Veins M_1 and M_2 completely fused in a single vein (M_{1+2}) Veins M_1 and M_2 separate); 2. scape elongate, about three times as long as pedicel (scape not elongate, at most twice as long as pedicel); 3. gonostyli internally fused to the hypandrium (gonostyli not internally fused to the hypandrium). The phylogenetic interrelationships of the three genera of Diochlistinae are shown in Textfig. 2. The list of characters is the following (plesiomorphic states in parentheses):





- 1. M_1 ends in R_1 (M_1 ends in C)
- 2. C ends beyond apex of M2 (C complete)
- 3. M_2 ends well above wing apex (M_2 ends slightly above wing apex, far from R_1)
- R₄ fused to R₅ apically (R₄ free from R₅ apically)
- 5. Vein $CuA_1 + M_3$ absent ($CuA_1 + M_3$ present)
- 6. Anatergite pilose (Anatergite bare)
- 7. Only middle spermatheca present (Three spermathecae present)
- Katatergite convex, tuberculate and mammiform, pilose (Katatergite convex only, bare)
- 9. Mid and hind coxae with spines (Coxae without spines)
- 10. Hind femur clavate (Hind femur not clavate)
- 11. Hind tibia carinate (Hind tibia cylindrical, not carinate)
- 12. First flagellomere two or more times as long as scape and pedicel together (First flagellomere subequal in length to scape and pedicel together)
- 13. Facial gibbosity long (Facial gibbosity short)
- 14. Katatergite tuberculate (Katatergite only convex, not tuberculate)
- 15. Mediotergite pollinose (Mediotergite bare)
- 16. Stem of veins R_4 and R_5 much shorter than stem of M_1 and M_2 between apex of discoidal cell and their bifurcations (Stem of R_4 and R_5 and stem of M_1 and M_2 long and subequal in length as measured between apex of discoidal cell and their bifurcations)

In the form of a dichotomic key, the three genera of Diochlistinae can therefore be recognized in the following manner:

KEY TO THE GENERA OF DIOCHLISTINAE

- C. complete; M₁ ends in C or in R₁, M₂, ends elightly above wing apex, far from R₁; R₄ and R₅ free, i. e., ending independently in R₁; CuA₁ + M₃ present, i. e., cell m₃ petiolate (Fig. 1). Proboscis subequal in length to eye height (Fig. 6). Katategite ("hypopleura") from convex to tuberculate and mammiform and pilose. Middle and hind coxae with several long and slender spines. Hind femur clavate on apical half (Fig. 9). Hind tibia with ventral keel (carinate). Anatergite ("postscutellar slopes") bare and shining. (Australia, Tasmania). Length, 12-25 mm
 - C ends beyond apex of M₂; M₁ ends in R₁; M₂ ends well above wing apex, in C, near end of R₁; R₄ fused to R₅ apically; CuA₁ + M₃ absent, i.e., cell m₃ not petiolate (Fig. 2). Proboscis from very short (shorter than length of subcranial cavity) to very elongate (Fig. 4). Katatergite convex, bare of hairs. Hind femur not clavate (Fig. 8). Hind tibia cylindrical. Anatergite long and densely pilose. Only central spermatheca present (Figs. 14-15); see also Artigas & Palma, 1979: Figs. 75-80. Male terminalia and aedeagus as in Figs. 10-13 (see also Artigas & Palma, 1979: Figs. 108-125, 138-139, 140-145). (Chile, Argentina). Length, 11-19 mm*Mitrodetus Gerstaecker*

2. VICARIANT BIOGEOGRAPHY OF THE MYDIDAE

Let's denote by D the Diochlistinae, by M the Mydidae and by $C_M D$ the sister-group of the Diochlistinae (i.e., the complement of the Diochlistinae in relation to the Mydidae).

We have that D is distributed in the southern tip of South America, Australia and Tasmania. $C_M D$ is world-wide, being sympatric with D in Southern South America and Australia and Tasmania.

Two hypotheses may be constructed to explain this distribution:

H1) We may postulate that a vicariant event se-

parated Pangaea in two portions: one that included the southernmost portions of that Supercontinent, against all the rest (the greatest part) of it, and that the ancestor of M was distributed all over Pangaea (primitive cosmopolitism). This vicariant event separated M into two distinct lineages, which eventually originated D and $C_M D$ (see textfig. 1). Later, through the disappearance of the barrier which caused this splitting of M or by accidental crossing of that barrier. $C_M D$ dispersed, and entered into sympatry with D, and the biogeographical pattern that we now see was obtained.

2

We find such a barrier in the Samfrau Geosynclinal, thus called because it interested the southern portion of South America, the southern portion of Africa and parts of Australia (SAM + (A)FR + AU(S) (Textfig. 3):



Textfig. 3. The Samfrau geosynclinal, apud Holmes, 1960.

If the Samfrau Geosynclinal is postulated as having caused the separation of Pangeae and of M, we would have, initially, D distributed "south" of it and $C_M D$ "north" of it. Later on, $C_M D$ dispersed "southwards" (of the Samfrau Geosynclinal), entering into sympatry with D. This pattern remained like that until the present. (For information on the Samfrau Geosynclinal, see, for instance, Harrington, 1942; Holmes, 1960; Theron, 1973).

The great inconvenient of this hypothesis is that we would have to place the origin of M at least in the Upper Carboniferous:

H2) We may postulate that both D and $C_M D$ have arisen by an unknown event of vicariance and were in total sympatry (primitive cosmopolitism) in Pangaea by Cretaceous times, as most (if not all families of Diptera), and that D became extinct all over the Supercontinent, except in Southern South America and Australia (with Tasmania), i.e., that the presence of D only in those two areas of the world is merely fortuitous.

This hypothesis does not involve an exagerated lowering of the age of the Mydidae, but involves a tremendous extintion of representatives of D.

We will adopt the second alternative, as there are evidences, in other families of Diptera, that

great extinctions have occurred. A spectacular example occurs within the Stratiomyidae. Woodley (1986) has convincingly shown that the Chilean genus Parhadrestia James is the sistergroup of the genus Cretaceogaster Teskey (a fossil from the Canadian amber (Upper Cretaceous)), and that both (united in the subfamily Parhadrestiinae by Wooley) are the sistergroup of all the other Stratiomyidae. The Parhadrestiinae show that they were amply distributed in Pangaea, both in Laurasia (as evidenced by Cretaceogaster and in Gondwana (Parhadrestia). Only Parhadrestia is still living; all the other representatives of Parhadrestiinae have been extinct (or were not yet collected) all over the rest of the world.

If the second hypothesis (H2) is accepted, we may predict the existence of fossil Diochlistinae in any part of the world, outside Southern South America and Australia (with Tasmania).

Hipothesis two can also be tested through the establishment of the phylogeny and vicariant biogeography of the sister-group of the Mydidae —the Apioceridae. According to our second hypothesis, the Apioceridae must have a history associated to the splitting of Pangeae into Laurasia and Gondwana, with all the further separations of these land-masses.

3. KEY TO THE AMERICAN GENERA OF MYDIDAE

wing and apex of R_1 (Fig. 3). Scape at most two times as long as pedicel

2

3

4

2(1) First tarsomere of hind leg usually five times as long as wide. Cell cup closed and petiolate. Robust flies, about 11-29 mm long. Hind trochanter with one to five spines. Hypandrium either entirely free from gonocoxites or fused to them only basally; gonostyli present or absent. Female tergite 10 with circlet of strong spines. (Southwestern United States, Mexico). Subfamily Ectyphinae
 First tarsomere of hind leg shorter, never five times as long as wide. Other combinations of characters

3(2). Prementum subequal in length to subcranial cavity, labella short and slightly wider

- 4(2) Cell r₄ open, usually very widely open
 5

 Cell r₄ closed or closed and petiolate
 9

7(5).Katepimeron pilose. Abdomen deeply and densely punctate. Alula with fringe of squamose hairs. Female tergite 10 with hairs. Female spermathecae as in Artigas & Palma, 1979, Figs. 81 and 83. Male terminalia: see Figs. 89-92 of Artigas & Palma, 1979. (Chile: Coquimbo to Talca). Length, 18-23 mm Katepimeron bare. Other combinations of characters 8 8(7) Anal lobe of wing less than 1/2 as broad as long. Alula with fringe of short fine hairs. Hind femur: 4-4.5, 4.5-5 times as long as broad. Female tergite 10 with spines. Male terminalia: see Artigas & Palma, 1979: Figs. 93-98, 134-137. Female spermathecae: see Artigas & Palma, 1979: Figs. 84-86. (Chile: between provinces of Anal lobe of wing about as broad as long. Alula with dense fringe of squamose hairs. Hind femur: 06, 97 times as long as broad. Female tergite 10 with spines. (Brazil: Santa Catarina). Length, 21-28 mm Eumydas Wilcox & Papavero. 9(4). Hind tibia cylindrical. (Americas). Subfamily Mydinae 10 Hind tibia with ventral keel (carinate). (United States to Peru). Subfamily Leptomydinae ... 21 10(9). Prementum about one-half length of subcranial cavity; labella attached to prementum near its midpoint and subequal in length to subcranial cavity. Anterior margin of subcranial cavity situated at about two-fifths distance from lower eye margin to base of antennae 11 Prementum subequal in length to subcranial cavity; labella attached to prementum near its apical one-half, and extending out at about a 90° angle. Anterior margin of subcranial cavity level with lower eye margin 12 11(10). Antenna short, first flagellomere widened apically and subequal in length to scape and pedicel together; second flagellomere as long as the three preceding segments. Vein CuA₁ + M₃ absent. Male terminalia as in Figs. 76-78 of Wilcox & Papavero (1971), Female spermathecae as in Figs. 35-36. (Guiano, Brazilian subregion). Tribe Dolichogasterini. Length, 20-27 mmDolichogaster Macquart First flagellomere of antenna slender and at least twice as long as scape and pedicel together; second flagellomere shorter than three preceding segments. Vein CuA₁ + M₂ present. Male terminalia as in Wilcox & Papavero (1975). Female spermathecae as in Figs. 37-38. (United State: Arizona to Argentina: Buenos Aires). Tribe Mes-12(10). Facial gibbosity about as broad as high. Female tergite 9 narrower apically than basally. Male terminalia with simple, or bifid and falciform gonostyli. (North and 13 South America). Tribe Mydini. Length, 15-60 mm Facial gibbosity about one and one-half times as broad as high. Female tergite 9 wider apically than basally, fluted (see Wilcox & Papavero, 1971: Fig. 61). Gonostyli bifid. Female spermathecae as in Figs. 39-40. (United States, Mexico). Tribe Phyllomydini. Length, around 21 mmPhyllomydas Bigot. 13(12). Hind tibia with ventral keel underdeveloped, visible only on the basal half (or less)

of the tibia; apical spur on hind tibia underdeveloped, always shorter than width of first tarsomere (still shorter, almost absent, in female).Epandrium trapezoidal. Female spermathecae as in Figs. 41-42. (Neotropical, except Chile). Subtribe Protomydina, Length, 20-40 mm*Protomydas* Wilcox, Papavero & Pimentel Gayana Zool. 54(3-4), 1990

Hind tibia with well-developed, very evident ventral keel, all along its length; apical spur of hind tibia well-developed in both sexes (longer in males), always longer than width of first tarsomere (up to two times as long as width of first tarsomere). Epandrium trapezoidal, subtrapezoidal or triangular	14
 14(13) Mesonotum without a definite pollinose pattern of stripes or spots (Americas). Subtribe Mydina Mesonotum with a very evident pattern of pollinose stripes or spots. (Neotropical, except Chile). Subtribe Stratiomydina 	15 19
 15(14). First tarsomere of hind leg long, at least subequal in length to tarsomeres 2-3 and always longer than tarsomere 5 First tarsomere of hind leg very short, subequal in length to tarsomere 2 and always shorter than tarsomere 5 	16 17
 16(15). Second flagellomere of antenna about six times as long as wide or more. Female spermathecae as in Figs. 43-45. (Neotropical, except Chile)	
 17(15). No strong, differenciated bristles on legs. Fore tibia with a dense patch of black and orange-red hairs. Alula broad, with a long, dense fringe of squamose hairs. Abdomen entirely cupreousred as wide as thorax. Female spermathecae as in Figs. 48-49. (Surinam, Brazil: Pará). Length, 29-32 mm	18
 18(17). Alula narrow, with a short, sparse fringe of hairs. Abdomen slender, narrower than thorax, mostly black, sometimes constricted in the middle. Female spermathecae as in Figs. 50-52. (Neotropical, except Chile). Length, 20-27 mm	
 19(14). First tarsomere of hind leg long, subequal in length to tarsomeres 2-3 and longer than tarsomere 5. Epandrium variable. First tarsomere of hind leg very short, subequal in length to tarsomere 2 and shorter than tarsomere 5. Katepimeron pilose (<i>Baliomydas cubanus</i> (Curran)) or bare. Epandrium trapezoidal, with a distinct spur on the inner posterior corner. (West Indies)	20
20(19). Tergites 2-5 with the usual sparse, short, recumbent pilosity, directed backwards. Epandrium subtrapezoidal or triangular. Katepimeron bare (sparsely pilose in <i>Stra- tiomydas colimas</i> Wilcox, Papavero & Pimentel). (Tropical lowland forests of Mexi- co and Central America, Peru) <i>Stratiomydas</i> Wilcox, Papavero & Pimentel Tergites 2-5 with long, dense, recumbent hairs, directed outwards. Epandrial halves triangular. Katepimeron pilose. (Guiano-Brazilian subregion)	

ACKNOWLEDGMENT

We are very grateful to Prof. Dr. Lajos Biro (Department of Geociencias, Universidad de Concepción) for providing us with data and bibliography about the Samfrau Geosynclinal.

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Manuscrito aceptado en septiembre de 1990







Figs. 1-3. Wings: 1. Triclonus sp.; 2. Mitrodetus sp.; 3. Mydas sp.



Figs. 4-9. Mitrodetus sp.: 4. head. 5. antenna. 8. leg. Triclonus sp.: 6. head, 7. antenna, 9. hind femur.







Figs. 10-13. *Mitrodetus dentitarsis* (Macquart): 10. male terminalia in lateral view, 11. same in dorsal view, 12. same in ventral view, 13. aedeagus in lateral view.







Figs. 16-20. *Triclonus gracilis* (Macquart): 16. male terminalia in lateral view, 17. same in ventral view, 18. same in dorsal view, 19. aedeagus in lateral view, 20. same in dorsal view.

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Figs. 21-23. *Triclonus gracilis* (Macquart): 21. apex of abdomen, lateral view, 22. same, dorsal view, showing position of spermathecae, 23. spermathecae with detail of capsule.



Figs. 24-25. Anomalomydas mackerrasi (Norris): 24. tip of abdomen showing position of spermathecae, 25. spermathecae.



Figs. 26.27. Opomydas limbatus (Williston): 26. tip of abdomen showing position of spermathecae, 27. spermathecae.



Figs. 28-30. Heteromydas bicolor Hardy: 28. tip of abdomen showing position of spermathecae, 29-30. spermathecae, in different views.

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Figs. 31.32. *Pseudorhopalia mirandai* (d'Andretta & Carrera): 31. tip of abdomen showing position of spermathecae, 31A. tip abdomen, lateral view, 32. spermathecae.



Figs. 33-34. *Miltinus viduatus* (Westwood): 33. tip of abdomen, showing position of spermathecae, 34. spermathecae and details of tips of spermathecae.



Figs. 35-36. *Dolichogaster brevicornis* (Wiedemann): 35. tip of abdomen, showing position of spermathecae, 36. spermathecae and tip of abdomen (tergite 9 flattened in the preparation).





Figs. 39-40. Phyllomydas bruessi Johnson: 39. tip of abdomen showing position of spermathecae, 40. spermathecae.



Figs. 41-42. *Protomydas coerulescens* (Olivier): 41. tip of abdomen showing position of spermathecae; 42. spermathecae and details (middle capsule with teratological growth).



Figs. 43-45. Gauromydas heros (Perty): 43. tip of abdomen showing position of spermathecae; 44. spermathecae; 45. detail of confluence of the three ducts of the spermathecae.



Figs. 46-47. Mydas clavatus (Drury): 46. tip of abdomen showing position of spermathecae; 47. spermathecae and detail of teratological growth of duct.



Figs. 48-49. *Ceriomydas crassipes* (Westwood): 48. tip of abdomen showing position of spermathecae; 49. spermathecae (notice extreme development of accessory glands).







Figs. 53-54. Nemomydas pantherinus (Gerstaecker): 53. tip of abdomen showing position of spermathecae; 54. spermathecae and detail of tip of spermatheca.



Figs. 55-56. *Pseudonomoneura hirta* (Coquillett): 55. tip of abdomen showing position of spermathecae; 56. spermathecae and detail of tip of spermatheca.



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