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STUDIES OF ASILIDAE (DIPTERA) SYSTEMATICS AND EVOLUTION. II. THE TRIBES OF DASYPOGONINAE

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STUDIES OF ASILIDAE (DIPTERA) SYSTEMATICS AND EVOLUTION. II. THE TRIBES OF DASYPOGONINAE

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ABSTRACT

The Asilidae subfamily Dasyopogoninae is divided in 5 tribes: Blepharepiini (1 genus), Lastaurini (11 genera), Isopogonini (16 genera), Megapodini (8 genera), and Dasyopogonini (34 genera). A brief diagnosis of the tribes, a list of their genera, their distribution, and a speculative history of their phylogeny in the light of the present knowledge of continental drift, are given.

1. INTRODUCTION

The Dasyopogoninae are distinguished from all other Asilidae by the presence of a more or less developed spur on the front tibiae. They include at present 70 genera, of which 69 considered as valid, and 1 (*Lycomax* Hull, 1962) maybe also valid, but not yet sufficiently characterized; some new genera from the Australasian region, related to *Austrosaropogon* Hardy, will be described in the near future.

Dasyopogoninae genera are deceptively closely related and relatively "poor" in diagnostic characters, the subfamily presenting a remarkable morphological homogeneity; in addition to that, derived characters seem to have appeared independently in many groups, by convergent or parallel evolution (e.g., reduction of antennal style, of chaetotaxy, closing of wing cells, etc.). This renders their subdivision very difficult and extremely trying for the systematist.

The present proposed classification is therefore highly tentative and will be tested in the forthcoming papers, where each "tribe" will

be separately revised. As a general picture, however, this tentative scheme of classification results into a logical and coherent geographical pattern, that seems to indicate that the groupings are not entirely artificial.

For this paper the same collections mentioned in Part I were used. To their curators my best thanks. Also abbreviations used are the same. Taxonomic references were also given in Part I; in the bibliography only references discussed here are given.

New abbreviations employed in this Part are:

- B Blepharepiini
- D Dasypogonini
- I Isopogonini
- L Lastaurini
- M Megapodini

2. KEY TO TRIBES

The key is still tentative, and tries to show the main phylogenetic tendencies within the Dasypogoninae. It is not a key for the "easy" inclusion and identification of all the genera. In some couplets only characters of one sex (the male) have been used. As soon as tribes are revised, another key, including all possible "deviations", will be presented.

1. Prosternum complete, fused with the pronotum, forming a complete ring; antennal style absent; marginal cell open; 4th posterior cell closed and petiolate; post-scutellar slopes bare; male genitalia with free hypandrium; female terminalia with spines on acanthophorites (Neotropical; two species occurring in Nearctic) BLEPHAREPIINI, trib. n.
 Prosternum dissociated into dorsal and ventral plates, broadly separated by membrane 2
2. Antennal style with 2 microsegments; fore tibial spur bristle-like, sigmoid; all wing cells open; post-scutellar slopes bare; male hypandrium free from epandrium; female terminalia with spines on acanthophorites, or formed from segment 6 onwards (Worldwide, except Oriental) ISOPOGONINI Hardy
 Antennal style one-segmented or absent 3
3. Male genitalia with a completely fused 9th segment (i.e., hypandrium coalesced to epandrium, forming a complete ring); antennal style one-segmented or absent; marginal cell, 4th posterior, 1st posterior and anal cells open or closed; post-scutellar slopes bare or pilose; female terminalia with or without spines on acanthophorites, in the latter case strongly modified

(mainly Ethiopian and Neotropical, a few species invading the Northern Hemisphere) MEGAPODINI Carrera
 Male hypandrium free from epandrium 4

4. Fourth posterior cell normally open (if closed, not petiolate) and third antennal segment normally without small bristles on the lower dorsal surface; antennal style one-segmented or absent; marginal cell open or closed; post-scutellar slopes bare; female terminalia with or without spines on acanthophorites; small to medium-sized flies (Palearctic, Nearctic, Neotropical and Australasian) DASYPOGONINI Macquart

Fourth posterior cell always closed and petiolate and third antennal segment always with small bristles on lower dorsal surface; marginal cell open; antennal style absent; post-scutellar slopes bare; female terminalia with spines on acanthophorites; medium-sized to large and robust flies (mainly Neotropical, one genus in the Nearctic) LASTAURINI, trib. n.

3. BLEPHAREPIINI, trib. n.

This tribe includes a single genus, *Blepharepium* Rondani, 1848, from the Neotropics, with 2 species occurring also in the Nearctic region. It may be immediately separated from all other Dasypogoninae by the primitive condition of the prosternum.

4. LASTAURINI, trib. n.

A mainly neotropical group of medium-sized to large and robust flies, with 1 genus occurring in the Nearctic. It is distinguished by the closed and petiolate 4th posterior cell and the small group of bristles on the lower dorsal surface of the third antennal segment; it lacks an antennal style, and differs from the Blepharepiini in the dissociated prosternum.

The Lastaurini could be included, along with other Dasypogoninae genera lacking antennal style, in the tribe Dasypogonini (see below). However, their strong resemblance to the Blepharepiini, the closed and petiolate 4th posterior cell (the 4th posterior cell may become closed in some other genera, but never petiolate), and the fact that they are almost exclusively neotropical, led me to consider them as a distinct tribe, which radiated in the Guiano-Brazilian region, being derived from the Blepharepiini. Loss of the antennal style is likely to have occurred several times within the Dasypogoninae, and the other asilid subfamilies.

List of genera:

1. *Allopogon* Schiner, 1866 (Neo)
2. *Caenarolia* Thomson, 1869 (Neo)

3. *Diogmites* Loew, 1866 (Neo, Nea)
4. *Lastaurax* Carrera, 1949 (Neo)
5. *Lastaurina* Curran, 1935 (Neo)
6. *Lastauroides* Carrera, 1949 (Neo)
7. *Lastauronia* Carrera, 1949 (Neo)
8. *Lastauropsis* Carrera, 1949 (Neo)
9. *Lastaurus* Loew, 1851 (Neo)
10. *Neodiogmites* Carrera, 1949 (Neo)
11. *Phonicocleptes* Lynch Arribálzaga, 1881 (Neo)

5. Tribe ISOPOGONINI Hardy

Isopogonini G. H. Hardy, 1948 : 118.

Hardy proposed this tribal name tentatively, in his key to Asilidae tribes. I have preferred to preserve this name for my concept of the tribe, instead of creating a new one; *Isopogon* Loew (now *Leptarthrus* Stephens) is a well-known genus, and, in spite of its derived ovipositor, can be very well the type-genus of the tribe.

The Isopogonini are a very easy group to recognize, of relatively small flies, with a weak, bristle-like spur on the fore tibiae, and a double-segmented antennal style.

Nerterhaptomenus G. H. Hardy, 1934 seems to belong here, in spite of the fact that Hardy declared that the spur on the fore tibia was absent. Hardy very probably overlooked this character, as the bristle-like spur of the Isopogonini is sometimes somewhat difficult to see. This genus is closely related to *Leptarthrus*.

List of genera:

1. *Alvarenga* Carrera, 1960 (Neo)
2. *Annamyia* Pritchard, 1941 (Neo)
3. *Aphamartania* Schiner, 1866 (Neo)
4. *Aspidopyga* Carrera, 1949 (Neo)
5. *Aterpogon* Hardy, 1930 (A)
6. *Comantella* Curran, 1923 (A)
7. *Cophura* Osten Sacken, 1887 (Nea, invading trans-Andean Pacific coast of South America down to Atacama desert)
8. *Hodophylax* James, 1933 (Nea)
9. *Leptarthrus* Stephens, 1829 (P, E)
10. *Nerterhaptomenus* Hardy, 1934 (A)
11. *Nicocles* Jaenicke, 1867 (Nea)
12. *Omninablautus* Pritchard, 1935 (Nea)
13. *Paraphamartania* Engel, 1930 (P)
14. *Questopogon* Dakin & Fordham, 1922 (A)
15. *Theromyia* Williston, 1891 (Ch)
16. *Theurgus* Richter, 1966 (P)

6. Tribe MEGAPODINI Carrera

Megapodini Carrera, 1949 : 5.

As will be seen in the revision of this tribe, no diagnostic character is shared by all genera, except the derived male genitalia (complete fusion of segment 9, forming a complete ring). I have regarded this group as monophyletic (as indicated by the concordance and sequence of many other morphological characters) and given to it tribal rank.

List of genera:

1. *Cyrtophrys* Loew, 1851 (Neo)
2. *Deromyia* Philippi, 1865 (Ch)
3. *Lagodias* Loew, 1858 (E, P, O)
4. *Megapoda* Macquart, 1834 (Neo)
5. *Pegesimallus* Loew, 1858 (E)
6. *Pronomopsis* Hermann, 1912 (Ch)
7. *Pseudorus* Walker, 1851 (Neo, Nea)
8. *Senobasis* Macquart, 1838 (Neo)

7. Tribe DASYPOGONINI Macquart

Dasypogonitae Macquart, 1838 : 14 (1839 : 130). (Including "subfamily" Archilaphriinae Enderlein, 1914b, and "tribes" Brachyrrhopalini Hardy, 1926; Chrysopogonini Hardy, 1934; Saropogonini Hardy, 1926; Thereutrini Hull, 1962).

An extremely diversified group, including genera with or without an apical, single style. It seems to be, however, a natural group, and the absence of style a derived condition which appeared several times in several regions. Hardy (1926, 1934) and Hull (1962) proposed some tribes for small groups of genera with minor derived characters; all these genera can trace their origin to the *Austrosaropogon*-group, and were not considered here as tribes.

List of genera:

1. *Aczelia* Carrera, 1955 (Neo)
2. *Apotechyla* Hull, 1962 (A)
3. *Araiopogon* Carrera, 1949 (Ch)
4. *Archilaphria* Enderlein, 1914 (P)
5. *Austenmyia* Carrera, 1955 (Neo)
6. *Austrosaropogon* Hardy, 1934 (A)
7. *Brachyrrhopala* Macquart, 1847 (A)
8. *Cabaza* Walker, 1851 (A)
9. *Chryseutria* Hardy, 1928 (A)
10. *Chrysopogon* Roeder, 1881 (A)

11. *Chylophaga* Hull, 1962 (A)
12. *Cleptomysia* Carrera, 1949 (Neo)
13. *Dakinomyia* Hardy, 1934 (A)
14. *Daptolestes* Hull, 1962 (A)
15. *Dasypogon* Meigen, 1803 (P)
16. *Erythropogon* White, 1914 (A)
17. *Lestomyia* Williston, 1889 (Nea)
18. *Lycomax* Hull, 1962 (?; no species included; cited only in key)
19. *Macrocolus* Engel, 1930 (Neo)
20. *Metalaphria* Ricardo, 1912 (A)
21. *Molobratia* Hull, 1958 (P, O)
22. *Neocyrtopogon* Ricardo, 1912 (A)
23. *Neoderomyia* Artigas, 1971 (Ch)
24. *Neosaropogon* Ricardo, 1912 (A)
25. *Oberon* Carrera & Papavero, 1962 (Ch)
26. *Opseostlengis* White, 1914 (A)
27. *Parataracticus* Cole, 1924 (Nea)
28. *Paraterpogon* Hull, 1962 (A)
29. *Rachipopogon* Ricardo, 1912 (A)
30. *Saropogon* Loew, 1847 (Nea, P, O)
31. *Stizochrymus* Hull, 1962 (A)
32. *Taracticus* Loew, 1872 (Nea)
33. *Thereutria* Loew, 1851 (A)
34. *Tocantinia* Carrera, 1955 (Neo)

8. GEOGRAPHICAL DISTRIBUTION

Examination of the Table and figs. 1 and 2 discloses the following facts:

- (i) The Blepharepiini exist only in the Neotropical and Nearctic regions; as will be seen, the Nearctic is invaded by only 2 species, the group being decidedly Neotropical;
- (ii) The Lastaurini are equally Neotropical in distribution, the Nearctic region having only one genus (with many species);
- (iii) The Isopogonini occur in all zoogeographical regions, except in the Oriental; the Nearctic and Neotropical regions with 5 genera, the Palearctic and Australian with 3, and the Ethiopian and Chilean with 1 genus each;
- (iv) The Megapodini are also worldwide, but do not occur in Australia; the same as with the Blepharepiini, it will be seen that penetration of the Northern Hemisphere is limited (very few species), and that the group is mainly Neotropical (4 genera in the Guiano-Brazilian subre-

gion and 2 in the Chilean subregion) and Ethiopian (2 genera, 1 with many species);

(v) The Dasypogonini are absent from the Ethiopian region; the Oriental region has a generalized Palearctic fauna; the group is therefore predominantly Nearctic, Palearctic, Neotropical, and especially Australian (18 genera known, or more or less 25% of the world genera of Dasypogoninae).

Conversely, examination of the fauna of each zoogeographical region shows that:

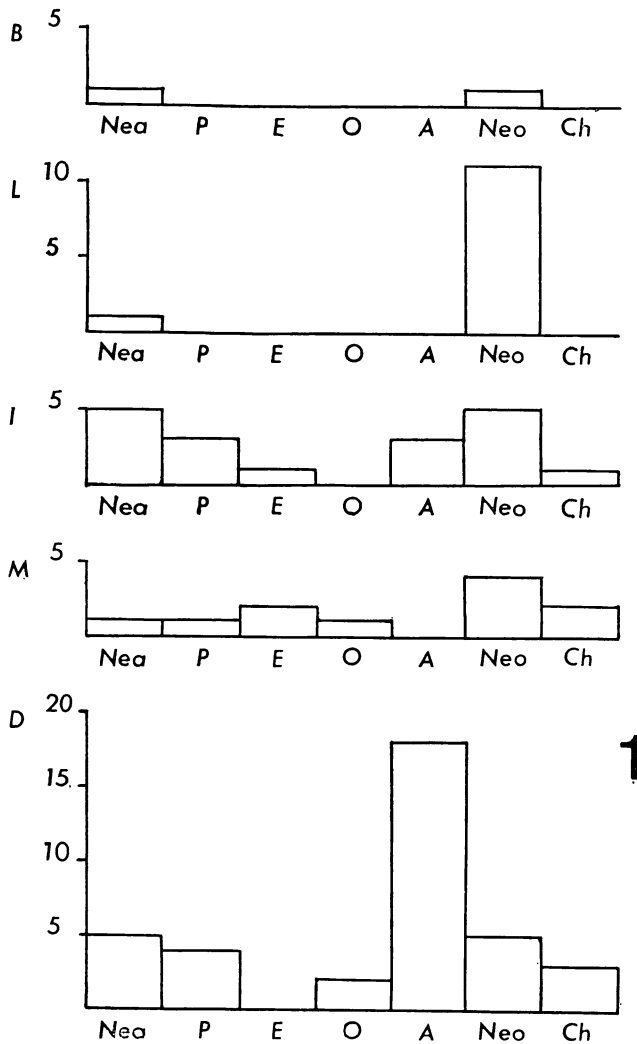


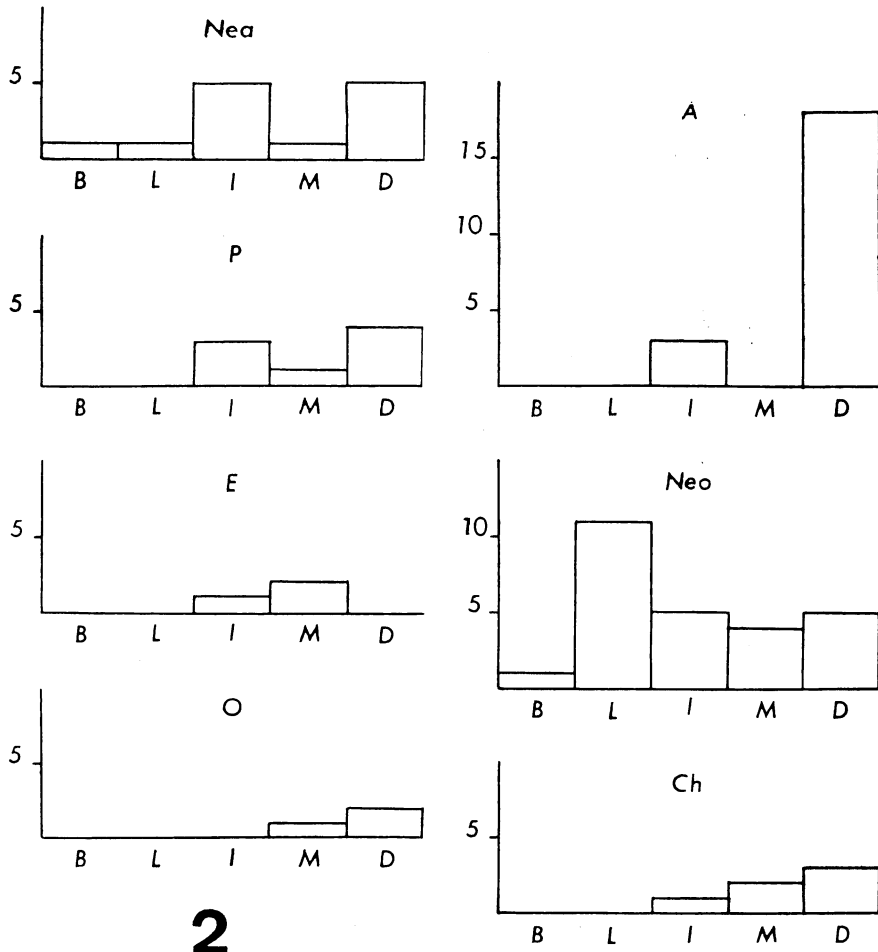
Fig. 1, Geographical distribution of tribes (number of genera in each tribe per zoogeographical region).

(i) The Nearctic region has representatives of all the 5 tribes, but the Blepharepiini, Lastaurini and Megapodini are Neotropical invaders;

(ii) The Palearctic region has only Isopogonini, Megapodini, and Dasyopogonini, but the second group is clearly an Ethiopian immigrant;

(iii) The Ethiopian region, along with the Oriental, is the poorest in genera (3 genera), and has only Isopogonini (widely disjunct) and Megapodini; at the species level, however, its fauna is immensely richer than the Oriental one;

(iv) The Oriental region is the poorest of the world in Dasyopogoninae, both in genera and species; all its genera are Palearctic in origin; that is to say, *no endemic Oriental genus of Dasyopogoninae is known*;



2

Fig. 2, Faunistic composition of the zoogeographical regions (number of genera of the different tribes in each zoogeographical region).

(v) The Australasian region, similarly to the Ethiopian, has only representatives of 2 tribes, but these are different : instead of Megapodini and Isopogonini, the Australasian region has Isopogonini and Dasypogonini, the latter being extremely abundant (18 genera known up to now) ;

(vi) The Neotropical region has representatives of all the tribes of Dasypogoninae, and two of them (Blepharepiini and Lastaurini) are practically endemic ;

(vii) The Chilean subregion lacks both Blepharepiini and Lastaurini.

Table

Number of genera per zoogeographical region

	B	L	I	M	D	Total
Nº of nominal genera	1	11	16	8	34	69
Nea	1	1	5	1	5	13
P	-	-	3	1	4	8
E	-	-	1	2	-	3
O	-	-	-	1	2	3
A	-	-	3	-	18	21
Neo	1	11	5	4	5	26
Ch	-	-	1	2	3	6

9. CONTINENTAL DRIFT AND THE EVOLUTION OF THE TRIBES

During the last years a great wealth of data has been published regarding plate tectonics and continental drift and their bearing on past plant and animal distribution. The brief discussion given below was entirely extracted from Dietz & Holden (1970) and especially from Keast (1971).

1. In the Permian, the Atlantic and Indian oceans were closed so that all continents were configured into the universal landmass of Pangaea. Dietz & Holden (1970) believe that Pangaea existed at the end of the Paleozoic, and suppose that Laurasia (North America plus Eurasia, but not including India) and Gondwana (all the southern continents plus the subcontinent of India) were originally separate geologic entities, but that they collided in the later Paleozoic, by moving towards a common trench in an ancient North Atlantic ocean to form Pangaea; then they subsequently parted again along approximately

the same geosuture with the formation of a new rift in the Triassic (Dietz & Holden, 1970 : 4045). Pangaea has remained intact until the end of the Paleozoic, i.e., the end of the Permian, -225 million years (l. c., fig. 2, p. 4943).

The Permo-Carboniferous glaciations (Hamilton & Krinley, 1967) and the *Gangamopteris-Glossopteris* associations (Schopf, 1970) indicate that evidence for a clustering of the southern continents around Antarctica in the Permian, and their continuity, is very good.

2. In the Triassic (the midpoint of which would be -200 m. y.) the breakup of Pangaea commenced. The southwest Indian Ocean rift was created, which split West Gondwana (South America and Africa) away from East Gondwana (Antarctica, Australia), while a Y-shaped junction lifted India off Antarctica (this is according to Dietz & Holden "reconstruction"; as shall be seen later, authors disagree about the exact dating of India's detachment). An independent North Atlantic-Caribbean rift also formed, which lifted Laurasia (North America and Eurasia) off South America and the bulge of Africa. North America however still remained attached to Europe. Spain remained in point contact with West Gondwana.

Faunistic and floristic interchanges among the southern continents, and between these and the northern continents were possible at this time. The Lower Triassic fauna of reptiles and amphibians recently discovered in the mainland of Antarctica not only proves that this continent supported vertebrate life early in the Mesozoic, but also it was probably important in exchanges between the southern continents. These Antarctic fossils largely duplicate those of the *Lystrosaurus* Zone of the Early Triassic of Africa, bear good resemblances to an equivalent Indian fauna, and have fair resemblances to a fauna in China (Colbert, 1971). Overlying the *Lystrosaurus* Zone in Africa is a *Cynognathus* Zone, dominated by reptiles belonging to that genus. This assemblage bears striking relationships to a counterpart in South America which is also dominated by *Cynognathus*. There are also counterparts in India and China (Colbert, 1971). This pair of Lower Triassic faunas is persuasive evidence for a continuing cluster of southern continents at this time (and therefore India could not have been already detached). The occurrence of these faunas in China (not a part of Gondwanaland, but of Laurasia), shows that Gondwanaland was not completely isolated from Laurasia at that time; also work on the Triassic floras of South America shows the persistence there at that time of a flora related to the Triassic floras of South America, Australia, and India (Menéndez, 1969).

3. By the end of the Jurassic (-135 m. y.) additional generations of new oceanic crust by seafloor spreading caused a further widening of the North Atlantic basin. Contact of Eurasia with Africa was still maintained between these continents, by Spain. Splitting along the pan-Antarctic and the Indo-Antarctic rifts continued. In the late Ju-

rassic or possibly in early Cretaceous an incipient South Atlantic rift was created within West Gondwana that commenced to drift these two continents apart.

According to Keast (1971) "by the Late Jurassic the picture of "exclusive", or nearly exclusive southern floras and faunas became obscured *in favor of dominance by more "cosmopolitan" types*" (italics mine).

4. By the end of the Cretaceous (-65 m. y.), the motions initiated in the Triassic continued. With the further opening of the Atlantic rift by sea-floor spreading, both North and South America moved westward, the North Atlantic opening about 1500 km, and the South Atlantic 3000 km or more. Within the Cretaceous, South America encountered the Andes trench and commenced to displace this trench to the westward without splitting or overriding it. The Andean fold belt resulted from this encounter. Africa drifted northward, about 10°, and continued its sinistral rotation, and this motion, together with a dextral rotation of the Eurasia plate to the north, caused an almost complete closure of the Tethys seaway. Africa was everywhere bounded by rifts except to the north; then Madagascar split away and dropped off. By the end of the period the pan-Antarctic rift extended eastward, initiating the rifting away of Australia from Antarctica (also according to Dietz & Holden; later we shall see other opinions on the separation of Australia). All the continents were now blocked out except for the join between Greenland and northern Europe.

According to Keast (1971 : 366) : "The Lower Cretaceous fresh-water faunas (Krommelbein, 1965a, 1965b), and certain spore-pollen floras (Freake, 1966) suggest : a junction or near junction of West Africa and Brazil at that time [see also Axelrod, 1970, for evidence based on Angiosperms]. This fits the sea floor spreading data [see also Maxwell et al., 1970]. The greater similarity between the Late Cretaceous dinosaur faunas of South America and North America, rather than South America and Africa would also fit the Dietz-Holden deduction that the Atlantic rift by that time formed an effective water barrier. It also supports the inference of increased opportunities for north-south interchanges between the two Americas. The newer writers on sea floor spreading and plate tectonics have not yet focussed on the finer details of the spatial relationships of these two continents in the later Mesozoic. There is of course, ample other geological evidence, that they were not actually joined (Jacobs et al., 1963; Lloyd, 1963; Haffer, 1970).

"The Upper Cretaceous flora of South America reveals virtually nothing about the spatial relationships of that continent relative to others. Angiosperms appeared and "they form a flora with elements similar to those which today occur in tropical and subtropical zones; although there are also enough plants of southern origin which indicate

an evident relation to the floras of Australia and New Zealand (Menéndez, 1969 : 559)."

According to Axelrod (1970) : "During the Early Cretaceous, ocean-floor spreading gradually opened up the tropical Atlantic and the Indian Ocean widened as the eastern segments of Gondwanaland were conveyed farther apart. At the same time, epeiric seas were advancing on all continents, reaching maximum extent during the Cenomanian. The resultant trend to widespread, more equable climate favored the invasion into the lowlands of angiosperms whose postulated origin was in mild uplands at low latitudes during pre-Cretaceous times. As tropical and subtropical lands were rafted farther apart by ocean-floor spreading following Albian-Cenomanian times, new taxa (species, genera, tribes, families) evolved in isolation. This accounts in part for the increasing richness of the three major tropical floras following the Cretaceous."

5. Finally, during the Cenozoic, according to Dietz & Holden, Antarctica rotated further westward. Australia experienced a remarkable flight northward, and New Zealand was split away from its east coast. The North and South Atlantic oceans continued to open; the rift that formerly passed west of Greenland now switched to the east and split Greenland away from northern Europe and extended through the Arctic Ocean. Africa moved slightly northward, continuing sinistral rotation. The Tethyan megashear became dextral for the first time, India collided with and underthrust Asia, throwing up the Himalaya fold belt by the collision (Eocene).

Several authors do not agree with Dietz & Holden's reconstruction or dating. Thus:

1. For India — Dietz & Holden (1970) assume a mid-Triassic separation, India then drifting northward across the Indian Ocean, finally abutting against Asia in the Eocene.

McElhinny (1970) suggests, based on paleomagnetic evidence, that the India-Madagascar-Antarctica block broke away from Africa between the mid-Jurassic and mid-Cretaceous, prior to the separation of the first two land masses from Antarctica.

Veevers et al. (1971) match Permian, Triassic and Jurassic rock sequences in Australia and India. They suggest, on this basis, that India and Australia ruptured in the latest Jurassic or earliest Cretaceous and that this is marked by basaltic extrusions, tuft depositions, and marine sediments in western Australia.

Francheteau & Sclater (1969) say separation occurred between middle Cretaceous and Cretaceous-Tertiary boundary.

Axelrod (1970) also says early Cretaceous, based on angiosperms.

In short, separation of India in early Cretaceous would be a general consensus, and would explain the presence there of certain dinosaur faunas (see Keast, 1971 : 366), while it was supposed to be in the middle of the Indian Ocean during the Cretaceous, according to Dietz & Holden.

Authors also disagree about the date of India's "collision" with Asia — Dietz & Holden (1970), and Heirtzler et al. (1968) say Eocene; McElhinny (1970), early Miocene; Fischer et al. (1971) and Veevers et al. (1971) at the end of Eocene; finally Larson & LaFountain (1970) say that it was as recently as 10,000,000 years ago.

2. For Southeast Asia — Ridd (1971) believes (with other authors) that also Southeast Asia was a part of Gondwanaland, and that it also drifted northward and collided against Asia, the Song Ma Fold and Fault Belt marking its separation from Asia. Stratigraphic evidences, the *Glossopteris* flora, and the fitting of Southeast Asia into Gondwanaland, seem to show that it adjoined India in the Triassic, but that separation may well have taken place in the Jurassic.

3. As pointed out by Keast (1970 : 346) "An important paper on the geological history and time of separation of South America and Antarctica has recently been published by Dalziel & Elliot (1971). They conclude that separation of South America and Antarctica occurred between the beginning of the Tertiary and 20-25 million years ago. Such a later separation of South America and Antarctica could have a great implication from the viewpoint of the direct transference of Southern Hemisphere floras and faunas."

4. Also according to Keast (1970 : 346) : "The date for the separation of Australia from Antarctica is given as Late Eocene by Heirtzler et al. (1968) rather later than the separation of New Zealand (Upper Cretaceous). Le Pichon (1968) suggests that New Zealand left Antarctica in the Paleocene, moving northward very rapidly at first. By the early Eocene its rate of movement had slowed considerably. When Australia broke free from Antarctica in the late Eocene it developed a rate of movement twice that of New Zealand. The two masses apparently were then moving in closely parallel paths and, for a time, came into closer contact, before separating more widely.

Creer (1964, 1970), after a study of Mesozoic pole positions suggested a much earlier date for the separation of Australia from Antarctica, the early Triassic. However, the Eocene date is based on sea-floor spreading data (Le Pichon, 1968; Le Pichon & Heirtzler, 1968; McElhinny & Wellman, 1969). Christoffel & Ross (1970) link a major change in the pattern of ocean-floor spread in the Antarctic, which occurred about the time of the Paleocene-Eocene boundary, with the event. Tarling (1971) suggests that Australia and Antarctica were connected until the Paleocene. Jones (1971) notes the occurrence of a marine transgression along the southern margin of Australia in the Late Eocene. In contrast to this, Veevers et al. (1971) suggest that Africa, Australia, and India, all began to drift north in the mid-Cretaceous. This date, as noted, is actually apparently too late for the separation of Africa (Dingle & Klinger, 1971).

In spite of the several controversies about the exact dating of the separation of the continents, some facts seem to be well established, and based on them, a speculative hypothesis on the formation and evolution of the Dasypogoninae tribes can be formulated.

1. The Asilidae, as many other families of flies, must have appeared in the Mesozoic. Absence of fossils is not at all a proof in contrary. Several other families of Brachycera are represented in the Mesozoic (Hennig, 1969 : 391; Ussatchov, 1971). I believe that the subfamilies of Asilidae were already differentiated somewhere between the Jurassic and Cretaceous.

2. The Dasypogoninae, in a first radiation, have probably originated 3 different branches (Fig. 3):

- i. The Blepharepiini, characterized by the primitive condition of the prosternum; this group probably became very soon restricted to South America; it is now impossible to know their past history; they present almost the same problem as the occurrence of Monotremata in Australia (Fooden, 1972);
- ii. The Isopogonini, also a primitive group, characterized by the two-segmented antennal style; this tribe probably radiated in Pangaea immediately after the separation of India and southeast Asia (?Cretaceous). This would explain their pre-

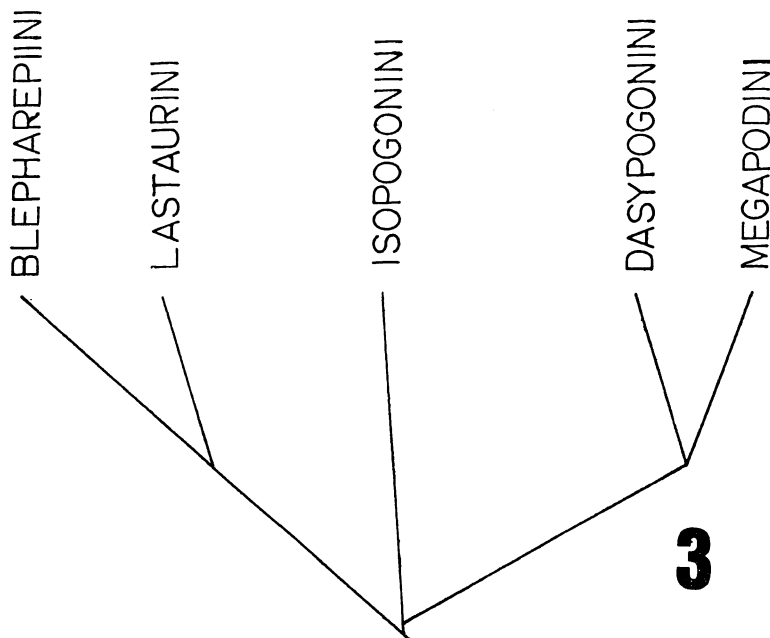


Fig. 3, Hypothetical phylogeny of the tribes of Dasypogoninae.

sence in all the present zoogeographical regions, except the Oriental;

- iii. The ancestral group of both the Dasypogonini and Megapodini; this stock also seems to have occupied all the continents after the separation of India and southeast Asia.

3. The great radiation of the Megapodini has probably occurred during the Cretaceous, coinciding with the breaking away of West Gondwana, and with the rise and dominance of angiosperms (Axelrod, 1970). The Megapodini, which are clearly a West Gondwanan group, were then isolated in South America and Africa, originating two different faunas. In South America they remained closely linked with forest formations, and probably entered in competition with the Isopogonini and especially with the Dasypogonini, which are now poorly represented. In Africa they had a strong radiation, occupying almost all the open formations, and have probably eliminated the Dasypogonini, which are now absent from Africa; they also have probably eliminated the Isopogonini, which have, as the Megapodini of Africa, spines on the acanthophorites; *Leptarthrus*, with a different type of ovipositor, and probably a different type of biology, seems to be the only survivor of the Isopogonini, but is now widely disjunct (Mediterranean area and southern Africa).

4. Meanwhile, in South America, the Blepharepiini had originated another group, the Lastaurini, that occupied all the forests of the Guiano-Brazilian subregion. The primitive Megapodini (with spinous acanthophorites) probably competed with the Lastaurini; this may explain the present limited and disjunct distribution of that former group; the more recent Megapodini, with a different type of ovipositor, and therefore probably a different type of biology, had the chance to avoid competition, and had a great radiation (see Part IV). One genus of Lastaurini penetrated North America, probably very early in the Tertiary, and there had a great radiation.

5. Finally, the Dasypogonini of Laurasia had a significant radiation, originating several dominant and aggressive genera, especially *Saropogon*. This group was not able however to radiate in Africa and the Guiano-Brazilian subregion; in Australia they had a strong radiation, originating several genera, with noticeable derived characters.

During the Late Tertiary, or more probably during the Pleistocene, some relatively limited interchanges of faunas between the southern and northern continents occurred : the Blepharepiini and Megapodini colonized North America, coming from the Guiano-Brazilian region; the African Megapodini expanded to the Palearctic and Oriental regions. Some Dasypogonini and Isopogonini expanded to the south, barely invading northwestern South America, and northern Africa.

So, the present distribution pattern was formed:

- i. The Neotropical region with representatives of all the 5 tribes;
- ii. The Ethiopian with a few relict Isopogonini, and the dominant Megapodini;
- iii. The Nearctic with some Isopogonini, some Dasypogonini, descendants of very old stocks, and a few immigrant Blepharepiini, Lastaurini and Megapodini;
- iv. The Oriental region only with a few Palearctic Dasypogonini and a few Ethiopian Megapodini invaders;
- v. The Australian region with only relict Isopogonini and Dasypogonini;
- vi. The Chilean subregion with a few relict Isopogonini and Megapodini, and some relatively recent Dasypogonini.

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