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Transantarctic relations of *Diachlorini* (Diptera: *Tabanidae*)¹

Abstract. *Diachlorini* are distributed in 8 vegetation zones, but it is only in Neotropis that they occupy the entire environmental range. Plesiomorphic, intermediate and apomorphic character states in *Diachlorini* were discussed. The definition of ancestral forms is based on plesiomorphic character states. Their occurrence in Australia is indicated by intermediate character states in east Australia and New Caledonia. A four-step similarity analysis resulted in two clusters of closely related plesiomorphic taxa, one including *Cydistomyia* TAYL. and *Nubiloides* COSC. & PHIL., and the other with *Cydistomorpha* TROJ. as the basis for all other clusters, but nearest to Neotropical *Stenotabanus* LUTZ-related taxa. Similarity analysis confirmed the hypothesis of much closer morphological relations between South American and Australian taxa, than between Australian and South African ones. Transantarctic hypothesis is confirmed.

Key words: *Diptera*, *Tabanidae*, *Diachlorini*, ancestral forms, origin, habitat preferences, timing, distribution routes.

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INTRODUCTION

Four isolated centres can be seen in the to-day distribution of the tribe *Diachlorini* s.str. (TROJAN 1997). Three of them fit a Gondwanan distribution pattern. The only exception is two genera, *Dasyrhamphis* END. and *Philipomyia* OLS., occurring in the Mediterranean Region. In comparison with „old” *Lepidoselagini* (MACKERRAS 1954, FAIRCHILD 1969) *Diachlorini* represent a younger branch of the subfamily *Tabanidae*, and their taxonomic position is nearest to the *Tabanini* (TROJAN, IWAN & WYTWER 1997). The new division of

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the subfamily *Tabaninae* (TROJAN 1994) makes necessary the re-examination of results and opinions concerning the questions of origin and migration routes of horse-flies, and also the timing of these events.

The discussion on the origin of supraspecific taxa of *Tabaninae* has a long tradition. HENNIG (1952) has provided the first outline of the problem. He supposed that the migration routes between Neotropical and Afrotropical horse-flies do not run across the Atlantic. He also expressed also the opinion that finding an answer for the question of migration channels is necessary for recognition of the basic systematic structure of the family. Two such hypothetical channels were proposed, the northern, or Lemurian, route, and the southern, or Antarctic, route. This concept was subsequently developed by OLDROYD (1957), who proposed two centres of evolution for *Tabanidae* :

1. A southern centre with dominating *Diachlorini* s. l. including a conservative group, now known as *Lepidoselagini*. This group has undergone extensive radiation connected with northward-directed expansion, they invaded those areas and settled tropics.

2. The northern centre was occupied by *Tabanini* and *Haematopotini*. From this centre they invaded the Afrotropical, Oriental and also Nearctic regions.

OLDROYD's concept can be defined as the bicentric hypothesis. However, his map (OLDROYD 1957: 52, map II) indicates only one radiation centre of *Tabanidae* in tropical South America, an area representing the highest taxonomic diversity of the family. Hennig's opinion that a high number of species cannot be accepted as a proof of the antiquity of the group was not taken into account. *Diachlorini*, evidently belonging to the southern centre, after OLDROYD (l.c.) originated in South America, and by the transantarctic route invaded the south-eastern part of the Afrotropical Region and southern part of Australia. The northern route through Arabian Peninsula, India and insular Orient to northern Australia was used only by *Philolichini* and *Rhinomyzini*, both of African origin.

Explanation of distribution and evolutionary events in the southern hemisphere is strongly influenced by paleogeographical concepts. All above treated opinions are based on the assumption of a stable position of continents. Actually, such opinions as this of HARTMANN (1986), that the Gondwanaland distribution pattern hypothesis is only a probable speculation even if it takes into account results of paleomagnetic, plate tectonic and deep-sea floor studies, are exceptional. At the same time, in the first volume of the „Fauna of Australia”, DYNE G.R. & WALTON D.W.(eds) (1987) and a group of co-authors broadly accepted the continental drift theory as the most probable basic concept for explaining the origin and composition of present Australian fauna.

The concept of a stable position of continents constrains the acceptance of continental bridges or corridors or the possibility of land animals living only a few days crossing large oceanic barriers. An example of such difficulties is given by MACKERRAS (1961: 105), who compared the horse-flies of New

Zealand and New Caledonia and assumed an existence of a Pleistocene land bridge between the two islands, which was necessary to explain the occurrence of *Protodasyommia* END. on both islands. However, the representatives of *Cydistomyia* TAYL. live only on New Caledonia. It was therefore indispensable to accept the risky concept of a one-way channel between these two islands.

For the sake of this paper I have accepted continental drift events as a basis for analysis of the distribution of *Diachlorini*. In morphological analysis I have distinguished plesiomorphic and apomorphic characters, especially of relict forms. Such treatment of the material enables the designation of primary and secondary centres of their radiation. Changing positions of land plates and islands, together with changing climatic conditions in successive geological periods, allow more precise indication of past events in the evolutionary history of the group. An other matter of interest is the habitat preferences of several groups of *Diachlorini*. Their occupance of tropical ecosystems seem to be quite fresh.

In many cases of evolution-related considerations on the origin of *Diachlorini*, ancestral forms are situated outside the area under investigations. Such procedure allows one to omit the somewhat complicated analysis of character states and the definition of characters in the ancestral group. It is, however, hardly possible when all taxa belonging to a tribe are examined.

If we take into account the sequence and timing of the Gondwanan plate break up, and related environmental events, and if we accept a view that the dissimilarity of related taxa increases with permanent isolation, the following working hypothesis can be proposed for the explanation of the present distribution of *Diachlorini*.

Hypothesis. The degree of dissimilarity between the taxa of *Diachlorini* of Gondwanan origin should be:

1. Greatest between Madagascar and the rest of Gondwanaland taxa.
2. Smaller between the taxa of India and other parts of Gondwanaland.
3. Still smaller between South African taxa and those of Australia (and South America).
4. Even smaller between the taxa of New Zealand (with New Caledonia) and Australia (with South America).
5. Smallest between Australian and South American taxa.

This hypothesis is easy to falsify. A similar view was expressed by HEATWOLE (1987) in relation to Australian fauna.

The first point is to be rejected, because there are no *Diachlorini* on Madagascar. Two species of *Tabanotelum* Oldr. occurring on the nearby Macarenes (Mauritius I.) cannot be taken as a proof of existence of a horse-flies stop between Africa and India because these islands of volcanic origin are quite young, and were formed in the process of sea floor spreading. Therefore they could not serve as a refugium for old African *Diachlorini* which should appear on Madagascar and Indian plates before 190 or 140 Mybp.

The same is true for Indian *Cydistomyia* TAYL., and their relations to African *Amanella* OLDR. or Australian *Cydistomyia* TAYL. need examination based on careful analysis of similarity between the species of this genus. The last three points of the hypothesis are open for considerations.

The aim and scope of the present paper is to perform an evolutionary analysis of Gondwanan *Diachlorini*, and particularly :

1. to analyse their habitat preferences and distribution throughout the Gondwanaland.
2. to examine numerical values of the character states for the purposes of the similarity analysis;
3. to define a set of characters and their states attributed to the ancestral form;
4. to indicate the most possible place of their origin;
5. to distinguish a group of closely related plesiomorphic taxa on the basis of the similarity analysis;

EVOLUTION OF GONDWANAN ENVIRONMENTS



A review of the Gondwanaland history (Annexe 1) was compiled from numerous sources. It was subsequently applied as an environmental background for distribution analysis of *Diachlorini*. Most data concerns to the Australian Region. Much less information was gathered on African and South American geological history, and the data on the evolution of the Antarctic environment are still largely covered with a thick layer of ice.









































































The occurrence of a large ice sheet covering a large part of the fused single Gondwana supercontinent on the Carboniferous-Permian boundary is a starting point for a discussion on the origin of the land biota of the southern hemisphere. At this time only the northern belt of Australia and India, the northern half of Africa and the entire northern and western part of South America were free of ice. Cool-adapted *Glossopteris* flora dominated on periglacial swamps, forming coal deposits. Progressive warming of the climate began in Upper Permian and a soft to warm humid climate dominated over all Gondwanan continents throughout the Mesozoic era. Changes in climatic conditions are connected there with the fragmentation of the previously fused Gondwanan continent. An important effect of this fragmentation is the closing of equatorial and establishment of southern circumpolar currents. In South America a secondary factor was the formation of the Andean mountain barrier. All these events are rather new in Gondwanan history, and after the Permian deglaciation there were favourable conditions for the spread of land insects over the whole undivided continent. This is the reason for attaching greater importance to the sea barriers, originating as a result of the break-up of the primarily undivided giant Gondwanaland, and also in the case of sea transgressions, than to the differences in climate.

The fragmentation of the Gondwanan plate (Table I) began 190 Mybp with the separation of Madagascar. Ten millions year later Gondwana was

separated from the northern part of Pangea, namely Laurasia, by a large Tethys II sea. The separation of India took place during the Lower Cretaceous, approximately 140 Mybp, and of the whole African continent, 120 Mybp. These dates are of great interest for tracing the evolution of animals. India, for nearly 95 My, and Africa, for more than 80 My, were separated from other parts of Gondwanaland, and also from Europe and Asia.

Table I. Fragmentation of the Gondwanaland throughout of earth history:

 fused continent,  isolated lands or islands.
Explanation of abbreviations: Af - Africa, An - Antarctica, Au - Australia, I - India, M - Madagascar, NC - New Caledonia, NZ - New Zealand, SA - South America.

No	Period	Mybp	M	I	Af	SA	An	Au	NZ	NC
1.	Permian to Jurassic	280-200								
2.	Jurassic	190								
3.	Early Cretaceous	140								
4.	Middle Cretaceous	120								
5.	Late Cretaceous to Palaeocene	80-65								
6.	Late Palaeocene	60-57								
7.	Late Eocene	45-37								
8.	Middle Oligocene	30								
9.	Miocene	20-10								

An other important event was the separation of New Caledonia and New Zealand from the eastern part of Gondwana 80 - 65 Mybp due to the expansion of Coral and Tasman seas. They moved a long distance away from the maternal continent. New Zealand has remained isolated till now, New Caledonia drifted northward, and there, in the Miocene, it came into contact with New Guinea owing to a chain of islands forming a bridge that enabled the exchange of fauna (TILLIER 1988).

The separation of Australia from Antarctica began in the Palaeocene 60 Mybp, but the exchange of fauna was for a long time possible throughout a Tasmanian bridge. Migration through the southern route was closed when the ice cap on the Antarctica covered the entire continent, which took place in the Upper Miocene, several million years before now. The northward motion of Australia resulted in a collision of the Australian and Asian plates. In effect, some parts of northern Australia were submerged, but other parts of its former northern edge emerged. In the Miocene New Guinea and most of islands constituting recent insular Orient were formed. AUDLEY-CHARLES (1983) suggest also a transfer from Australia to the Asian continent of some fragments of land, namely southern Tibet, Burma, Thailand, Indochina and Malaya. I want here to indicate only that the insular bridge enabling the exchange of fauna between Australia and Orient was opened only in the Miocene, and during the last glaciation of the North Hemisphere a large land bridge was open due to the lowering of the sea level on the Indian Ocean and the Pacific 180 to 100 m below the present depth. The long isolation of Australia from India was interrupted for a short period in Pleistocene.

HABITAT PREFERENCES OF GONDWANAN *DIACHLORINI*

The long-lasting isolation of the four areas settled by *Diachlorini* exposed them to different environmental conditions. At present they occur in several vegetation zones, chiefly in hot and hot temperate climates. In the Palearctic Region they are distributed around the Mediterranean Sea, in the macchia vegetation type. In the Oriental and Australian regions they live in more humid climate. The greatest degree of differentiation is seen in situation we meet in South America. The majority of species occurring in the Neotropical and Nearctic regions are distributed northward of the line dividing Argentina into a southern part with more continental, temperate and cold climates, and a northern part moister and hotter, with prevailing tropical climates (FAIRCHILD 1969, TROJAN 1997). Among American *Diachlorini* other than those belonging to the *Cydistomyia* series, 28 genera with 342 species are distributed northward of this boundary, chiefly in the tropical or subtropical zones. The only exception is *Nubiloides* COSC. & PHIL. with 2 species living in the cold temperate rain forest (DARLINGTON 1965).

Table II. Ranges of plesiomorphic taxa of the *Cydistomyia* series in vegetation zones

Region	Genus	Number of species in the vegetation zone							
		Desert and semi-desert	Mediterranean	Savanna	Sub-tropical forest	Tropical rain forest	Temperate mixed forest	Cold temperate rain forest	Montane
Afrotropical	<i>Amanella</i> & <i>Canalicula</i>	0	8	9	0	0	0	0	0
	<i>Tabanotelum</i>	0	0	0	0	2	0	0	0
	<i>Stenotabanus</i> cluster	2	0	6	7	44	2	0	5
Neotropical	<i>Agelanius</i>	0	0	0	0	0	0	8	2
	<i>Nubiloides</i>	0	1	2	0	0	0	2	0
Oriental	<i>Cydistomyia</i>	0	0	0	5	16	0	0	0
Australian	<i>Cydistomyia</i>	0	0	0	14	70	0	0	0
	<i>Chalybosoma</i>	0	0	0	0	3	0	0	0
	<i>Chasmiella</i>	0	0	0	0	20	0	0	0
Total		2	9	17	26	155	2	10	7

The *Cydistomyia* series, distributed in four zoogeographical regions (Table II), merits special attention. Two Neotropical genera occurring south of the climatic boundary are added for comparison. Afrotropical genera are found in two vegetation types, the savanna and the forest savanna, and in Mediterranean-type vegetation with an addition of mixed forest (USHER 1972). Two species of *Tabanotelum* OLDR. found on Mauritius I. live in a tropical forest zone. Much greater differentiation is seen among Neotropical representatives. The *Stenotabanus* cluster is distributed in six vegetation zones, although the majority of its species prefer the tropical rain forest. Two other genera, *Agelanius* ROND. and *Nubiloides* COSC. & PHIL., belong to other

series, but they bear many apomorphic states of characters and therefore are included there for the sake of further analysis. They occur there chiefly in the cold temperate rain forest zone (RATCLIFE 1984), which dominated in the past over large area of the Gondwanan continent. In Oriental and Australian Regions habitat preferences of *Diachlorini* are limited to tropical and subtropical forests.

NUMERICAL VALUES OF CHARACTERS

The characters and their states listed below (Table III, IV, V) and applied to the similarity analysis of the taxa of the *Cydistomyia* series, were also used for the purposes of defining of the set of characters of ancestral forms.

Table III. Character states distinguishing the core of the *Cydistomyia* series

No	Character	Plesiotypic state value = 0	Intermediate state value = 0.5	Apotypic state value = 1
1	Head	flattened	hemispherical	strongly inflated
2	Frontal callus	touching subcallus	separated from subcallus	linear or reduced
3	Face	pruinose	–	with shining spots
4	Scape	cup-like or conical	hood-like	pipe-like, oval or inflated
5	Pedicel	cup-like	cup-like with dorsal hook	pipe-like
6	Basal plate	short	moderate	elongate
7	Wings	transparent unpatterned	fumigated	patterned or wholly dark
8	Bazicoستا	bare	with few setulae	wholly setulose
9	Legs	normal	–	incrassate or elongate

In cladistic analyses (RATCLIFE 1984) all character states are divided into two groups: plesiotypic, corresponding to „old” or ancestral forms, and apotypic representing „young” or advanced evolutionary changes. Most plesiotypic character states are seen in genera belonging to the *Cydistomyia* series. Only they were selected for analysis, with one additional genus *Chasmia* END., closely related to *Chasmiella* END., both occurring on New Guinea. All characters were divided into three groups. The first group of nine characters was used earlier for determining the core of the *Cydistomyia* series (Table III) (TROJAN 1998). A second group of characters (Table IV) is used for description of numerous genera of *Diachlorini* in all series. The last group of characters (Table V), applied rarely and only for distinguishing single genera, plays an additional role.

The division of character states into plesiotypic and apotypic, though legitimate in species-level analyses, is hardly applicable in relation to genera. This is especially true for species-rich genera with broad distribution ranges, as they frequently exhibit great variability in characters. We find there plesiotypic and apotypic states of characters, but also their intermediate forms, and in some cases variability is demonstrated over the whole range of character states. These four groups are distinguished for the purpose of the similarity analysis. Three of them are tabularized below, the whole range of the character variability received the value 2

The first group of characters is connected with the definition of the core of the *Cydistomyia* series (Table III).

The list of characters enumerated in the above table does not exhaust the number of characters of evolutionary significance. 15 such characters found in the *Cydistomyia* series were taken into account in the similarity analysis (Table IV). They are related to the head and wing morphology.

Table IV. Additional character states in the *Cydistomyia* series

No	Character	Plesiotypic state value = 0	Intermediate state value = 0.5	Apotypic state value = 1
10	Postocular rim	broad	narrow	lacking
11	Eyes	haired	with some microscopic hairs	bare
12	Frons	diverging	parallel-sided	converging
13	Frontal index	1-3.0	3.1-4.0	> 4.0
14	Ocellar tubercle	distinct with ocelli	developed without ocelli	lacking
15	Subcallus	flat	swollen	inflated
16	Face	flat	produced	inflated
17	Parafacial index	0.9-1.4	1.5-1.6	> 1.6
18	Basal plate	pipe-like	obtuse-angled	with dorsal tooth or process
19	Length of the proboscis in relation to the head height	shorter	equal	longer
20	Labellae of the proboscis	fleshy	partly sclerotized	wholly sclerotized
21	Palpi	short	moderate	elongate
22	Palpi	slender	swollen basally	wholly swollen or flattened
23	Base of the costal vein	without groove	-	with groove
24	Vein R4	appendiculate	angulate	smoothly curved

Moreover five unique characters (Table V) were included. They were applied to taxonomic studies for the sake of distinguishing single genera of the tribe. Evolutionary significance can be easily ascribed to most of their states.

Table V. Unique character states distinguishing the genera in *Diachlorini*

No	Character	Plesiotypic state value = 0	Intermediate state value = 0.5	Apomorphic state value = 1
25	Bands on eyes	2 or more	1	0
26	Tibiae	unicolorous darkened at the tip	-	contrastingly coloured
27	Body tegument	mat	-	metallic
28	Abdomen shape	flattened	-	convex or tapering
29	Style annuli	4	-	3 or less

ORIGIN OF THE DIACHLORINI

Recent distribution studies (TROJAN 1997) indicated that *Diachlorini* never settled in large areas of North America, Europe and Asia. In continental Orient only six species were found in India (STONE 1975), but their origin needs examination. They were not found in Thailand (BURTON 1978), Malay Peninsula (PHILIP 1960), Indochina Peninsula, in the oriental part of China (WANG ZUNG-MING 1983, 1994) or in Japan (MURDOCH & TAKAHASHI 1969). All countries mentioned above have habitats favourable enough for *Diachlorini*.

Such a distribution pattern indicates a post-Jurassic origin of the tribe, when all parts of Gondwanaland were separated from Euramerica and Asioamerica by the large sea barrier of Tethys II, and the sea level rise submerged a great part of former lands (SUTTON 1978). This view can be supported by the distribution pattern of older *Lepidoselagini*. They are commonly found chiefly in the southern part of Gondwanan continents, but are represented in the Holarctic Region by numerous relict forms (TROJAN 1996).

If zero states are to be applied in the description of ancestral forms of *Diachlorini* they should be interpreted as follows: Body of medium size, mat tomented, with oval flattened, unpatterned abdomen. Head flat with broad postocular rim. Eyes haired with two or more bands. Frons diverging, index not exceeding 3.0. Ocellar tubercle distinct with well developed ocelli. Frontal callus touching subcallus. Face and subcallus flat without shining spots. Prarfacial index 1.5 to 1.6. Scape and pedicel cup-like, basal plate rather short, pipe-like, four style annuli. Proboscis shorter than head height, labellae soft. Palpi short slender. Wings transparent without pattern. Bazicostal plate bare, costal vein without groove at the base, vein R4 appendiculate. Legs normal with unicolorous tibiae, sometimes darkened at the tip.

This set of characters is close to that proposed by MACKERRAS (1964: 97) for the ancestor of Oriental and Australian *Diachlorini*. The fusiform shape of the frontal callus can be discussed only in relation to Australian and Oriental forms. These of Afrotropical and Neotropical regions have frequently a square lower frontal callus.

Of special meaning for the analysis of the origin of *Diachlorini* are the characters applied for distinguishing tribes of the subfamily *Tabaninae* (TROJAN, IWAN & WYTWER 1997). Intermediate states of these characters can indicate proximity to ancestral forms which can occur in *Lepidoselagini*. Two such characters have a greater significance: the setulosity of the bazicostal plate and an intermediate parafacial index.

The frequency of the above discussed states of the two characters shows that in *Lepidoselagini* (Table VI) nearly 6.3 % of the species examined have the intermediate form of the parafacial plate, and 15.8% have a setulose bazicostal plate.

Table VI. Parafacial index and the setulosity of basicostal plate in *Lepidoselagini* occurring in four regions

Region	Examined		Parafacial index			Bazicostal plate		
	Genera	Species	1.0-1.4	1.5	>1.5	bare	with few setulae	wholly setulose
Neotropical & Nearctic	21	50	49	1	0	45	5	0
Australian & Oriental	10	30	25	5	0	30	0	0
Afrotropical	3	5	5	0	0	5	0	0
Palaearctic	4	10	10	0	0	1	4	5
Total	38	95	89	6	0	81	9	5

A similar make up of the values of characters under examination (Table VII) was compiled for the species of *Diachlorini*. It makes possible the comparison of their variability in the four distribution centres of the tribe. The number of species with intermediate parafacial plates is much lower, only 2.1%, and while those with bazicostal plates with few or numerous setulae account for 15.9%.

Both characters, the parafacial index and the setulosity of the bazicostal plate are of different importance for evolutionary analysis. They are also unevenly distributed.

An increasing number of setae occurring on the basicostal plate indicates changes leading towards *Tabanini*. Such intermediate forms occur among *Lepidoselagini* in Neotropical *Eristalotabanus* KROEB. and *Phorcotabanus* FAIRCH., and in Nearctic in *Anacimas* END. and *Microtabanus pygmaeus* (WILL.). A wholly setulose bazicostal plate is found in *Leucotabanus* LUTZ. A greater number of intermediate forms occurs among Palaearctic *Lepidoselagini*. Only *Nanorrhynchus* KROEB. has a bare bazicosta. In *Ochrops* SZIL. and *Glaurops* SZIL. it bears a few setulae and in Mediterranean *Mouchaemyia* OLS. five species have a wholly setulose bazicostal plate. This places this genus among the candidates for the status of ancestral forms for *Tabanini*. In Neotropical *Diachlorini* the bazicosta with a few setulae is found in 11 genera, but their affinity to the tribe *Tabanini* needs examination.

Table VII. Parafacial index and bazicostal setulosity of *Diachlorini* in four centres of their distribution

Region	Examined		Parafacial index			Bazicostal plate		
	Genera	Species	1.0-1.4	1.5	>1.5	bare	with few setulae	setulose
Neotropical & Nearctic	31	96	0	0	96	74	20	2
Australian & Oriental	7	42	0	3	39	41	1	0
Afrotropical	3	3	0	0	3	3	0	0
Palaearctic	2	4	0	0	4	4	0	0
Total	43	145	0	3	142	122	21	2

Intermediate forms of parafacial plates can indicate transitional forms and areas between *Lepidoselagini* and *Diachlorini* or *Tabanini*. Such intermediate values of the parafacial index are seen among *Lepidoselagini* in North American *Microtabanus pygmaeus* (WILL.) and in five species of East Australian *Cydistomorpha* TROJ. In *Diachlorini* the number of intermediate forms is lesser, and only three New Caledonian species of *Cydistomyia* TAYL., namely *C. brachypalpus* TROJ., *C. risbeci* MACK. & RAG. and *C. tiwakai* TROJ., have parafacial index values equal to 1.5.

A comparison of numbers of the intermediate forms of parafacial plates in both tables (Table VI, VII) indicates the only area of overlap in the Australian Region. Both above mentioned genera, *Cydistomorpha* TROJ. and *Cydistomyia* TAYL. have completely bare bazicostal plates, without any setulae. Such junction between these two characters indicates the Australian Region as the only place where the origin of the tribe *Diachlorini* can be documented. North American *Microtabanus pygmaeus* (WILL.) bears some setulae on the bazicostal plate, and occurs in an area which cannot be accepted as the place of origin of *Diachlorini*. Earlier analyses (TROJAN 1997) showed that all North American *Diachlorini* have their ancestors in the Neotropical Region. An additional argument is that among *Lepidoselagini* of the Neotropical, Palaearctic and Afrotropical regions no intermediate forms in the shape of parafacial index have been found to date.

DEGREE OF SIMILARITY WITHIN THE *CYDISTOMYIA* SERIES

The TYTAN package of dissimilarity measures was employed for the analysis of the degree of similarity between the taxa of the *Cydistomyia* series. Four measures were applied: the Euclidean distance, Manhattan metric, Czekanowski-Soerensen index and Marczewski-Steinhaus index. The values of similarity index (s) obtained by calculations based on all these measures range from 0 for minimum similarity, to 1 for maximum similarity. A similarity measure can be easily converted into a dissimilarity index (d), $d=1-s$. The analytic procedure was divided into three stages in accordance

with the proposals discussed above (Table III-V). Only phylogenetically classified characters were taken into account.

The first stage of analysis encompasses the characters distinguishing the *Cydistomyia* series. Character states were defined and tabularized (Table VIII).

Table VIII. Distribution of distinctive character states among the genera of the *Cydistomyia* series, character names and states as listed in the Table III.

Genus	Character numbers								
	1	2	3	4	5	6	7	8	9
<i>Cydistomyia</i>	0	3	0	0	0	2	0	0	0
<i>Chalybosoma</i>	0	0	1	0	0	1	0	0	0
<i>Chasmiella</i>	0	3	0	0	0	1	0	0	0
<i>Chasmia</i>	1	0	0	1	0	1	0	0	0
<i>Amanella</i>	0	0	0	0	0	1	0	0	0
<i>Canalicula</i>	1	0	0	0	0	0.5	0	0	0
<i>Tabanotelum</i>	1	1	0	0	0	1	0	0	0
<i>Agelanius</i>	0.5	1	0	0	0	0	0	1	0
<i>Stenotabanus</i>	1	0	0	0	0	1	0	0	0
<i>Roquezia</i>	0	0	0	0	0	0	0	0	0
<i>Cretotabanus</i>	0	0	0	0	0	0.5	0	0	0
<i>Wilkersonia</i>	0	0	0	0	0	1	0	0	0
<i>Teskeyellus</i>	1	1	0	0	0	0.5	0	0	0
<i>Erioneura</i>	1	0	0	0	0	1	1	0	0
<i>Hemichrysops</i>	1	0.5	0	0	0	0	1	0.5	0
<i>Pseudacanthocera</i>	0	0	0	0	0	0.5	1	0.5	0
<i>Selasoma</i>	0	0	1	0	0	1	1	0.5	1
<i>Spilotabanus</i>	0	0	1	0	0	0.5	1	0.5	0
<i>Stypommisa</i>	0	0	0	0	0	0.5	0.5	0.5	0
<i>Philpotabanus</i>	0	1	0	0	0.5	0.5	1	0.5	0

Among four clusters distinguished using the Marczewski-Steinhaus index, three contain a mixture of taxa occurring in South America, Africa and New Guinea, while the last one represents only South American genera. Similar results were obtained when the Czekanowski-Soerensen index was applied. Other measures, namely the Manhattan metric and the Euclidean distance showed similarity indices greater than 0.95 for most of the genera analysed. Also these methods brought together taxa from different regions. First set of characters came out as too small to provide results sufficient for the examination of the problem.

In the second stage the analysis was supplemented with 15 additional characters (Table IV). Their states are shown below (Table IX).

Examination of the results showed that two measures of similarity, the Czekanowski-Soerensen and Marczewski-Steinhaus indices, do not reflect affinities between the taxa. Four subgenera of *Stenotabanus* Lutz were each classified into a different cluster of genera. Geographical affinities are also unreflected in an analysis based on these two measures. The Euclidean distance showed the proximity of Afrotropical *Amanella* OLDR. to Neotropical *Roquezia* WILK., *Cretotabanus* FAIRCH. and *Wilkersonia* FAIRCH. & BURG.

And *Stenotabanus* LUTZ was included in the same cluster as *Canalicula* OLDR., *Tabanotelum* OLDR. and *Teskeyellus* PHIL. & FAIRCH. All measures showed the affinity of *Chasmiella* END. to *Cydistomyia* TAYL. The Manhattan metric resulted in two big clusters, the first including *Agelanius* ROND. and six more specialised genera of tropical and subtropical regions of South America, the second containing all taxa of the *Cydistomyia* series core and additionally the taxa from New Guinea and Australia as well as *Tabanotelum* Oldr. and *Teskeyellus* PHIL. & FAIRCH. The picture of affinities becomes clearer, but the the problem of the degree of differences between South American, African and Australian taxa remains unsolved.

Table IX. Distribution of additional character states among the genera of the *Cydistomyia* series, character names and states as in table IV

Genus	Character numbers														
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Cydistomyia</i>	1	2	0.7	4.1	2	0	0	1.8	2	0	1	1	1	0	2
<i>Chalybosoma</i>	1	1	1	3.5	2	1	0	2.0	2	0	0	1	0	0	0
<i>Chasmiella</i>	1	2	0.5	3.8	2	0	0	2.0	1	0	1	1	0	0	1
<i>Chasmia</i>	0	1	0	3.0	1	0	1	2.5	0	1	0	1	0	0	1
<i>Amanella</i>	2	0.5	1	4.5	2	0	0	1.6	1	0	0	1	2	0	0
<i>Canalicula</i>	0	0	1	4.9	2	1	0	2.5	2	0	0	1	2	1	1
<i>Tabanotelum</i>	2	0.5	0	5.9	2	0	0	1.9	1	0	0	1	0	1	2
<i>Agelanius</i>	1	0	1	3.0	0	1	0	2.1	2	0	1	1	0	0	0
<i>Stenotabanus</i>	0	1	1	4.5	1	0	0	2.1	1	0	0	1	2	1	0
<i>Roquezia</i>	0	1	2	5.0	2	0	0	2.0	1	0	0	0	2	1	0
<i>Cretotabanus</i>	0	1	2	6.7	1	0	0	3.3	1	0	0	0	2	0	2
<i>Wilkersonia</i>	1	1	2	3.3	0	1	0	2.0	0	0	0	0	2	0	0
<i>Teskeyellus</i>	2	1	1	3.0	2	0	0	1.8	1	0	0	0	2	0	0
<i>Erioneura</i>	1	1	1	4.0	2	0	1	2.2	2	0	2	1	0	0	2
<i>Hemichrysops</i>	2	0	0	4.8	2	1	0	2.7	0	0	2	1	2	0	2
<i>Pseudacanthocera</i>	1	1	1	5.0	0	0	0	4.0	1	0	1	1	1	0	1
<i>Selasoma</i>	2	1	2	5.0	2	1	0	3.0	1	0	0	1	3	0	0
<i>Spilotabanus</i>	2	0.5	0	2.4	1	0	0	1.8	2	0	0	1	0	1	2
<i>Stypommisa</i>	2	2	1	4.3	1	0	1	2.8	1	0	1	1	0	1	2
<i>Philpotabanus</i>	2	1	2	7.5	2	0	0	5.0	2	0	0	1	0	1	2

In the third stage of analysis the data matrix was supplemented with unique characters described above (Table V), whose states are tabulated below (Table X).

The clusters of taxa obtained by this analysis reflect more adequately the relations between the genera of *Diachlorini*, especially when the Euclidean distance and Manhattan metric are applied. The lowest similarity ($s = 0$) is found in *Chasmia* END., a genus close to, but not included in the *Cydistomyia* series. *Philpotabanus* FAIRCH. and *Selasoma* MACQ. exhibit values between 0.25 to 0.05. A similarity value of 0.3 divides all remaining genera into two distinct clusters. The first of them includes *Agelanius* ROND., *Erioneura* BARR., *Hemichrysops* KROEB., *Pseudacanthocera* LUTZ, *Stypommisa* END. and *Spilotabanus* FAIRCH., all of which were excluded from the previous analysis.

together with Mexican *Teskeyellus* PHIL.& FAIRCH., a montane relict of the Northern Hemisphere. This group of taxa, bearing many apomorphies and distributed chiefly in the tropical part of South America, can hardly be regarded as a parental group for Gondwanan *Diachlorini*.

At the same time all characters with states greater than 2 were removed, because they are related to the range of the character variability rather than to the character states.

Table X. Distribution of unique characters among the taxa of the *Cydistomyia* series, names of characters and the values of their states as in the table V.

Genus	Character numbers				
	25	26	27	28	29
<i>Cydistomyia</i>	1	0	0	0	0
<i>Chalybosoma</i>	1	1	1	0	0
<i>Chasmiella</i>	1	0	0	1	0
<i>Chasmia</i>	1	0	0	1	0
<i>Amanella</i>	0.5	0	0	0	0
<i>Canalicula</i>	1	0	0	0	0
<i>Tabanotelum</i>	1	0	0	0	0
<i>Agelanius</i>	1	0	0	0	0
<i>Stenotabanus</i>	0	0	0	0	0
<i>Roquezia</i>	0	0	0	0	0
<i>Cretotabanus</i>	0	0	0	0	0
<i>Wilkersonia</i>	0	0	0	0	0
<i>Teskeyellus</i>	1	0	0	0	1
<i>Erioneura</i>	1	0	0	0	0
<i>Hemichrysops</i>	1	0	1	0	0
<i>Pseudacanthocera</i>	1	0	1	0	0
<i>Selasoma</i>	1	0	1	0	0
<i>Spilotabanus</i>	1	0	0.5	0	0
<i>Stypommisa</i>	1	0	0.5	1	0
<i>Philipotabanus</i>	1	0	0	0	0

Thus a limited set of taxa contains a nearly pure core of the *Cydistomyia* series. When the Manhattan metric is used for similarity calculations, it is divided into two clusters by the similarity value $s = 0.37$. The first cluster includes only Neotropical *Stenotabanus* LUTZ. with its relatives, *Roquezia* WILK., *Cretotabanus* FAIRCH. and *Wilkersonia* FAIRCH.& BURG. In the second cluster *Canalicula* OLDR. and *Tabanotelum* OLDR. are distinguished from the remaining genera by the similarity value of 0.42. A similar value of the measure is seen in *Chalybosoma* OLDR. South African *Amanella* OLDR. is placed near to *Cydistomyia* TAYL. by the value $s = 0.50$. The highest similarity degree, $s = 0.85$ was shown by the last two genera of the cluster, *Chasmiella* END. and *Cydistomyia* TAYL.

The main result of the similarity analysis was the opportunity to make up a set of most similar taxa for further examination, the true core of the *Cydistomyia* series. It includes 6 Neotropical taxa, *Agelanius* ROND., *Nubiloides* COSC. & PHIL., *Stenotabanus* LUTZ., *Wilkersonia* FAIRCH. & BURG., *Cretotabanus* FAIRCH. and *Roquezia* WILK. The Oriental and Australian group includes *Cydistomyia* TAYL., *Chalybosoma* OLDR. and *Chasmiella* END. From Afrotropis are *Amanella* OLDR., *Tabanotelum* OLDR. and *Canalicula* OLDR. To this set of genera, *Cydistomorpha* TAYL. was added as an intermediate form between *Lepidoselagini* and *Diachlorini*.



Fig. 1. Dendrogram of dissimilarity between plesiomorphic forms of *Diachlorini* calculated by using 21 characters and Czekanowski-Soerensen measure.

All four measures were applied. Best clustering was done using the Marczewski-Steinhaus and Czekanowski-Soerensen measures (Fig. 1). The first cluster with the similarity value, $s=0$, is *Cydistomyia* TAYL. and *Nubiloides* COSC. & PHIL. All measures have *Cydistomorpha* TROJ. as nearest to *Cretotabanus* FAIRCH., *Wilkersonia* FAIRCH. & BURG. and *Roquezia* WILK. In both cases Australian and Neotropical taxa have the highest similarity values. The remaining genera, namely *Chalybosoma* OLDR., *Amanella* OLDR., *Chasmiella* END., *Canalicula* OLDR., *Tabanotelum* OLDR. and *Agelanius* ROND. constitute a geographically differentiated cluster of more apomorphic forms. Special attention must be paid to the position of *Cydistomorpha* TROJ. which is placed at the basis of all clusters of plesiomorphic *Diachlorini*, except the above mentioned *Cydistomyia*-*Nubiloides* cluster.

CONCLUDING REMARKS

The results discussed above may be used for the the sake of falsification of the hypothesis formulated in the introduction to the present paper. The degree of similarity is highest between the taxa of cold southern South America and hot New Guinea, New Caledonia and east Australia, namely

between *Cydistomyia* TAYL. and *Nubiloides* COSC. & PHIL. Eastern Australian *Cydistomorpha* TROJ., representative of intermediate forms of *Lepidoselagini*, can be regarded as real ancestral form by virtue of their place at the basis of all other clusters, but nearest to subgenera of Neotropical *Stenotabanus* LUTZ. In this manner African *Diachlorini* seem to be apomorphic forms of the tribe distributed in hot temperate climate with Mediterranean and savanna vegetation. Such habitat adaptations do not occur in Australian and Oriental Regions and are rather exceptional among Neotropical taxa.

These considerations do not lead, however, to the transfer of the place of origin from South America to Australia. More realistic, in my opinion, is the view that large unfragmented Gondwanaland was a cradle of *Diachlorini*. This view is additionally supported by the climatic history of Antarctica. Intermediate forms between *Lepidoselagini* and *Diachlorini* are eliminated from America, Africa and Orient. At present they exist only in Australian Region.

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STRESZCZENIE

[Tytuł: Transantarktyczne związki *Diachlorini* s.str. (Diptera: *Tabanidae*)]

Dotychczasowe hipotezy wyjaśniające rozmieszczenie gondwańskich *Diachlorini* wywodzą je z Ameryki Południowej drogą północną z Afryki przez Madagaskar, Indie i wyspy Orientu do Nowej Gwinei i Australii; lub

południową z Ameryki Południowej przez Antarktydę do Afryki Południowej oraz Australii i dalej poprzez wyspy Orientu do Indii. Obie te hipotezy oparte na koncepcji stałej pozycji kontynentów wymagały weryfikacji ze względu na nowe rozwiązania systematyki podrodziny *Tabaninae* oraz postępy w paleogeografii i paleochronologii półkuli południowej.

Autor przyjął jako podstawę analizy rozmieszczenia *Diachlorini* obszaru Gondwany teorię dryftu kontynentalnego. Zestawiono również dane o chronologii wydarzeń paleogeograficznych i towarzyszących im warunkach środowiskowych, jak również o barierach morskich pojawiających się wraz z fragmentacją kontynentu Gondwany i zanikających lokalnie w Plejstocenie.

Analiza rozmieszczenia *Diachlorini* wykazała, że zasiedliły one 8 stref roślinnych, jednak większość z nich jest związana z klimatem tropikalnym i subtropikalnym. Najszersze spektrum środowiskowe zasiedlają neotropikalne i nearktyczne gatunki z pokrewieństwa *Stenotabanus* Lutz. W Regionie Neotropikalnym dwa rodzaje, *Agelanius* Rond. i *Nubiloides* Cosc. & Phil. Obydwa posiadają wiele plezjomorfii i są po części związane z występującym w zimnej strefie klimatu umiarkowanego lasem deszczowym ze znacznym udziałem *Nothofagus*. Ten typ lasu w przeszłości dominował na obszarze całej Gondwany.

Ustalono listę cech oraz ich stanów plezjomorficznych, apomorficznych i przejściowych i na ich podstawie określono przypuszczalny wygląd grupy wyjściowej dla *Diachlorini*. Najbardziej prawdopodobnym miejscem powstania plemienia jest Australia. Formy przejściowe między *Lepidoselagini* i *Diachlorini* zachowały się do dziś we wschodniej Australii i na Nowej Kaledonii.

Wielostopniowa analiza podobieństw między rodzajami oparta na czterech miarach, Marczewskiego-Steinhaus, Czekanowskiego-Soerensena, odległości miejskiej i euklidesowej, wykazała, że najwyższy stopień podobieństwa występuje między plezjomorficznymi rodzajami Południowej Ameryki i Regionu Australijskiego. *Cydistomyia* TAYL. i *Nubiloides* COSC. & PHIL. stanowią parę takich rodzajów najbardziej zbliżonych do siebie i zarazem odrębnych od pozostałych. Forma pośrednia, należąca do *Lepidoselagini* australijska *Cydistomorpha* TROJ. znajduje się u podstaw podziału wszystkich pozostałych rodzajów plezjomorficznych na grupy, przy czym najbliższym jej zgrupowaniem jest pokrewieństwo południowo-amerykańskiego *Stenotabanus* LUTZ.

Analiza podobieństwa morfologicznego w obrębie plezjomorficznych form *Diachlorini* pozwoliła na udowodnienie hipotezy o gondwańskim pochodzeniu plemienia *Diachlorini*. Formy przejściowe zachowały się jedynie na obszarze Regionu Australijskiego, we wschodniej Australii i na Nowej Kaledonii.

ANNEXE 1.

Some more important plate tectonic and environmental events in the Gondwanaland history

Period	Date ± Mybp	Position of continental plates and sea barriers	Climate and environmental events	Vegetation and fauna	Authority
Carboniferous – Permian boundary	320-270	Fused Gondwana and Euroamerica.	Cold and wet. Glaciation of the southern Gondwana.	lacking	SCHWARZBACH 1961; WHITE 1990.
Lower Permian	270-260	Fused Gondwana and Euroamerica.	Cool temperate climate. Coal deposites.	Periglacial Glossopteris flora.	WHITE 1990.
Upper Permian	260-245	Fused Gondwana and Euroamerica.	Progressive warming of the climate.	Decrease of Glossopterids, origin of Conifers, Cycadophytes & seed ferns.	FRAKES, MC GOWRAN & BOWLER 1987; WHITE 1990.
Triassic	245-208	Fused Gondwana and Euroamerica.	Hot-arid climate from equator to 50° N & S, more humid in high latitudes.	Dicroidium flora of ferns. Flourishing of conifers, cycadophytes, gingkophytes	WHITE 1990.
Jurassic	208-144	Whole Gondwana	Warm climate throughout the globe with high rainfall	Unified flora over all lands: conifers, cycadophytes, gingkophytes, tree ferns and ferns.	WHITE 1990;
Lower Jurassic	190 180	Madagascar separated from Africa. New Zealand elevated.			HARTMANN 1986; KAMP 1980;
Upper Jurassic	180-160	Gondwana separated from Laurasia by the large Tethys II sea.			HEATWOLE 1987.
Cetaceous	144-66.4	Both Americas broadly separated by the sea. Bering bridge open for the biota migration.	Soft climate over all lands from Alasca to Antarctica	Unified vegetation of broad-leaved mixed forests	GOSE, SCOTT & SWARIZ 1980; HARTMANN 1986
Lower Cretaceous	144-125 140	Sea level rise. Great part of continents submerged. India breaks away from Gondwana.	Climate cooling in Australia		WHITE 1990 HEATWOLE 1987

Lower Cretaceous	144-125 144-66 120	Argentina (Patagonia) overflowed by the sea. Fragmentation of Australia into a number of islands. Africa breaks away from Gondwana	Sea transgression		HARTMANN 1986 MAIN 1987 HEATWOLE 1987
Upper Cretaceous	97-66.4 95 80 80	Continental shelves 6 times as extensive as at present (partly submerged). Australia begins the breaking away from Antarctica. New Zealand moved away from Gondwana. New Caledonia separated from Australia and New Zealand.	Hot subtropical climate. High humidity, cold to mild temperatures. Expansion of Tasman & Coral Sea.	Tropical rain forest broadly distributed. Nothofagus flora established .	SUTTON 1978; WHITE 1990; FRAKES, MCGOWRAN & BOWLER 1987; HEATWOLE 1978; TILLIER 1988.
Tertiary Paleocene	66.4-1.6 60	Separation of Australia from Antarctica	Cooling of the climate. Hot-wet climate with high rainfall	Nothofagus flora replaces tropical forms	CROOK 1981; MAIN 1987; HEATWOLE 1987;
Paleocene - Oligocene	66.4-23.7	Africa (Namib, Kalahari & Sahara). South America (Peru, Columbia, Bolivia & Jamaica)	Arid climate. Arid climate		SCHWARZBACH 1961;
Eocene	57.8-36.6	New Caledonia	Hot-arid climate		SCHWARZBACH 1961;
Lower Eocene	57.8-52	Australia	Tropical warm-wet climate	Nothofagus rain forest widely distributed.	FRAKES, MCGOWRAN & BOWLER 1987;
Middle Eocene	45	Collision of India with Asian plate. Break up of the Tasmanian bridge between Antarctica and Australia	Equatorial current closed.		POWELL & al. 1985; WHITE 1990;
Upper Eocene	42-36.6	Antarctica Australia	Ice sheet starts to develop. Temperature and humidity decreases, aridization of the climate.	Vegetation still present. Nothofagus rain forest decreases. Dry adapted vegetation develops.	WHITE 1990;

Oligocene	36.6-23.7	Fusion of North and South America. South America separated from Antarctica. Land connections between Gondwanan continents closed.	Circumpolar current established. Climate cooling	Migration of plants & animals begins.	GOSE, SCOTT & SWARTZ 1980; KATZ 1982; FRAKES, MCGOWRAN & BOWLER 1987;
Miocene	23.7-5.3	New Guinea and Insular Orient emerged as a result of collision of Australian and Asian plates. Antarctica Australia	Progressive cooling of the earth climate. Ice sheet is northward 200 km more than recently.	Exchange of fauna between Orient and Australia begins. Tropical rain forest still remains.	SCHUSTER 1972; RATCLIFE 1984; MAIN 1987; HEATWOLE 1987; WHITE 1990.
Pleistocene	1.6-0.01	Pacific sea level fell 180-100 m below present depth. South East Asia, New Guinea and Australia connected by land and insular bridges. Tierra del Fuego connected with South America. Tasmania connected with Australia. Australia New Guinea South America. Amazonia was a large inland sea .	Climate cooling Aridisation of the climate increases. Mountains & highlands with tropical wet climates established. During pluvial periods.	Recent flora develops. Tropical flora transferred from Australia to New Guinea. Tropical rain forest starts to develop.	AUDLEY-CHARLES & HOLJER 1973; THENIUS 1972; DARLINGTON 1965; WHITE 1990; RATCLIFE 1984; COLINVAUX 1989.
Holocene	0.0147	New Zealand Tasmania New Guinea New Caledonia	Deglaciation	Large areas of <i>Nothofagus</i> rain forest and conifers. <i>Nothofagus</i> forests only in high mountains.	DARLINGTON 1965; BRIDGEWATER 1987; DARLINGTON 1965; BONNET DE LARBOGNE, TILLIER A., TILLIER S. 1991.