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Geographical Distribution of Tabanomorpha (Diptera, Brachycera): Athericidae, Austroleptidae, Oreoleptidae, Rhagionidae, And Vermileonidae[1]

Charles Morphy Dias Santos[2]

1. Agência de fomento: CAPES. 2. Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, e-mail: charlesmorphy@gmail.com

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Abstract. The infraorder Tabanomorpha traditionally includes the families Tabanidae, Athericidae, Rhagionidae, and Vermileonidae. The new family Oreoleptidae was placed among the tabanomorphan, as well as some controversial groups as Austroleptidae and Spaniidae, but there is no agreement on the phylogenetic relationships of the groups considered as belonging to the infraorder. Here is presented the geographical distribution of the tabanomorphan families Rhagionidae, Vermileonidae, Athericidae, Austroleptidae and Oreoleptidae, followed by comments on the biogeography of each group. The origin of Tabanomorpha probably dates back to the early Mesozoic, during the Triassic or even earlier, which somehow explains its widespread distribution all over the biogeographical regions, pointing to a great influence of plate tectonics in generating nowadays distribution. Nevertheless, despite the initial attempts to solve the problem, the biogeographical evolution of Tabanomorpha is still scarcely known. In order to properly reconstruct its historical area relationships, every biogeographical analysis depends on up-to-dated distributional information, and, hence, reliable lists of distribution are a starting point to a broad comprehension of the evolution of life in space.

Key words: Biogeographical regions, Diptera, geographical distribution, Tabanomorpha.

Distribuição Geográfica de Tabanomorpha (Diptera, Brachycera): Athericidae, Austroleptidae, Oreoleptidae, Rhagionidae e Vermileonidae

Resumo. A infraordem Tabanomorpha tradicionalmente inclui as famílias Tabanidae, Athericidae, Rhagionidae e Vermileonidae. A nova família Oreoleptidae foi posicionada entre os Tabanomorpha, assim como alguns grupos controversos como Austroleptidae e Spaniidae, mas não há concordância sobre as relações filogenéticas entre os grupos considerados como pertencentes à infraordem. Aqui é apresentada a distribuição geográfica das famílias de Tabanomorpha Rhagionidae, Vermileonidae, Athericidae, Austroleptidae e Oreoleptidae, seguida por comentários sobre a biogeografia de cada grupo. A origem dos Tabanomorpha provavelmente remonta ao Mesozóico Inferior, durante o Triássico ou mesmo antes, o que de alguma forma explica sua ampla distribuição por todas as regiões biogeográficas, apontando para uma grande influência da tectônica de placas na geração da distribuição atual. No entanto, apesar das tentativas iniciais para resolver o problema, a evolução biogeográfica dos Tabanomorpha ainda é pouco conhecida. Com vistas a reconstruir apropriadamente as relações históricas entre as áreas, qualquer análise biogeográfica depende de informação atualizada sobre distribuições, e, conseqüentemente, listas de distribuição confiáveis são um ponto de partida para uma ampla compreensão da evolução da vida no espaço.

Palavras-Chave: Diptera, distribuição geográfica, regiões biogeográficas, Tabanomorpha.

Traditionally, the infraorder Tabanomorpha (Diptera, Brachycera) includes the families Tabanidae, Athericidae, Rhagionidae, and Vermileonidae. The recently described family Oreoleptidae (Zloty *et al.* 2005) was also placed among the other tabanomorphan families. For some authors (Woodley 1989; Sinclair *et al.* 1994; Yeates 2002; Zloty *et al.* 2005), *Pelecorhynchus* Macquart should be raised to the family status and equally placed within the infraorder, while others as Nagatomi (1982b), Stuckenberg (2001) and Santos (2006) retain the group as a genus of rhagionids. There are also controversies about the phylogenetic position of *Austroleptis* Hardy, which is sometimes considered as incertae sedis within Rhagionidae or receives family status, and Spaniidae (Stuckenberg 2001), two families often considered as belonging to Tabanomorpha.

According to literature (e.g., Woodley 1989; Sinclair 1992; Stuckenberg 2001; Yeates 2002), three synapomorphies sustain the monophyly of Tabanomorpha: larval retractile head, a brush above the larval antennae and beside the labrum, and a convex and bulbous clypeus in adults. In fact, these characters are not so widely disseminated among the tabanomorphan families, which made its relationships with the other Diptera still an open question. The same way, the lack of clear synapomorphies to delimit each level of the tabanomorphan phylogeny, especially regarding some genera of Rhagionidae, causes much of the remaining uncertainty about higher-level relationships.

This paper presents the geographical distribution of Tabanomorpha, excluding the greatly diversified family Tabanidae. The intent is to make an update of the list of distribution made by Nagatomi (1982a) in order to provide a database for further systematic and biogeographical studies. The online version of the BioSystematic Database of World Diptera (Thompson 2007) was used as the main source of information, as well as published papers and catalogs (e.g. James 1968, 1975; Nagatomi 1982a; Evenhuis 1994; Santos 2005, 2006; Santos & Amorim 2007a), and examinations of the material deposited in the Museu de Zoologia da Universidade de São Paulo (MZ-SP). Based on the presented distribution, some comments on the biogeographical history of Tabanomorpha are made, pointing to further questions that should be faced to allow to a more complete reconstruction of the evolution of the infraorder.

Family Rhagionidae

The family Rhagionidae is worldwide distributed (Nagatomi 1982a,b; Santos 2005, 2006; Santos & Amorim, 2007a). The Rhagionidae is considered one of the most archaic Diptera, probably dating back to Triassic (Krzeminski & Krzeminska 2003). The diversification of the family is remarkable after the Jurassic (Rohdendorf 1938; Kovalev 1981; Zhang 1993; Mostovski 2000; Zhang *et al.* 2006).

The phylogenetic relationships within the Rhagionidae are uncertain. The family has included a large number of genera now accepted to be more related to other families of lower Brachycera. Nagatomi (1982b) recognized three subfamilies of

Rhagionidae: Rhagioninae, Spaniinae and Austroleptinae. Later, STUCKENBERG (2001) proposed that these subfamilies should be ranked as families, splitting the Rhagionidae *lato sensu* into Rhagionidae *sensu strictu*, Spaniidae and Austroleptidae. In Rhagionidae *s.s.*, Stuckenberg placed the genera: *Alloleptis* Nagatomi & Saigusa, *Arthroceras* Williston, *Arthroteles* Bezzi, *Atherimorpha* White, *Bolbomyia* Loew, *Chrysopilus* Macquart, *Desmomyia* Brunetti, *Pelecorhynchus* Macquart, *Rhagina* Malloch, *Rhagio* Fabricius, *Schizella* Bezzi, *Solomomyia* Nagatomi, *Stylospania* Frey, and *Symphoromyia* Frauenfeld. In Spaniidae fit the genera *Spania* Meigen, *Litoleptis* Chilcott, *Spaniopsis* White, *Spatulina* Szilady, and *Ptiolina* Zetterstedt, while in Austroleptidae fell the single genus *Austroleptis* Hardy. Studies made by SINCLAIR (1992), WIEGMANN *et al.* (2000), and YEATES (2002) do not completely agree with the classification above, and the relationships within Rhagionidae are still waiting for better resolution.

STUCKENBERG (2001) raised two autapomorphies of his Spaniidae: an antennal style unsegmented, laterally compressed, and pterostigma filling apex of cell R1. However, the Spaniidae status is debatable and the presumed autapomorphies seem not consistent in a deep morphological exam (SANTOS 2006). The five genera of Spaniidae *sensu* Stuckenberg are placed below among the rhagionids, as traditionally seem in the literature. This way, the Rhagionidae contains 49 genera whose species number and distribution are as follows (Table 1):

- *Alloleptis* Nagatomi & Saigusa: 1 species from Oriental region (Celebes).
- *Archirhagio* Rohdendorf: 2 fossil species, from Palearctic region: 1 from the Upper Jurassic of Kazakhstan, and 1 from the Jurassic of China (Nei Mongol).
- *Arthroceras* Williston: 7 species – 3 species from Palearctic region: 2 from Japan (Tsurugiyama and Mitaki, Musashi), and 1 from the former USSR (Ussuri); 3 from Nearctic region, from USA (1 from Washington, 1 from Washington, Oregon, Idaho, Colorado, and 1 from Michigan, Ontario, and New York); and 1 species from Oriental region, from China (Tienmushan, Zhejiang Province).
- *Arthroteles* Bezzi: 4 species from Afrotropical region: 3 from South Africa, and 1 from Cape Province.
- *Atherimorpha* White: 48 species – 12 species from Afrotropical region (2 from South Africa, 4 from Cape Province, 2 from Lesotho, 3 from Natal, and 1 from Transvaal); 15 species from Neotropical region: 12 from Chile (Llanquihue, Puerto Montt, Chiloe Island, Valdivia, Valparaiso, Perales, Concepcion), 2 from Argentina (Rio Negro, Bariloche), 1 from Brazil (Rio de Janeiro and Minas Gerais); 21 species from Australian region: 14 from Australia (10 from New South Wales, 1 from Victoria, 1 from Western Australia, 1 from Australian Capital Territory, and 1 fossil species from the Lower Cretaceous of Victoria), and 7 from Tasmania.
- *Bolbomyia* Loew: 6 species – 2 species from Palearctic region: 1 from the former USSR (Bolscherjetsk, Kamtschatka), and 1 fossil species from Eocene/Oligocene of Baltic region; 4 species from Nearctic region, from USA (Alaska, New York, Washington, Idaho, Virginia, Tennessee, North Carolina, and Michigan).
- *Chrysopilus* Macquart, ca. 319 species, distributed as follows:
  Palearctic region, 69 species: 20 from European territory, 11 from Russia and former USSR, 2 from Europe and Asia (Iran and Lebanon), 9 from China, 3 from Tibet, 19 from Japan, and 1 from Morocco. There are 4 fossil species, 2 from the Eocene / Oligocene of England, 1 from the Oligocene of Germany, and 1 from Baltic Amber (Eocene / Oligocene).
  Afrotropical region, 39 species: 28 from Madagascar, 3 from South Africa, 2 from South Africa, Zimbabwe, Kenya and Uganda, 1 from Cameroun, 1 from Congo, 1 from Rhodesia, 1 from Ivory Coast, 1 from Uganda, and 1 from Mawambi-Ukaika.
  Neotropical region, 70 species: 4 from Argentina, 2 from Bolivia, 17 from Brazil (11 from Southeastern, 2 from Amazonian basin, 1 distributed from North of Brazil to Guyana, 2 from Guyanian shield, and 1 distributed from Brazil to Colombia and Venezuela), 3 from Guyana, 1 from Chile, 1 from Colombia, 1 from Colombia and Venezuela, 3 from Costa Rica (1 distributed from Costa Rica to Peru), 3 from Cuba, 1 from Guadeloupe, 1 from Jamaica, 10 from Mexico, 6 from Panama (1 distributed from Panama to Guyana), 11 from Peru (2 distributed from Peru to Bolivia), 2 from Puerto Rico, 1 from Saint Vincent and the Grenadines, and 3 labeled only as "South America" (type-locality unknown).
  Nearctic region, 31 species distributed all over the USA, with 1 species endemic to Alaska, and 4 species extended to Canada (British Columbia, Manitoba, Alberta and Newfoundland).
  Oriental region, 76 species: 2 from Borneo (1 from Borneo to Malayan peninsula), 11 from China, 10 from India, 9 from Java (2 from Java to Sumatra, and 1 from Java to Philippines), 1 from Laos, 4 from Malayan peninsula, 14 from Myanmar (2 from Myanmar to India, 1 from Laos, 1 from Myanmar to Taiwan and Vietnam, and 1 from Myanmar to Taiwan and Philippines), 1 from Nepal, 1 from Nicobar Islands, 7 from Philippines, 4 from Sri Lanka, 5 from Sumatra, and 7 from Taiwan (2 from Taiwan to India, 1 from Taiwan to India and Philippines, and 2 from Taiwan to Japan).
  Australian region, 34 species: 19 from Australia (New South Wales, Capital Territory, Queensland, Victoria, and Southern Australia), 1 from Lord Howe island, 1 distributed from Australia to New Caledonia, 1 from Fiji, 2 from Indonesia (Maluku), 6 from New Guinea, 1 from New Zealand, 2 from Tasmania, 1 distributed from Tasmania to New Caledonia, and 1 from the Oriental and Australian region, widespread from Orient to New Guinea.
- *Desmomyia* Brunetii: 2 species – 1 species from Palearctic region (Xizang, Nyingchi, in Tibet); and 1 species from Oriental region (highlands of India).
- *Gallia* Krzeminski & Krzeminska: 1 fossil species, from Palearctic region (Triassic).
- *Glutops* Burgess: 11 species – 4 species from Palearctic region: 3 from Japan (Shinano, Ehime, Hida), and 1 from Russia; 7 species from Nearctic region, from USA territory, especially California, with 2 species with distribution extended to Canada (British Columbia).
- *Grimmyia* Ansorge: 1 fossil species from Palearctic region, Jurassic of Germany.
- *Ija* Kovalev: 1 fossil species from Palearctic region, Lower/Middle Jurassic of Russia.
- *Jersambromyia* Grimaldi & Cumming: 1 fossil species from Palearctic region, Cretaceous of New Jersey.
- *Jurabrachyceron* Kovalev: 1 fossil species from Palearctic region, Lower/Middle Jurassic of Russia.
- *Kubekovia* Kovalev: 1 fossil species from Palearctic region, Middle Jurassic of Russia.
- *Litoleptis* Chillcott: 1 species from Nearctic region, from Alaska.
- *Longhuaia* Hong: 1 fossil species from Palearctic region, Cretaceous of China (Hebei).
- *Mesobolbomyia* Grimaldi & Cumming: 1 fossil species from Palearctic region, Cretacic amber of Lebanon (Jezzine area)
- *Mesorhagiophryne* Hong & Wang: 2 fossil species from Palearctic region, Cretaceous of China (Shandong province).
- *Mesostratiomyia* Hong & Wang: 1 fossil species from Palearctic region, Cretaceous of China (Shandong province).
- *Mongolomyia* Kovalev: 1 fossil species from Palearctic region, Lower Cretaceous of Mongolia.
- *Neorhagio* Lindner: 3 species from Neotropical region: 1 from Chile (Santiago), and 2 from Mexico (Jaltenango, Reserva El Triunfo).
- *Omphalophora* Becker: 3 species from Palearctic region: 2 from former USSR, and 1 from Europe (Finland).
- *Palaeoarthroteles* Kovalev & Mostovski: 1 fossil species from Palearctic region, from the Mesozoic of Russia, Chitinsk

Region, River Daya.

- *Palaeobolbomyia* Kovalev: 6 fossil species from Palearctic region: 2 from the Middle-Upper Jurassic of Kazakhstan (Chimkent, Chayan, Karatau-Mikhailovka), 1 from the Middle-Upper Jurassic of Mongolia (Bayanhongor Aymag, Bahar), 3 from the Jurassic of Russia (1 from Siberia and 2 from Yakutia, Kempendyai).
- *Palaeobrachyceron* Kovalev: 6 fossil species from Palearctic region: 5 from the Lower/Middle Jurassic of Russia, and 1 from the Jurassic of Germany (Pomerania, Grimmen).
- *Paleochrysopilus* Grimaldi & Cumming: 1 fossil species from Palearctic region, from the Cretacic amber of Lebanon (Bcharee area).
- *Palaeostratiomyia* Rohdendorf: 1 fossil species from Palearctic region, from the Upper Jurassic of Kazakhstan.
- *Pelecorhynchus* Macquart: 37 species – 6 species from Neotropical region, from Chile (Valdivia, Llico, Magallanes, and Arauca); 31 species from Australian region: 25 from Australia (New South Wales, Victoria, Queensland, and Western Australia), and 6 from Tasmania.
- *Protorhagio* Rohdendorf: 1 fossil species from Palearctic region, from Kazakhstan (Upper Jurassic).
- *Pseudoerinna* Shiraki: 2 species – 1 species from Palearctic region, from Japan (Kyoto), and 1 species from Nearctic region, from USA (California).
- *Pseudoglutops* Makarkin & Sidorenko: 1 species from Palearctic region, from Russia (Primorskii Krai).
- *Ptiolina* Zetterstedt: 29 species – 16 species from Palearctic region: 11 from Europe, including Russia, and 5 species from Japan; 12 species from Nearctic region: 1 from Canada (Quebec), and 11 from USA territory (Colorado, Michigan, Oregon, New York and Washington, including 6 from Alaska); and 1 species from Oriental region, from Nepal.
- *Ptiolinites* Kovalev: 5 fossil species from Palearctic region (Lower Cretaceous): 2 from England (Dorset: Durlston Bay, and Surrey, Capel, Clockhouse Brickworks), 1 from Spain (Sierra del Montsec, Santa Maria de Meia, La Cabrua), 1 from Mongolia, and 1 from Russia (Transbaikalia, Baissa, Vitim River).
- *Rhagina* Malloch: 2 species from Oriental region: 1 from Java (Pangerango), and 1 from China (Guangxi-Zhuang).
- *Rhagio* Fabricius: 165 species – 106 species from Palearctic region: 52 distributed throughout Europe, 15 from Japan, 1 from Lebanon, 2 from Turkey, 17 from China, 2 from Northern Africa (Algeria and Tunisia), and 10 from Russia (1 from Russia and Japan, and 1 from Russia, China and Mongolia). There are 9 fossil species: 7 from Baltic Region (Eocene / Oligocene), 1 from Oligocene of Germany, and 1 from Oligocene of USA; 3 species from Neotropical region: 1 from South America, and 2 from Mexico (Tuxpango); 24 species from Nearctic region, distributed throughout USA territory, especially California and surroundings, with a species distributed from North American west coast to Alaska; 32 species from Oriental region: 12 from China, 5 from India, 2 from Indonesia (Java), 1 from Japan (Ryukyu Islands), 2 from Malaysia, Borneo, and Sabah, 2 from Myanmar, 1 from Philippines, 5 from Sumatra, and 2 from Taiwan.
- *Rhagiophryne* Rohdendorf: 1 fossil species from Palearctic region, from Kazakhstan (Upper Jurassic).
- *Scelorhagio* Zhang: 1 fossil species from Palearctic region, from the Jurassic of China (Laiyang Basin, Shandong Province).
- *Schizella* Bezzi: 3 species from Oriental region, from Philippines (Luzon and Mindanao).
- *Sinorhagio* Zhang, Yang and Ren: 1 fossil species from Palearctic region, Middle Jurassic, Daohugou Formation of Inner Mongolia.
- *Solomomyia* Nagatomi: 1 species from Australian region, from Solomon Islands.
- *Spania* Meigen: 4 species – 3 species from Palearctic region: 2 from Japan and 1 from all parts of Europe excluding Balcan Peninsula; 1 species from Nearctic region, from Maine (USA).
- *Spaniopsis* White: 7 species from Australian region: 6 from Australia (New South Wales and Western Australia), and 1 from Tasmania.
- *Spatulina* Szilady: 2 species from Palearctic region: 1 from Europe and 1 from China (Shaanxi, Shiquan).
- *Stratiomyopsis* Hong & Wang: 1 fossil species from Palearctic region, from the Upper Jurassic of China (Laiyang Basin, Shandong Province).
- *Stylospania* Frey: 1 species from Oriental region, from Philippines (Samar).
- *Symphoromyia* Frauenfeld: 42 species – 14 species from Palearctic region: 2 from China (Qinghai, Menyuan and Gansu, Jone), 1 from Uzbekistan, 2 distributed throughout Europe, 1 from former USSR, and 8 fossil species (5 from Eocene / Oligocene of Baltic region, 2 from Oligocene of France, and 1 from Oligocene of USA); and 28 species from Nearctic region, 27 from the USA territory, especially California and surroundings, and 1 from Canada (Quebec).
- *Taschigatra* Mostovski & Jarzembowski: 2 fossil species from Oriental region, from Lower Jurassic of India (Andhra Pradesh. Adilabad, Sirpur Taluka).
- *Zarzia* Zaitzev: 1 fossil species from Palearctic region, from the Upper Cretacic amber of Russia.

FAMILY VERMILEONIDAE

The position of Vermileonidae among the Tabanomorpha is not well understood. As pointed by TESKEY (1981), the placement of Vermileonidae among the Lower Brachycera has been the subject of speculation, since some of its features are shared with different brachyceran groups. Wing characters, as the weak anal angle and alula or the narrowing of both cells m3 and cup, suggest a relationship with some Asilomorpha. In the analysis made by YEATES (2002), Vermileonidae is the sister-group of all other Tabanomorpha, and included within this infraorder. The family contains 11 genera whose species number and distribution are as follows (Table 2):

- *Alhajarmyia* Stuckenberg: 1 species from Afrotropical region (Oman, Western Hajar).
- *Isalomyia* Stuckenberg: 1 species from Afrotropical region (Madagascar).
- *Lampromyia* Macquart: 13 species – 9 species from Palearctic region: 3 from Canary Island, 2 from Spain, 1 from France, Spain, Algeria and Canary Island, 2 from Morocco, and 1 from northwest Africa (Morocco and Algeria); 4 species from Afrotropical region, 2 from South Africa e 2 from Zimbabwe.
- *Leptynoma* Westwood: 7 species – 1 species from Palearctic region, from Namibia, Brandberg; 6 species from Afrotropical region, 4 from South Africa (Cape) and 2 from Namibia (Uguchab River and Luderitz District).
- *Namaquamyia* Stuckenberg: 1 species from Afrotropical region, from Sudan.
- *Protovermileo* Hennig: 1 fossil species from Palearctic region, from Baltic Amber (Eocene/Oligocene).
- *Vermileo* Macquart: 10 species – 3 species from Palearctic region: 1 from Greece (Crete), 1 from southern France, and 1 from Spain and Portugal (Cercadilla & Los Molinos); 1 species from Afrotropical region, from Sudan; 3 species from Neotropical region: 1 from Mexico (Guerrero), 1 from Jamaica, and 1 from Cuba (Trinidad Mountains); 3 species from Nearctic region: 1 from California (Alta Meadow), 1 from California to New Mexico and Colorado, and 1 from Mexico.
- *Vermilynx* Stuckenberg: 2 species from Afrotropical region: 1 from South Africa (Namaqualand) and 1 from South Africa and Namibia.
- *Vermiophis* Yang: 7 species from Palearctic region, from China (Shaanix, Gansu, Beijing, Shadong, Hubei, and Tibet).
- *Vermipardus* Stuckenberg: 13 species from Afrotropical region, 12 from South Africa (Trasnvaal, Cape and Natal), and 1 from

Table 1. The distribution of the Rhagionidae genera.

Genus	Palearctic	Nearctic	Oriental	Afrotropical	Australian	Neotropical
Alloleptis			1			
Archirhagio	2 fossils (Upper Jurassic)					
Arthroceras	3	3	1			
Arthroteles				4		
Atherimorpha				12	21	15
Bolbomyia	1 + 1 fossil from Eocene/Oligocene	4				
Chrysopilus	65 + 4 fossils from Eocene/ Oligocene	31	76	39	34	70
Desmomyia	1		1			
Galia	1 fossil (Triassic)					
Glutops	4	7				
Grimmyia	1 fossil (Jurassic)					
Ija	1 fossil (Lower / Middle Jurassic)					
Jersambromyia	1 fossil (Cretaceous)					
Jurabrachyceron	1 fossil (Lower / Middle Jurassic)					
Kubekovia	1 fossil (Middle Jurassic)					
Litoleptis		1				
Longhuaia	1 fossil (Cretaceous)					
Mesobolbomyia	1 fossil (Cretaceous)					
Mesorhagiophyrne	2 fossils (Cretaceous)					
Mesostratiomyia	1 fossil (Lower Cretaceous)					
Mongolomyia	1 fossil (Lower Cretaceous)					
Neorhagio						3
Omphalophora	3					
Palaeoarthroteles	1 fossil (Mesozoic)					
Palaeobolbomyia	6 fossils (Middle-Upper Jurassic)					
Palaeobrachyceron	6 fossils (Lower / Middle Jurassic)					
Paleochrysopilus	1 fossil (Cretaceous)					
Palaeostratiomyia	1 fossil (Upper Jurassic)					
Pelecorhynchus					31	6
Protorhagio	1					
Pseudoerinna	1	1				
Pseudoglutops	1					
Ptiolina	16	12	1			
Ptiolinites	5 fossils (Lower Cretaceous)					
Rhagina			2			
Rhagio	98 + 9 fossils from Eocene/ Oligocene	26	32			3
Rhagiophryne	1 fossil (Upper Jurassic)					
Scelorhagio	1 fossil (Jurassic)					
Schizella			3			
Sinorhagio	1 fossil (Middle Jurassic)					
Solomomyia					1	
Spania	3	1				
Spaniopsis					7	
Spatulina	2					
Stratiomyopsis	1 fossil (Upper Jurassic)					
Stylospania			1			
Symphoromyia	6 + 8 fossils from Eocene/Oligocene	28				
Taschigatra			2 fossils (Lower Jurassic)			
Zarzia	1 fossil (Cretaceous)					

Table 2. The distribution of the Vermileonidae genera.

Genus	Palearctic	Nearctic	Oriental	Afrotropical	Australian	Neotropical
Alhajarmyia				1		
Isalomyia				1		
Lampromyia	9			4		
Leptynoma	1			6		
Namaquamyia				1		
Protovermileo	1 fossil (Eocene/ *Oligocene)*					
Vermileo	2	3		1		4
Vermilynx				2		
Vermiophis	7					
Vermipardus				13		
Vermitigris			4			

Lesotho (Basutoland).

- *Vermitigris* Wheeler: 4 species from Oriental region: 2 from Indonesia (Sumatra and Borneo), 1 from India (Malayan peninsula), and 1 from China (Guangxi).

FAMILY ATHERICIDAE

Athericidae was erected by STUCKENBERG (1973), with the inclusion of several genera previously associated with Rhagionidae. There are few doubts on the monophyletic status of the family, often positioned as the sister-group of Tabanidae (WOODLEY 1989; SINCLAIR *et al.* 1994; YEATES 2002; ZLOTY *et al.* 2005) based on shared characters as elongated gonocoxal apodemes and long endophalic tines. The following distribution of Athericidae is quite different from NAGATOMI's (1982a) because he treated *Atherix*, *Ibisia*, *Pachybates*, *Suragina* and *Xeritha* as *Atherix sensu lato*. Athericidae contains 13 genera whose species number and distribution are as follows (Table 3):

- *Asuragina* Nagatomi & Yang: 1 species from Oriental region, from Yunnan.
- *Athericetes* Mostovski, Jarzembowski & Coram: 5 fossil species (Lower Cretaceous) from Palearctic region: 4 from England (Surrey and Dorset), and 1 from Russia (Buryat ASSR).
- *Atherix* Meigen: 22 species – 16 species from Palearctic region: 2 from Russia (Alasezberg and Siberia), 1 from Yugoslavia (Plasa), 1 from Roumania (Baile Herculane), 1 from Japan (Shinano Province), 2 from Croatia (Dalmatia: Zelenika), 2 from Syria (Ghazir), 2 from Germany, 1 from France, 1 from England, 1 from Morroco and Algeria, and 1 widespread from Europe to Japan. There is a fossil species from Oligocene of France; 2 species from Neotropical region: 1 from Bolivia (Mapiri), and 1 from Peru (Rosalina, Meshagua, and Pichis) and Bolivia (Mapiri); 3 species from Nearctic region: 2 from Canada and USA (1 from Quebec and 1 from Northwest territories to Quebec, and also California and Georgia), 1 from USA (Washington); and 1 species from Oriental region, from Nepal.
- *Atrichops* Verrall: 9 species – 5 species from Palearctic region: 1 from Greece and Turkey, 1 widespread in Europe, and 3 from Japan (Honshu); 1 species from Afrotropical region, from Kenya; 1 fossil species from Nearctic region, Oligocene of USA; and 2 species from Oriental region, from Thailand.
- *Dasyomma* Macquart: 32 species – 21 species from Neotropical region: 17 from Chile (Valparaiso, Galvarino, Valdivia Province, Chiloe, Santiago, Aconcagua Provinces, and Casa Pangue), 4 from Argentina (Rio Negro, Bariloche, and Chubut, Valle del Lago Blanco); 11 species from Australian region, 7 from Australia (New South Wales, Western Australia and Camberra), and 4 from Tasmania.
- *Ibisia* Rondani: 2 species from Palearctic region: 1 from Morocco, and 1 from France.
- *Microphora* Krober: 1 species from Australian region, from Papua New Guinea (Bismarck Arch).
- *Pachybates* Bezzi: 3 species from Afrotropical region, from South Africa.
- *Succinatherix* Stuckenberg: 2 fossil species from Palearctic region, Baltic Amber (Eocene/Oligocene).
- *Suragina* Walker: 45 species – 4 species from Palearctic region,

Table 3. The distribution of the Athericidae genera.

Genus	Palearctic	Nearctic	Oriental	Afrotropical	Australian	Neotropical
Asuragina			1			
Athericetes	5 fossils (Lower Cretaceous)					
Atherix	15 + 1 fossil (Oligocene)	3	1			2
Atrichops	5	1 fossil (Oligocene)	2	1		
Dasyomma					11	21
Ibisia	2					
Microphora					1	
Pachybates				3		
Succinatherix	2 fossils (Eocene / Oligocene)					
Suragina	4	1 (NE+NT)	22 + 2 (OR+PA)	12	3	3
Suraginella					1	
Trichacantha				1		
Xeritha						1

from Japan (Kagoshima, and Iriomote-jima); 12 species from Afrotropical region: 4 from South Africa, 2 of them with distribution extended to Zimbabwe and Mozambique, 2 from Uganda, 2 from Madagascar, 1 from Zimbabwe, 1 from Cameroun, 1 from Nigeria, and 1 from Congo; 3 species from Neotropical region: 1 from Northern Brazil, and 3 from Mexico (Cordova, Angangueo, Oaxaca, with one species from Guerrero to Texas, USA); 21 species from Oriental region: 2 from Myanmar (Amherst District and Dawna Hills), 4 from India (Assam, West Bengal, and Parensnath Hill), 1 from Vietnam (Tonkin: Hoa-Bin), 1 from Malaya Peninsula (Sunhei Tahan, Pahang), 2 from Sri Lanka, 4 from Philippines (Luzon and Mindanao), 4 from China (Guangxi-Zhuang and Yunnan), 3 from Indonesia (Celebes and Java); 2 species from Palearctic and Oriental region, from Japan and India; 3 species from Australian region, from Indonesia (Maluku).

- *Suraginella* Stuckenberg: 1 species from Australian region, from Australia (Queensland).
- *Trichacantha* Stuckenberg: 1 species from Afrotropical region, from South Africa.
- *Xeritha* Stuckenberg: 1 species from Neotropical region, from Brazil (Santa Catarina, Nova Teutônia).

FAMILY AUSTROLEPTIDAE

As Spaniidae, Austroleptidae was erected by STUCKENBERG (2001) based on former NAGATOMI's (1982b) recognition of three rhagionid subfamilies. Such family status is doubtful, but further analyses are necessary. Austroleptids are small (from 3.5–5.0 mm), soft-bodied flies with humped thorax, short legs and large wings, with males usually darker than females. The distribution of the Austroleptidae is as follows:

- *Austroleptis* Hardy: 8 species – 5 species from Neotropical region, from south Chile and Patagonia; and 3 species from Australian region, from Australia (New South Wales and Tasmania).

FAMILY OREOLEPTIDAE

Oreoleptidae is a new family described by ZLOTY *et al.* (2005) based on the monotypic genus *Oreoleptis* Zloty, Sinclair & Pritchard. *Oreoleptis torrenticola* is from Nearctic region, from Alberta (Canada). The adult oreoleptids resemble the ground plan of adult Tabanomorpha and is hardly distinct from rhagionids, but their larvae stage is truly incomparable to any other family of this infraorder.

COMMENTS ON THE DISTRIBUTION OF TABANOMORPHA

After the description of the extinct rhagionid *Gallia alsatica* (KRZEMINSKI & KRZEMINSKA 2003), the earliest fossil record of Tabanomorpha was pushed back to Lower/Middle Triassic (ca. 240 million years ago). As is widely known, the fossil register is a great source of information to biogeographical reconstruction and, combined with geological reconstructions, allows to the depiction of plausible hypotheses about the spatial evolution of biological groups. Some recent reconstructions of the geological scenario since the Paleozoic – for detailed reconstructions, see MCLOUGHLIN (2001), and SANMARTIN & RONQUIST (2004) – points to a general consensus around 180–160 mya as the age of Pangaean break-up. This way, it seems obvious to consider a Pangean origin for Tabanomorpha, with a further radiation of the infraorder after the split of Pangaea in Laurasia and Gondwana, which probably began 165–150 mya, in the Jurassic.

Among the Tabanomorpha, the families Rhagionidae and Athericidae (as well as Tabanidae) are widely distributed, encompassing all biogeographical regions (NAGATOMI 1982a). The bulk of diversity of Vermileonidae is in Afrotropical region, with some species described to Palearctic, Oriental and Nearctic regions, and three species with Neotropical distribution, from Mexico and Central America.

Despite the uncertainties on the monophyletic status of Rhagionidae, an old origin for the group is highly probable, not just because of the widespread distribution of its most diversified genus (*Chrysopilus*) – supporting an ancient Pangean origin consistent with the vicariancist paradigm – but also because of the great sort of Triassic and especially Jurassic fossils of the group (ROHDENDORF 1938; KOVALEV 1981; ZHANG 1993; MOSTOVSKI 2000; ZHANG *et al.* 2006). However, it is common some conflict between distributions, which often suggests hypotheses of ancient origins for the clades, and the (non)existence of old aged fossils compatible with such proposals. The greatly diversified *Chrysopilus* is an example. The earliest records of the genus are from England Eocene/Oligocene compression fossils and from Baltic Eocene/Oligocene amber (EVENHUIS 1994). Based on the current widespread distribution of the genus and the rather diversified assemblage of Jurassic rhagionids, NAGATOMI (1982a) extrapolated the age of the group suggested by the fossil record advocating an ancient origin for *Chrysopilus*, maybe Middle Jurassic, when there was a unique supercontinent. This position was lately followed by AMORIM & SILVA (2002) and YEATES (2002). Based on a single wing impression, MOSTOVSKI *et al.* (2003) redescribed the Lower Cretaceous rhagionid *Simulidium priscum* Westwood, remarking a great resemblance between the fossil and extant *Chrysopilus*. The single difference is in vein R_{2+3}, but it is far from unexpected, since R_{2+3} varies considerably in *Chrysopilus* species (SANTOS & AMORIM 2007a). Notwithstanding, tabanomorphan wings are very conservative among and within the families, which allows us to consider that the described wing of the fossil *Simulidium* could be comfortably ascribed to *Chrysopilus* (or some closely related genus), dating back the origin of the genus at least to the Cretaceous.

Among the Rhagionidae, the distribution of some genera supports a Laurasian origin, after the first split of Pangaea. *Bolbomyia*, *Glutops*, *Pseudoerinna*, *Symphoromyia* and *Spania* have species described for Palearctic and Nearctic regions. *Arthroceras* and *Ptiolina* accord to the Holarctic pattern, but are also distributed in Oriental region. Notwithstanding, CRANSTON (2005) points to the sometimes confused, even disrupted, patterns of Laurasian taxa – northern hemisphere patterns tend to be complex and difficult to interpret, and the strictly vicariancist perspective can be not enough to comprehend such patterns. The fact that *Bolbomyia* and *Symphoromyia* have fossils from Eocene/Oligocene could somehow suggests a more recent origin for both genera but, as commonly accepted, the lack of fossils should not be taken as the nonexistence of ancient species older than the available paleontological register.

STUCKENBERG (2000b; 2002; 2003) made some important discussions regarding the biogeography of Vermileonidae. He recognized two well-defined vermileonid groups, the Laurasian genera (composed by *Vermileo*, *Vermiophis*, *Vermitigris*, and all the Nearctic species of the family) and the African genera (*Alhajarmyia*, *Lampromyia*, *Leptynoma*, *Vermilynx*, *Namaquamyia*, *Vermipardus*, and *Isalomyia*). In fact, the distribution of *Vermileo* extrapolates the Northern territories, with species occurring in both Afrotropical and Neotropical regions. This can push back the origin of the genus to the boundary Permian–Triassic or can be explained due to dispersal events or due to expansion of the distribution, which seems to be the case especially for the Neotropical species, distributed in a continuum with the Nearctic ones. Some of Stuckenberg's African genera have species described also in Palearctic region, as *Lampromyia* and *Leptynoma*, but it does not invalid the possible existence of an African group of vermileonids, since the Palearctic distribution of these two genera is restricted to Southern European and Northern African areas, which turn the possibility of dispersion events to explain the current distribution into plausible hypotheses.

The infraorder Tabanomorpha is also a good source of evidences to comprehend gondwanan distributions in a vicariancist scenario. According to De Jong (2003), if a taxon occurred in Gondwana before its break-up, it is expected to found its sister-groups in fragments of the former austral landmass, e.g. Australian relatives in South American region. Considering vicariance, the supposed gondwanan groups must have at least the same age as the break-up. In order to be considered a gondwanan group, the taxon must be endemic to some of the recognized gondwanan areas (South America, Australia, New Zealand, New Caledonia, New Guinea, Tasmania, Africa and, in some cases, India and south Asian archipelagos), must have a sister-group relationship with a taxon endemic to other gondwanan remnants, and must be old enough in order to could had responded to the vicariance events of continental drift. In fact, the role of vicariance and dispersal in molding the distribution of currently gondwanan groups is still debatable. Regarding the Tabanomorpha, there are several groups with distribution that fit with the circum-antarctic pattern of disjunctions (taxa present in the Southern landmasses like South America, tropical Africa and Australian region) and which can be interpreted through a vicariancist perspective plus dispersal events and secondary expansions of distribution.

As pointed by Nagatomi (1982a) in other terms, two rhagionid genera have circum-antarctic distribution: *Atherimorpha* (with 12 Afrotropical species, 21 Australian species, and 15 Neotropical species), and *Pelecorhynchus* (31 Australian species and 6 Neotropical species). The bulk of *Atherimorpha* diversity is in Australian region, with 14 species from Australia – including one fossil from Lower Cretaceous of Victoria, indicating Mesozoic origins –, and seven species from Tasmania. In Neotropics, the genus is widely distributed in Chile (12 species), with two species from Argentina, and a single species from Brazilian Atlantic forest. There are still 12 atherimorphan species from Southern Africa. From the 31 Australian species of *Pelecorhynchus*, six are endemic to Tasmania, and 25 are widely distributed in Australia. The Neotropical species are known from Chile. The genus *Austroleptis*, probably the sister-group of the remaining Tabanomorpha, also fits this circum-antarctic pattern, with five species from Neotropical region (Chile and Patagonia), and three species from Australian region.

There are some interesting aspects about the distribution of Athericidae. As Rhagionidae, the widespread distribution of some of its genera points to a Pangean origin of the family – e.g. *Suragina*, which is distributed in all biogeographical regions. The distribution of *Atherix*, with 16 described species from Palearctics, three from Nearctics, two from Neotropics, and a single species from Oriental region, suggests a very ancient origin for the genus, probably during Pangean times as well, despite the poor fossil record, with a single species from Oligocene. *Atrichops* have species in all Northern Hemisphere, with a unique species described for Afrotropical region. If the genus is Laurasian, the African occurrence can be explained as an individual dispersion event – or a secondary expansion – from Northern terrains but if the origin of *Atrichops* is still more ancient, it is easy to suppose that the diversity of the genus is actually underestimated. *Dasyomma* is clearly part of the Gondwanic element (Stuckenberg 2000a). The genus is distributed in Australian (11 species) and Neotropical regions (21 species). The 21 Neotropical *Dasyomma* are distributed in Chile (17 species) and Argentina (four species). In Australian region, the 11 described species of the genus are known from Australia and Tasmania. Other two genera, *Suraginella* and *Xeritha*, also seem to be part of the Gondwanic element. *Suraginella* has a single species described for Australia (Queensland), and *Xeritha* has a single species described for South America (in Southern Brazilian territory). Both genera share great morphological similarities (wings, head, and terminalia) and, if close phylogenetic affinities could have been found between them, a common Gondwanic ancestor could be hypothesized (Stuckenberg 2000a).

It is worth mentioning that, following an alternative reconstruction of the fragmentation of Pangaea (MCCARTHY *et al.* 2007), the patterns presented by *Atherimorpha*, *Pelecorhynchus*, *Austroleptis*, and *Dasyomma* should be considered as transpacific and not circum-antarctic. In such model, the sequence of split of Pangaea is different from the orthodox model, with Western South America and Australia still connected after the separation of Antarctica and Afrotropical region from the other gondwanan terrains.

Despite the initial attempts to solve the problem, the biogeographical evolution of Tabanomorpha is still deeply unknown. The infraorder is widespread, with some genera distributed throughout all biogeographical regions, corroborating the hypothesis of a very ancient origin for the group, during Pangean times. Unfortunately, the number of taxa known from the Triassic fossil register is still limited, and some of the present “Pangaeic” distributions may reflect exclusively the effects of subsequent stochastic intra-hemispheric (Cranston 2005) and trans-continental dispersal events. In certain cases, the paleontological data seems to be a source of conflict. Anyway, the limitedness of the fossil record should not be seen as a dead-end to the biogeographical reconstruction of any group – phylogenies and biogeographical analysis are much strengthened by the inclusion of fossil data but they are not strictly dependant on suck kind of evidence.

Regarding the Tabanomorpha, its vast amount of genera and species turns the reconstruction of the biogeographical affinities of the infraorder into an almost prohibitive task, demanding some kind of taxonomic sampling. Furthermore, the subject should be considered under a phylogenetic perspective (Santos & Amorim 2007b) since phylogenies are powerful tools in providing biogeographical information. With a reliable phylogeny at hand, biogeographical hypotheses could be obtained and compared to biogeographical patterns from different taxonomic groups in the search for congruent (general) patterns. This way, an important effort should be toward a reliable resolution of the phylogenetic relationships among Tabanomorpha, followed by a historical biogeographical analysis, which depends on up-to-dated lists of distribution. As distributional data are fundamental requirements for any biogeographical analysis, the geographical distribution of some of the greatly diversified tabanomorphan families is a starting point to a broad comprehension of the spatial evolution of the infraorder.

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