Climate and the Phylogeny and Distribution of Tabanidae[1]

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This presentation grew out of efforts to explain to myself the present distribution and origins of the Neotropical Tabanidae. As I attempted to decide which groups seemed precinctive and which may have come from outside the region, I got involved in comparative studies of other faunas, possible migration routes, problems of primitive vs. specialized, and considerations of times on a geological scale. The striking similarities between the Chilean and Australian faunas especially needed explanation, but other similarities and differences also did not seem explainable on the basis of intercontinental migration. I read Shapley (1953), Kendrew (1961), Nairn (1961), Harrington (1962), Darlington (1965), and whatever else I could find on zoogeography and Paleoclimatology and tried to fit the proposals of Mackerras (1950, 1954, 1959, 1961) and Oldroyd (1957) into the picture as I saw it. The results do not by any means satisfy me, but have convinced me that a zoned climate and some form of continental drift have had an overwhelming influence on the present distribution and evolution of at least this group of Diptera, and should probably be taken into account in any similar study of insect distribution and evolution.

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The most difficult exercise in taxonomy is the determination of phylogenies, or probable lines of descent. When this must be done in the virtual absence of fossils, the exercise becomes one of determining the possibilities of a series of more or less educated guesses. The ranking of taxa in the order of their degree of primitiveness or specialization can be done on the basis of comparative morphology, but the results are relative and often ambiguous. This is because one must first rank characters, or structures, and their rankings are very likely to show little or no correlation among different structures in the same taxon.

The use of geographic distribution seems to be one of the few ways of checking the reality of morphologically based phylogenies. But it is very difficult to avoid circular arguments here. One is likely to assume that a taxon is primitive because it has a relict type of distribution, and decide that therefore its morphological characters are primitive. Taxa having characters established as primitive in this way are then used in efforts to define relict areas or bridge wide gaps in distribution.

If, however, one considers climate as another and independent factor, and introduces it into phylogenetic speculations, other relationships and correlations appear which may serve as additional checks on the reality of morphologically based phylogenies.

In what follows I have used the horse flies as an example of the use of climatic and geographic factors in checking a phylogeny based largely on morphology. I have done this primarily because it is the group with which I am most familiar, and one about which others, especially Mackerras (1954, 1955) have established what appear to me valid morphological criteria as to what characters and taxa are primitive or specialized. It has the further advantage of being almost worldwide in distribution and not showing a great variety or great extremes of structural diversity or adaptive dependence on other organisms. So far as known, no Tabanidae are parasitic nor do any depend on plants for food. Most adult horse flies appear to need a meal of vertebrate blood to mature a full complement of eggs, but there is a possibility that autogeny may occur in these, while others are exclusively flower or nectar feeders or take no food as adults. Thus dependence on vertebrates has probably not been an absolute limiting factor to their distribution. Comparatively little is known of the larval stages. The evidence available suggests that they show little diversity in structure and may utilize a wide variety of terrestrial and aquatic habitats. The known larvae apparently feed on any available invertebrates of suitable size, including other Tabanidae, or possibly on detritus or microorganisms. In any case there appears to be little close dependence on other organisms and few limiting environmental factors affecting the larvae. The adults are strong fliers and are evidently capable of extended over-water flights. This fact is evidenced by the wide distribution of some species and the presence of continental species on offshore or even quite distant islands such as the Galapagos and Mauritius. The presence, then, of Tabanidae, even of precinctive species on islands such as the West Indies, Fiji, and Samoa, does not necessarily indicate land connections.

The classification of the family accepted here is largely the work of Mackerras (1954). He divides the family into 3 main subfamilies, the Pangoniinae, Chrysopsinae, and Tabaninae, mainly on the morphology of the genitalia. The Scepsidinae, originally included as a 4th subfamily, was later abandoned Mackerras (1959 in litt.).

The Pangoniinae are regarded as the most primitive and are divided into 4 tribes. Of these, the Pangoniini is regarded as comprised of primitive and specialized moieties, the Scionini as also containing primitive and specialized elements, the Philolichini as being more homogeneous and mainly specialized. The Scepsidini contains but 1 primitive but aberrant species, not further treated here.

The Chrysopsinae stand in most respects between the Pangoniinae and Tabaninae, and are also divided into 3 tribes. The Bouvieromyini is believed to be the most primitive, but has some relatively specialized elements. The Chrysopsini are rather uniform structurally and only a few genera have been distinguished, though the species are numerous. The Rhinomyzini are all quite specialized.

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The 3 tribes of Tabaninae are the Diachlorini, Haematopotini, and Tabanini. The Diachlorini is both the most primitive and the most diverse, containing primitive and specialized moieties. The Haematopotini consists essentially of a single large and rather homogeneous group and 2 or 3 other monotypic genera. All are rather specialized. The Tabanini may be polyphiletic. It contains both specialized and primitive forms, but in my view none are either so primitive or so specialized as some Diachlorini. It is the largest tribe in the family, but the bulk of the species are placed in 2 genera.

The classification just outlined is based largely on morphology, and the terms *primitive* and *specialized* as used here refer to the ranking of the taxa, based primarily on the ranking of key characters. These latter characters, in general, are considered primitive as they approach the condition found in presumed ancestral forms, such as the Nematocera, specialized as they depart from them, either by reduction or increase in complexity. I realize that this is a controversial field, but there is not space to go into the details of the reasons for believing that the scheme outlined here does, in the main, reflect relationships.

Age

The Tabanidae are probably an old group. The evidence for this is scanty and mostly indirect. Fossil Tabanidae are few and unsatisfactory, consisting mainly of wings, and none are older than Oligocene. These all appear to represent modern genera. The fossil record of other Diptera is not extensive, though Brues et al. (1954) stated that Nematocera are known from the lower Jurassic and both Orthorhapha and Cyclorhapha from middle or late Jurassic. Hennig (1954) also believed that many nematocerous and brachycerous families were in existence by the Jurassic. The only extinct families known are from the Jurassic. Tillyard (1937) felt that Diptera arose in late Permian or early Jurassic. Cretaceous amber has yielded Empididae and 6 living genera of Chironomidae (Carpenter et al. 1936). A living genus of Bombyliidae has been reported from the Eocene (Hennig 1966, p. 56) and the living genus *Olbiogaster* (*Anisopodidae*) from the Jurassic (Stuckenberg 1962, p. 204). It thus appears probable that nearly all the present families of lower Diptera may have become differentiated by middle Mesozoic times, and that a large proportion of the genera, at least of Nematocera and lower Brachycera, were in existence before the end of the Cretaceous. Therefore, I assume that the Tabanidae existed as a family by early Triassic times and that the subfamilies, surely, and tribes probably were established before the beginning of the Tertiary, possibly early in the Cretaceous.

Morphological evidence, though relative, also tends to confirm that Tabanidae are rather primitive and hence relatively old. The wing venation is little reduced, mandibles are present in most species, the antennae are multisegmented, the genitalia quite simple, and ocelli are retained in many forms.

Distribution and *Climate*

When one considers the terrestrial environment in a broad way, certain facts of major importance to insect life seem evident. There is land where insects can live and there is salt water where they can't live. Both land and water are at the bottom of an ocean of air the chemical composition of which is practically uniform, but with physical characteristics that are not. There are several physical characteristics of the atmosphere which can and do affect insects, but the most basic and widespread, and the only one here discussed, is temperature.

To animals like insects, dependent on external heat for activity, zones of cold climate are barriers to dispersion which may be as effective as salt water. The fact that very many insects have developed adaptations to enable them to live in cold climates, while extremely few have invaded the marine environment, means only that cold is less of a barrier. No insects appear to be able to remain active, that is to feed and reproduce, at temperatures more than 2 or 3 degrees below the freezing point of water, even in such hostile environments as the Antarctic continent (Gressitt 1967).

I believe that insects as a class, and probably most orders and families, evolved in the Tropics, and by Tropics I mean areas where the temperature rarely if ever is low enough to stop insect activity. In respect to the Tabanidae this seems to me evident in the cases of the subfamilies, tribes, and most genera. If this is so, then the ability to survive and reproduce outside the Tropics is an acquired adaptation (Ross et al. 1964), although one that has evolved repeatedly at different times and places and in different groups. The Diptera seem to have been unusually successful in this respect, as they are a dominant group in cold climates. The only holometabolous insects on the Antarctic continent are 2 Diptera (Gressitt 1967).

From the insect point of view, there are actually 2 kinds of cold climate, probably needing different adaptive mechanisms to permit survival. One is the so-called continental type, with essentially tropical summers but long and very cold winters. This is characteristic of the large land masses in the North Temperate zone. The other is a constantly cool climate, without great seasonal variations. The temperature, because of local factors of topography, wind, etc., seldom is below freezing for very long, and seldom reaches tropical temperatures. Sunlight is often deficient because of excessive cloud cover. This kind of climate is prevalent especially on islands, on high mountains in the Tropics, and along coasts bathed by ocean waters with temperature contrasting markedly with that to be expected on the adjacent land, such as Chile and western Europe. Insects inhabiting the continental type need physiological adaptions primarily to survive in a resting stage—egg, larva, pupa—or behavioral adaptations to escape the severe conditions by migrating or seeking protected environments. Those inhabiting the 2nd type of climate must evolve physiological mechanisms operative throughout the life cycle.

Although adaptation to cold is a common phenomenon among insects, I believe it has led to some interesting evolutionary results. In the Tabanidae at least there are few authentic cases of cool adapted taxa at any level invading the Tropics, except at high altitudes where temperatures are low. On the other hand, there are numerous tropical genera with cool adapted species, and numerous tropical species have invaded cool environments. The tropical environments are furthermore well known to have far richer and more diverse insect faunas. Among the Tabanidae, for example, the Neotropical fauna has about 3 times as many species as the Nearctic. The 3 largest genera in tropical America include about 31% of the total species, while in temperate North America about 74% of the total species belong to the 3 largest genera. In temperate South America, about 60% of all species belong to a single genus. It is also generally accepted that though species are fewer, individuals tend to be more abundant in temperate climates. In my own collecting of Tabanids this is certainly my strong impression, though I have seen no precise comparative studies on the subject.

This fact, if it is a fact, of more severe interspecific competition and heavier selection pressures in the tropics would mean that successful adaptation to cold and consequent movement out of the Tropics would also mean movement into an environment of lower competition and lessened selection pressure. It would then follow that evolution would be slowed in cool climates, and that movement by a cool adapted taxon back into the Tropics would be increasingly difficult.

Now if the assumptions and deductions just made in regard to cool adaptation prove applicable to a substantial number of cases, a further corollary seems to me very probable. Since movement of insects is more prevalent into cool regions from the Tropics, and differentiation and specialization—evolution—are slower in the cool areas, there should be a gradual accumulation of less specialized taxa in cool areas. In other words, cool climatic areas act somewhat as traps for primitive stages in the evolution of a group. When these areas become, in addition, isolated by other barriers unfavorable to the group involved, so that immigration from the Tropics is restricted, a population with a high proportion of precinctive forms will result. Depending on the times of contacts and isolations, the fauna will to a certain extent reflect its history. Thus Chile has been very effectively isolated by high mountains and deserts, probably throughout the Tertiary, from any immigration directly from the Tropics. Its tabanid fauna is highly precinctive and includes only a very few elements of obvious or recent tropical derivation. On the other hand, emigration of cool adapted types from Chile has occurred northward along the cool Andes, and probably eastward through mountain gaps in temperate latitudes into southern Argentina.

The distribution of the various tribes is:

PANGONIINI.—The unspecialized genera occur in eastern and western Nearctic, southern Brasil and Chile in the Neotropics, the southern tip of Africa, in scattered localities in the Palearctic from Spain to northern Japan, in temperate Australia and the south island of New Zealand. The specialized genera occur from northern Argentina and Chile to south-central U. S., and in the Mediterranean region of Europe and North Africa.

SCIONINI.—The unspecialized genera are in the eastern Nearctic and temperate to subtropical Neotropical, and in Australia, New Guinea, and New Zealand. The specialized genera are all Neotropical, from Mexico to northern Argentina, but apparently not in Chile.

PHILOLICHINI.—This tribe replaces the Scionini in the Old World, occurring throughout Africa south of the Sahara, with 1 genus in Algeria and Morocco, and a few species in India, Mauritius, Indonesia, and New Caledonia.

BOUVIEROMYINI.—The unspecialized members of this tribe occur in the eastern Nearctic, Chile, Temperate South Africa, with 1 species widespread north to the Congo Basin, northeastern Asia and Japan, and eastern and southern Australia. The specialized genera are all in the Old World, South and Tropical Africa, Madagascar, Seychelle Islands, Indonesia, New Guinea, and Australia, with 2 species in north India and south China.

RHINOMYZINI.—This specialized tribe is mainly in tropical Africa and Madagascar, with a few species in south India, Ceylon, and Indonesia.

CHRYSOPSINI.—The bulk of the species are tropical, in South America and Africa, but well represented in the Nearctic and Palearctic. There are far fewer species in the Oriental region, and only 3 occur in the Australian region and one in Chile.

DIACHLORINI.—The unspecialized genera occur in the south-temperate Neotropical, including the high Andes mountains, the southern tip of Africa, Madagascar, Mauritius, the mountains of south India, and the Australian region, including Tasmania and New Zealand and New Caledonia. Only a few beach or coastal species extend into New Guinea. The specialized genera cover the tropical Neotropics and southeastern Nearctic, the Mediterranean region, eastern Africa, Madagascar, Mauritius, Ceylon, Java, Philippines, Celebes, and the Australian region east to Fiji, but not Tasmania or New Zealand. The temperate species are very few as compared with the tropical.

HAEMATOPOTINI.—More than 90% belong to a single genus, with the bulk of the species African and Oriental. They are well represented in the Palearctic, extending north beyond the Arctic Circle in Scandinavia, and a few species are Nearctic. None occur in the Neotropical or Australian regions with the exception of 1 doubtful record from New Guinea, and none in Madagascar.

TABANINI.—This tribe is worldwide, but best represented in the Old World tropics and the North Temperate regions. About 20 species occur in Australia, mostly in the north and east, none reaching Tasmania, New Caledonia, or New Zealand. Only 4 species are known from Madagascar and about 6 from Chile.

The discussion of climate has suggested an explanation of the preponderance of primitive forms in cooler climates, or at least the occurrence of most primitive relicts outside the tropics. However, it has not done much to explain some of the knottier problems in distribution, except to make certain hypotheses more unlikely. Thus the remarkable resemblances between the Southern Hemisphere temperate faunas seem increasingly unlikely to be the result of migrations by way of any Northern Hemisphere land bridge. Furthermore, the present wide disparity between African and Neotropical tropical faunas argues a lack of effective migration routes via either north or south, or any at all recent contact. The general similarity between Nearctic and Palearctic faunas, especially their more boreal elements can be, and usually is, explained by the presence of the Bering land bridge, although this may not be the whole story. To put it briefly, there appear to be 2 separate cool adapted faunas in the North and South Temperate zones, both containing primitive relicts and both having their relationships preponderantly with faunas at the same latitudes. Between lie largely specialized faunas, almost entirely unrelated as between the Neotropics and Africa, but showing a number of similarities as between the Neotropics and Tropical Australia, with the Oriental region seeming to be a mixing area for African and Australian elements.

Table 1 shows the number and the percentage of species belonging to each subfamily in each of the main zoogeographical regions and to each tribe in each subfamily. Note the general similarity in tribes between the Australian and Neotropical, except for the reversal of representation of Bouvieromyini and Chrysopsini. One species of *Chrysops* in Australia, 2 species of *Mesomyia* in Chile. The same holds true more or less with the Palearctic and Nearctic regions, but the reversal here is

Table 1. Number and percentage of species of Tabanidae belonging to each subfamily in each of the main zoogeographical regions and to each tribe in each subfamily.

	Neotropical		Nearctic		Australian		African		Palearctic		Oriental[a]		Totals
	Species	%	Species	%	Species	%	Species	%	Species	%	Species	%	Species
Pangoniinae	267	27.1	23	7.8	89	38.0	85	14.4	39	8.4	4	1.1	507
Pangoniini	102	38.0	22	95.6	21	23.5	2	2.3	36	92.3			183
Scionini	165	61.5	1	4.4	68	76.4							234
Philolichini							83	97.6	3	7.7	4	100	90
Chrysopsinae	73	7.2	87	29.8	37	15.8	158	26.9	66	14.1	41	11.9	462
Bouvieromyiini	2	2.7	2	2.3	36	97.3	68	43.0	2	3.1	8	19.5	118
Chrysopsini	71	97.2	85	97.7	1	2.7	45	28.5	64	96.9	26	63.4	292
Rhinomyzini							45	28.5			7	17.0	52
Tabaninae	646	65.4	183	62.3	108	46.1	344	58.6	361	77.4	298	86.9	1940
Diachlorini	481	72.6	16	8.7	88	81.4	30	8.7	12	3.3	18	6.0	645
Haematopotini			5	2.7			184	53.4	57	15.7	80	26.8	326
Tabanini	165	25.5	162	89.0	20	18.5	130	37.7	292	80.9	200	61.7	969
Totals	986	33.8	293	10.0	234	8.0	587	20.1	466	16.0	343	11.7	2909

[a] Estimated. No recent catalog published.

between Scionini and Philolichini. The Oriental and African regions resemble each other hardly at all, nor does either show much similarity to any other region.

I think I have shown that the probabilities favor an origin within a tropical climatic area for the Tabanidae and its divisions down to tribes, and that a record of sorts of past more primitive character states is to be found in the relicts preserved in cool refugia in both Temperate zones. It is also evident, I believe, that neither the place nor relative time of origin of the family or any of its subfamilies can be ascertained from the available evidence. In the case of the tribes, I believe it is possible to arrange them in a relative chronological sequence as to origin. I consider that the Pangoniini, Bouvieromyini, and Diachlorini contain the most primitive elements of their respective subfamilies. I should think that Scionini evolved quite early from Pangoniini, and that the Philolichini were either a later offshoot of Scionini, or arose in a different and separated place, from Pangoniine stock. The Chrysopsini are a conservative yet successful group which has left few primitive relicts, and those all in the North Temperate Zone of both hemispheres. The dominant genus *Chrysops* is numerically tropical, but is very well represented in the Nearctic and Palearctic. It may form an exception to the assumption that cool adapted species do not reenter the Tropics, or it may prove on more detailed analysis to be polyphiletic. The bulk of the species are in the Neotropics and Africa. I can make no guess as to time and place of origin. The Rhinomyzini are all tropical and largely specialized. They probably arose fairly late from Bouvieromyini and most probably in the Old World. Haematopotini appear to have arisen from either a somewhat specialized Diachlorine ancestor or from some Tabanine stock close to Diachlorini. Since they are unknown in the Neotropics or Australia and very little represented in the Nearctic, and show no markedly primitive relicts, I should think that their time of origin was fairly late and in the Old World Tropics, probably north of the equator. The Tabanini are so numerous, widespread, and diverse that I am intrigued by the possibility that they may be polyphyletic, though much careful analysis will be needed to sort out the primitive stocks. The fact that hardly any have reached South Temperate latitudes is noteworthy. They form the highest percentage of the fauna in the Nearctic, progressively less in Palearctic, Oriental, and Ethiopian, though they are the preponderant group in all. Primitive forms are nearly all in the North Temperate zone, none in the South. If they are monophyletic they must have arisen quite early from Diachlorini, probably in the Eastern Hemisphere. If polyphyletic, there may have been 2 centers of origin, the Neotropics and probably the Orient.

The probable times of origin of the subfamilies, or in other terms, their most primitive tribes, their wide distribution, and the concentration of primitive types in cool areas, particularly in the Southern Hemisphere, suggest to me that they may have arisen on a southern tropical land mass, or group of partially connected land masses, at a time when these masses included more habitable cool areas either because they were farther south than the present southern continents, or because the worldwide temperatures were higher, probably both. The tribes with more restricted distributions and few or no primitive relicts in the south may have arisen at a later time when either the present northern land masses were farther south or after the northward drifting, and separating, complexes of southern land masses had made contact with the northern. Since evidence is rapidly accumulating that there *has* been continental drift, speculation as to its effect, especially on organisms with history including times when this may have occurred, is stimulating, if possibly premature. At the moment, I see no alternative to such speculations in attempting to explain the origins of the Tabanidae.

Since presentation of this lecture I have had a chance to read several additional papers bearing on this general problem. Axelrod (1959) believes that the Angiosperms, the flowering plants, originated in the Tropics in pre-Cretaceous times, and that the Tropics formed a much broader belt, from 45° N to 45° S latitude. He believes that the climate in Mesozoic was much more uniformly warm. Although he notes that Angiosperms appeared earlier in northern latitudes than in southern, he explains this on edaphic factors and chances of fossilization rather than on continental drift. Graham (1964) in discussing the fossil record of plants also believes the mesozoic climate more uniformly warm, or a much broader tropical band. But he notes that Cretaceous temperatures calculated from oxygen isotopes show comparable temperatures in Denmark at 56° N latitude and Australia at 25° S latitude, which fact suggests that either the tropical band was farther north or the continents farther south. Brundin (1965) believes the distribution and phylogeny of the Chironomidae, worked out by Hennig's methods, give clear evidence of the existence of Gondwanaland and an Antarctic center of origin. He believes the north temperate sister-groups reached their present homes by moving through the Tropics at high altitudes. Axelrod and Bailey (1968) in discussing possible reasons for extinction of the Dinosaurs at the end of the Cretaceous, suggest that the mesozoic was a time of equable climate because of lack of high mountains and presence of extensive shallow continental seas. Mountain building at end of Cretaceous and withdrawal of seas caused greater variation in temperatures and extinction of dinosaurs which were unable to adapt. Other organisms, especially mesozoic floras, retreated to Southern Hemisphere areas of equable climate. Hennig's (1966) detailed study of the Diptera of New Zealand does not contribute much to the question, as he appears to assume a Northern Hemisphere origin for the Diptera and does not take into consideration possible climatic shifts.

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