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## **The relict forms of *Lepidoselagini* (Diptera: Tabanidae) in the Holarctic Region<sup>1</sup>**

**Abstract.** Bicentric versus monocentric concept of *Tabaninae* evolution are discussed. Recent division of the subfamily, including redefinition of the tribe *Lepidoselagini*, opened the possibility of tracing plesiomorphic taxa in Northern Hemisphere. 9 such genera with 26 species are distributed in Holarctic. They occur chiefly in arboreal centers. The disjunction of *Glaucoptis* Szil. and partly of *Ochrops* Szil. indicates preglacial occurrence of the tribe in Northern Hemisphere.

**Key words:** *Diptera: Tabanidae, Lepidoselagini*, relict forms, Holarctic Region

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The analysis of the distribution of plesiomorphic forms of the subfamily *Tabaninae* carried out by older students resulted in the opinion that they: 1. are concentrated in temperate and cool areas of the Southern Hemisphere (FAIRCHILD 1969: 248), 2. are common to South America and Australia (OLDROYD 1957: 51) and 3. have typical Gondwanaland distribution (MACKERRAS 1954: 448). These opinions in conjunction with the commonly accepted view on triassic origin of the family and the posterior documentation of the continental drift theory (DIETZ and HOLDEN 1970) assume the only centre of the evolution and dispersion of *Tabaninae*. The subsequent break-up of Gondwanaland resulted in the formation of secondary centres, which were nevertheless always connected with the southern parts of the Southern Hemisphere. All other centres were settled by incomers from this primary centre. This opinion was best expressed and illustrated by OLDROYD (1957). Such a concept can be named the monocentric hypothesis of the horse-flies evolution and distribution.

The Northern Hemisphere is considered a domain of modern forms of the subfamily *Tabaninae*. According to OLDROYD (1957) the invasion of *Tabanus* L.

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and *Haematopota* MEIG. into the Afrotropical Region started from the Mediterranean Region. The oriental centre forwarded some waves of invaders towards New Guinea, Northern Australia and Pacific islands. These lands were successfully settled by *Tabanus* L. (MACKERRAS 1971). FAIRCHILD (1971) admits that South American species of this genus are also of northern origin.

These views assume the existence in Northern Hemisphere of evolution and dispersion centres, but no plesiomorphic forms have been found there as yet. Two explanations of this question are possible: 1. they became extinct during a glacial disaster of the Quaternary; 2. we don't know how to find them.

While not exploring the above statements at length, one should consider the validity of the concept of monocentric vs bicentric or polycentric development of the subfamily *Tabaninae*.

There are no grounds for *a priori* rejecting the hypothesis of bicentric development of the subfamily *Tabaninae*. The first centre was situated in Gondwanaland, the other, in Laurasia. While the existence of the first centre is well supported nowadays, the other requires additional explanations and arguments. They are as follows:

1. The area of Laurasia in the mid-Triassic extended from the Equator to the North Pole and had a well developed coastline both in the West and the East. Owing to this, there was a wide spectrum of habitats allowing multiple faunal groups to develop.

2. At the time when the family *Tabanidae* was being formed, i. e. about 200 million years ago, the line of junction between Gondwanaland and Laurasia was very long, about the distance between San Francisco and New York or Madrid and Moscow. This made possible migrations of the fauna in both directions.

3. In the Jurassic, diversified *Tabanomorpha* fauna inhabited the area of Asia (ROHDENDORF 1964).

4. The degree of taxonomic diversification of the tribe *Tabanini* in the Northern Hemisphere provides grounds for the opinion (FAIRCHILD 1969, OLDROYD 1957) that this group invaded the Southern Hemisphere. It must, therefore, have developed earlier in Laurasia.

The hypothesis assuming two primary evolutionary radiation centres of *Tabanidae* in Gondwanaland and Laurasia, both inhabited by a group descending from a common ancestor, is in my opinion better supported than the hypothesis allowing of only one centre situated in Gondwanaland. The separation of the southern and northern continental plates in the Jurassic resulted in the isolation of the Gondwanaland and Laurasian centres. Since then the evolution of *Tabanidae* continued independently in each of them, except the periods of mainland union when faunal migrations occurred. Further fragmentation of continental plates in the late Cretaceous and Tertiary led to the establishment of a number of secondary centres where *Tabanidae* evolved independently. Locating the secondary centres and assigning to them a specific group of *Tabanidae* taxa is the goal of future investigations on *Tabanidae*.

The fundamental issue raised here is the verification of the hypothesis of the existence of a primary evolutionary radiation centre of *Tabanidae* in

Laurasia, inhabited by plesiomorphic representatives of *Lepidoselagini* just as it can be seen in the Southern Hemisphere.

The recent division of the subfamily *Tabaninae* is based partly on the course of the frontoclypeal suture. Its lower branches divide the face into frontoclypeus and parafacial plates. The face with a small frontoclypeus and broad parafacial plates has a parafacial index ranging from 0.9 to 1.4, which is exceptional among *Tabanidae* and even among *Tabanomorpha*. A large frontoclypeus and narrow parafacial plates prevail in horse-flies (TROJAN 1994a).

Both types of the facial structure can be found in *Diachlorini* sensu MACKERRAS (1954), while in *Tabanini* a face with narrow parafacial plates is the prevailing pattern. 39 supraspecific taxa were excluded from both tribes. The taxa are distinguished by apomorphic, broad parafacial plates. They have been included into a separate tribe (TROJAN 1994b) which, following the principles of zoological nomenclature, was given the name of *Lepidoselagini* LUTZ (1913) after one of the few tropical representatives of this newly defined tribe. However, it is *Dasybasis appendiculata* MACQ. from Australia which is the typical representative of the taxon from the morphological viewpoint as well as its most plesiomorphic form.

Zoogeographically, *Lepidoselagini* are distributed in the temperate and cool climate zone as well as in the mountains of the Southern Hemisphere with small offshoots in warmer areas. Such a distribution pattern is Gondwanaland-like, which at least is indicative of Jurassic appearance of the group. The researchers on the *Tabanidae* in the Southern Hemisphere fauna (MACKERRAS 1954, OLDROYD 1957, FAIRCHILD 1971) concur as regards such distribution of plesiomorphic forms within the subfamily *Tabaninae*. Such forms are not referred to in studies of the subfamily in the Northern Hemisphere, either in Northern America (STONE 1938, PHILIP 1965) or Palaearctic (LECLERCQ 1966, CHVALA, LYNEBORG and MOUCHA 1972, VILOVICH 1968).

The question of the presence of plesiomorphic *Lepidoselagini* forms in Laurasia is also the question of whether ice sheet advance on large areas in Europe, Asia and America could have led to the extinction of all relict forms, morphologically similar to the group of ancestors of the whole subfamily.

The examination of the supraspecific taxa of *Tabanini* and *Diachlorini* of the Palaearctic and Nearctic Regions reveals the existence of 26 species of 9 genera of the tribe *Lepidoselagini* (Tab. I.) in Holarctic so far (TROJAN 1994c). In its southern part, except the maximum glacier limits in Würm (Europe) and Wisconsin (North America) stages, the area contains a number of refuge areas. DE LATTIN (1967) labels them as dispersion centres of the fauna after glacier recession. These centres harbour two types of fauna: arboreal and eremial. In Palaearctic 15 dispersion centres of arboreal fauna and 8 of eremial fauna can be distinguished, while in Nearctic the figures are 10 and 6 respectively. Of the 26 *Lepidoselagini* species known from Holarctic, 25 occur in refuge areas for arboreal fauna, while just one species, namely *Anacimas dodgei* (WHIT.), has been reported from a refugium for eremial fauna (Kansas). The greatest number of *Lepidoselagini* species (9) inhabit the Mediterranean and Caspian centres with 5 species found in the Mexican centre, 3 in Virginian and Flori-

Table I. The occurrence of *Lepidoselagini* in dispersion centers of the Holarctic Region.

No	Genus	Species number in the Holarctic Region	Arboreal centers in the										Eremial center (Kansian)	Other centers	
			Palaeartic					Nearctic							
			Mediterranean	Kaspian	Iranian	Nepalian	Manchurian	Oregonian	Mexican	Arizonian	Virginian	Floridan			
1	<i>Aegialomyia</i> PHIL.	1											1		
2	<i>Anacimas</i> END.	3										2	1	1	
3	<i>Bolbodimyia</i> BIG.	1								1	1				
4	<i>Holcopsis</i> END.	4								4					
5	<i>Microtabanus</i> FAIRCH.	1										1	1		
6	<i>Nanorrhynchus</i> OLS.	1			1										
7	<i>Ochrops</i> SZIL.	2				2									2
8	<i>Mouchaemyia</i> OLS.	10	8	1		1									
9	<i>Glaucope</i> SZIL.	3			1			1							1
Total		26	8	1	2	1	2	1	5	1	3	3	1	3	

dan centres and 1–2 in the remaining ones. The absence of *Lepidoselagini* in the centres situated in South and East Asia with the exception of Nepal and the Ussuri centres indicates that the eastern part of Palaeartic did not contain or preserve plesiomorphic forms of the subfamily *Tabaninae* even though the glacier-free areas were much greater there than in Europe. However, since many plesiomorphic forms of the subfamilies *Chrysopsinae* and *Pangoniinae* as well as other *Tabanomorpha* families have actually survived in these refugia, it can be assumed that *Lepidoselagini* had not inhabited this area in the period before glaciation. This attachment of *Lepidoselagini* of Holarctic to refuge areas indicates that the taxa with plesiomorphic characters displayed significant conservatism in the postglacial periods and many of them have remained in warmer areas outside the temperate zone.

In Holarctic the “freezing” of the plesiomorphic forms was less marked than in the Southern Hemisphere. Here, the role of the cool ecological trap could have been played by the tundra and northern taiga areas where the winter period exceeds 150 or even 200 days, and the summer period is limited to two months (ANDREEVA 1984). Similar conditions are observed in the alpine zone of the mountains in Holarctis. The tundra and tundra-forest areas are inhabited mostly by species of the genus *Hybomitra* END. The species occurring in the north have a broad frons, which is undoubtedly a plesiomorphic character in *Tabanidae*. However, forms with a parafacial index similar to 1.0–1.3 are not reported. They are, therefore, evolutionarily younger forms. The absence of “old” *Lepidoselagini* in the traps in northern Holarctic can be explained on the

basis of the fact that the tundra is a young biot. What is more, there were warmer spells in the postglacial period when the pine and spruce forests of the taiga reached as far as the northern shores of the mainlands. The tundra biot was then forced out and survived only in a residual form, nor was the primary fauna of the tundra preserved. The present fauna of the area may be considered evolutionarily young.

High-mountain traps present a different situation. 8 species of Holarctic *Lepidoselagini* occur in the high-mountain zone. Three of them belong to the Holarctic genus of *Glaucops* SZIL. (Fig. 1). At least two of them are reported nowadays from areas which subject to glaciation in the Würm period (Wisconsin). Their present distribution can thus be considered secondary. The other

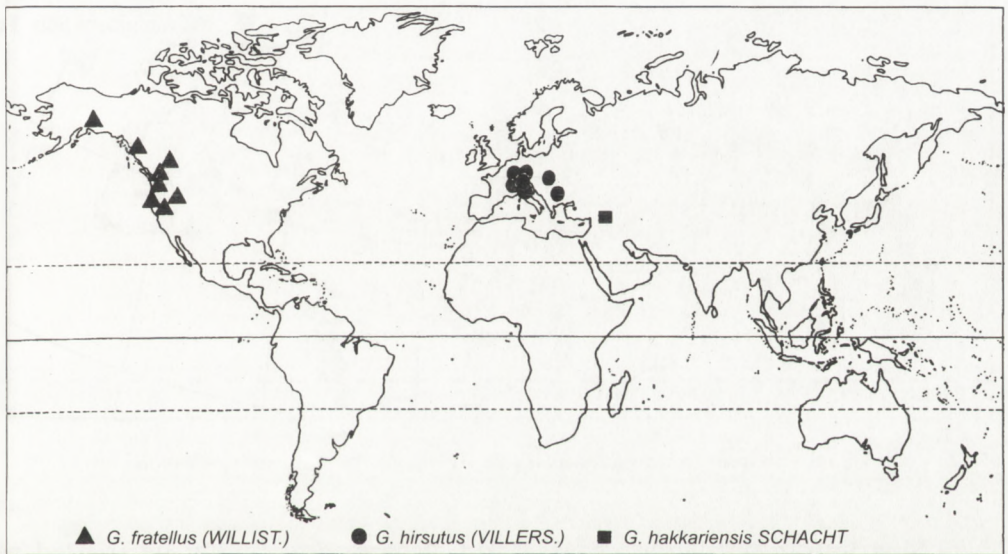


Fig. 1. The distribution of *Glaucops* SZIL. in the Holarctic Region.

high-mountain genus is *Holcopsis* END. associated with the mountains of Central Mexico. It is found at altitudes of 2,500–3,000 m above sea-level, but 1,500–2,000 m below the snowline. It is a zone of mixed pine-oak forests (PECHUMAN 1969), where the climate corresponds to the temperate climate of the plains. The last high-mountain representative of *Lepidoselagini*, the Caucasian *Mouchaemyia caucasi* (SZIL.), inhabits the submontane zone and cannot be considered a species frozen in an ecological trap. The other species of *Mouchaemyia* OLS., however, exhibit circummediterranean distribution (Fig. 2).

Stronger affinities of plesiomorphic forms of *Lepidoselagini* to cold high-mountain ecological traps are observed mainly in South America where representatives of the genus *Archiplatius* END. and related genera occur in the mountains as far as the ice-sheet border.

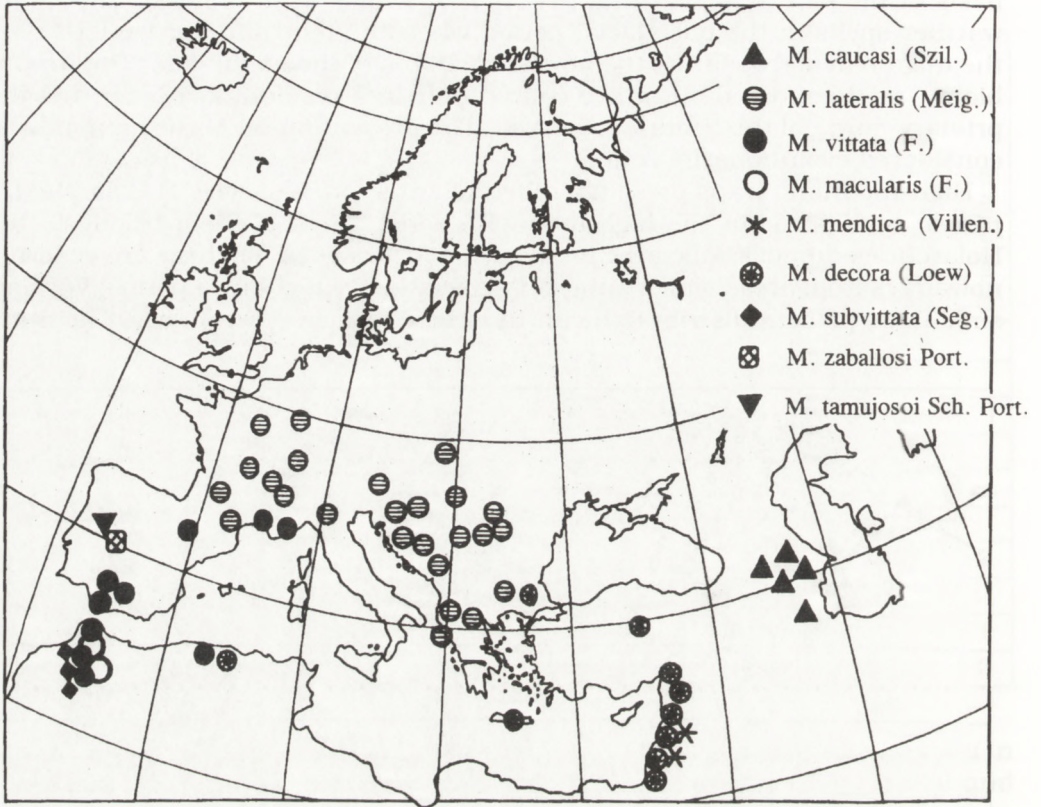


Fig. 2. The distribution of *Mouchaemyia* Ols. in the Palearctic Region.

The distribution of *Glaucops* SZIL. and *Ochrops* SZIL. could be treated as some of the few exceptions requiring further interpretation. The former genus is associated, at least in Europe, with the high-mountain alpine zone. It occurs in moorlands situated in the border zone between mountain-pine forests and mountain pastures (PARVU 1985, SCHACHT 1983). Its present distribution is of secondary nature, and no refuge areas are known either in Europe or in North America where species of this genus could have survived mountain glaciation of the Würm period (Wisconsin). On the other hand, *Ochrops plebeius* (FALL.) (Fig. 3) follows a disjunctive distribution pattern, occurring in the Manchuria-Ussuri refuge area in the East, and in typical relict sites of moorlands, particularly *Sphagnum*-associated highmoors, in Europe. While it may be assumed that in the glaciation periods in Europe there were many bogs with which the genus *Ochrops* SZIL. is associated, it is still difficult to explain the absence of representatives of this genus in boggy areas in Siberian taiga. A certain hint is given by SCHWARZBACH (1961) who mentions the disappearance of the tundra zone in Siberia in the postglacial period, which could also have led to extinction of the moorland fauna. This problem cannot be regard-

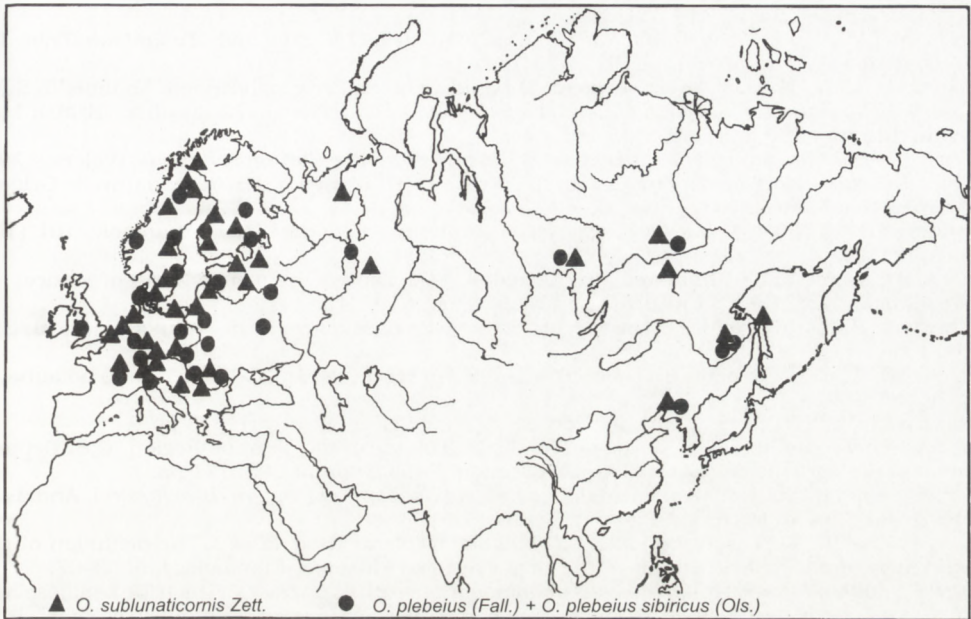


Fig. 3. The distribution of *Ochrops* SZIL. in the Palearctic Region.

ed as fully explained. However the disjunction of the area of *Glaucops* SZIL. and *Ochrops* SZIL. indicates preglacial origin of the taxa under discussion.

The above review shows that:

1. There existed two evolutionary radiation centres of the plesiomorphic forms of the tribe *Lepidoselagini*: in Gondwanaland and in Laurasia.
2. The occurrence of these plesiomorphic forms in the Northern Hemisphere is associated predominantly with refuge areas with a stable, rather temperate and warm climate.

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STRESZCZENIE

[Tytuł: Formy reliktowe *Lepidoselagini* (*Diptera: Tabanidae*) w Regionie Holarktycznym]

Wyodrębnienie w obrębie podrodziny *Tabaninae* plemienia *Lepidoselagini* pozwoliło na weryfikację koncepcji dotyczących ewolucji i rozmieszczenia form plezjomorficznych. Wysunięto koncepcję dwóch centrów ewolucji: gondwańskiego i laurazjatyckiego przeciwko koncepcji monocentrycznej, która wiąże rozwój i występowanie grupy z półkulą południową. W Holarktyce występuje 9 rodzajów *Lepidoselagini* z 26 gatunkami, głównie w refugiach fauny leśnej. Rozmieszczenie dysjunktywne rodzajów *Glaucops* SZIL. i *Ochrops* SZIL. wskazuje na występowanie plemienia *Lepidoselagini* na półkuli północnej w okresie przedlodowcowym.