

How far advanced was Diptera evolution in the Pangaea?

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Abstract – The accumulation of descriptive data of recent and fossil diversity is the base of systematic knowledge but can not alone answer major evolutionary questions. Last century brought a huge amount of information and new paradigms moving our understanding of Diptera evolution to high standards. However, the interface of descriptive data and analytical tools to date was still not sufficient to determine which groups of Diptera were already present in the Pangaea before its break-up in the Jurassic. The presence of fossils demonstrates that some groups were present at that time, but are not per se evidence of absence of groups – the nature of the palaeontological record is such that clade age inferences based on fossils tend to be very conservative. Biogeographical analyses considering vicariance, support much more precise evolutionary reconstructions, but demand refined phylogenetic reconstruction and distributional data not available for key groups. The constraints of the methods involved with evolutionary inferences are considered, as well as a checklist of fossil and biogeographical data so as to infer how far advanced was Diptera evolution in the Pangaea. The fossil record points to a Cretaceous / higher Tertiary diversification of the schizophorans, while biogeographical data may show some evidence of intercontinental disjunction in schizophoran families due to tectonics. The phylogenetic support for this data, however, is insufficient to support conclusions. The answer to these questions allows understanding whether the presence of calypterate and acalypterate groups in different continents is due to large waves of south to north or north to south invasions after continents were split or to vicariance related to tectonics.

Résumé – Où en était l'évolution des Diptères dans la Pangée? – L'accumulation de données décrivant la diversité, récente et fossile, est le fondement de la connaissance systématique mais elle ne suffit pas pour répondre aux questions essentielles sur l'évolution. Le siècle écoulé a apporté quantité d'informations et de nouveaux paradigmes, qui ont énormément fait progresser notre compréhension de l'évolution des Diptères. Cependant, la compréhension des données descriptives et les outils analytiques n'ont pas suffi jusqu'à présent à déterminer quels groupes de Diptères existaient dans la Pangée avant son démantèlement au Jurassique. La présence de fossiles démontre que certains groupes étaient présents à cette période, mais non que d'autres étaient absents – la nature des données paléontologiques est telle que l'estimation de l'âge des clades fondée sur des fossiles est très conservatrice. Les analyses biogéographiques examinant la vicariance permettent des reconstructions évolutives beaucoup plus précise, mais exigent une reconstruction phylogénétique et des données sur la distribution qui ne sont pas disponibles pour les groupes clés. Dans le but d'estimer le niveau d'évolution atteint par les Diptères dans la Pangée, nous avons pris en compte les contraintes liées aux méthodes d'inférence évolutive ainsi qu'une liste des données fossiles et biogéographiques. Les données fossiles suggèrent une diversification des schizophores au Crétacé / Tertiaire supérieur, tandis que les données biogéographiques semblent indiquer que la disjonction intercontinentale des familles de schizophores est liée à la tectonique. La phylogénie ne permet cependant pas de tirer des conclusions précises. La réponse à ces questions permet de savoir si la présence de groupes calyptères et acalyptères sur les différents continents est due à de grandes vagues d'invasion du Sud vers le Nord, ou du Nord vers le Sud, après la séparation des continents, ou à une vicariance liée à la tectonique.

PHYLOGENY, PALAEONTOLOGY AND BIOGEOGRAPHY: COMPOSING A PICTURE OF DIPTERA EVOLUTION

There was a time in which the understanding of dipteran diversity corresponded to the description

or redescription of species and to the gathering of these species on the base of similarities. This period can be traced mainly from Linnaeus's early works to the first decades of the XXth century. The effort of these first systematists and the many excellent descriptions produced was the base upon which the building of present knowledge was constructed. An understanding of the Diptera in a historical perspective, however, is

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more recent and grew in the XXth century with the interlacing of three complementary approaches: phylogeny, palaeontology and biogeography.

The impact of the concept of evolution in XIXth century Zoology can be realised, for example, through Haeckel's papers (e.g., Haeckel 1886). However, it took some time before phylogenetic discussion of any kind entered Diptera systematics. F.W. Edwards was one of the earliest systematists who tried to draw phylogenetic conclusions in the Diptera (e.g., Edwards 1925). Furthermore, Edwards (1925) was able to launch a discussion of rudiments of phylogenetic concepts. A thorough consideration of the phylogenetic method, however, came with Willi Hennig. Hennig has a long list of publications on the taxonomy of many dipteran families, and many of his papers included phylogenetic considerations. Discussions about the higher level phylogeny of the Diptera can be found in Hennig (1968, 1969, 1973), but the *Flügelgeäder und System der Dipteren unter Berücksichtigung der aus dem Mesozoikum beschriebenen Fossilien* (Hennig 1954) still stands as a landmark by the originality it has in many respects: it is an early contribution in the phylogenetic period and is the very first effort to combine in a single paper recent and fossil groups using cladistic methodology.

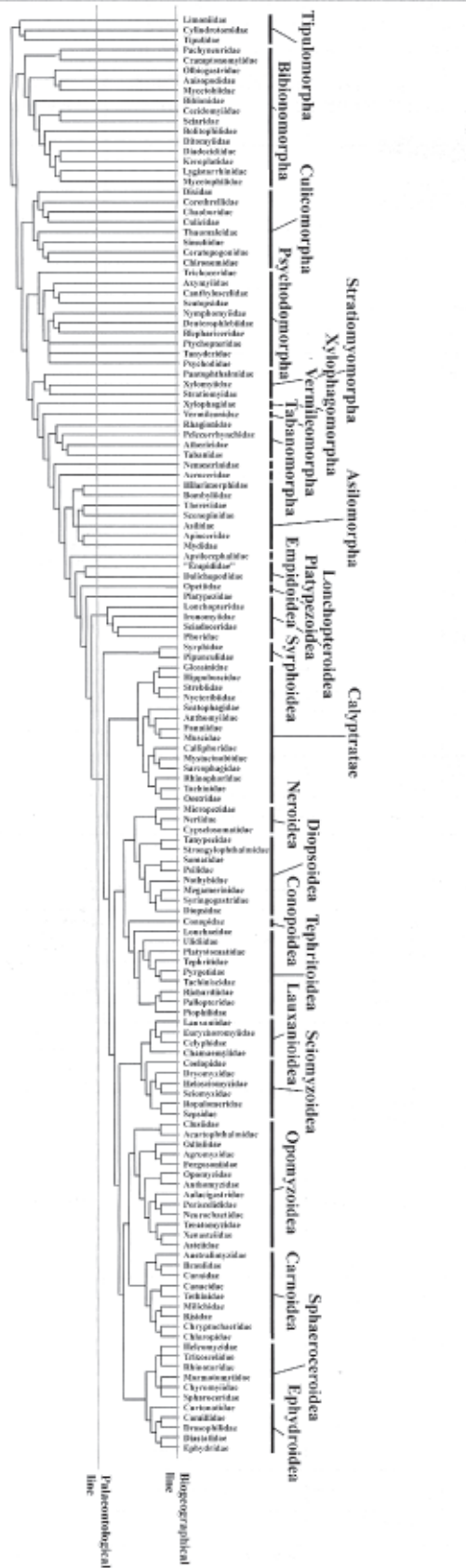
Another source of change in systematics came from biogeography. Dispersionists had only dispersionist concepts and dispersionist reconstructions to offer as explanations for taxonomic biogeographical disjunctions. Hennig (1960) himself proposed some dispersionist reconstructions for some dipteran taxa, as well as some conceptual contributions to a dispersionist biogeography. With the advent of vicariance biogeography (Croizat 1958, 1964, 1976; Croizat, Nelson & Rosen 1974; Rosen 1975, 1978; see Nelson & Platnick 1981; Humphries & Parenti 1986), biogeographic reconstructions could finally recognise both dispersion or vicariance as possible causes of disjunction. The development of modern biogeography, however, is quite recent and not much has been published to date on Diptera biogeography.

Finally, a major contribution to the understanding of Diptera evolution comes from palaeontology. Many early authors described fossil species of Diptera, but particularly thorough contributions came from A. Handlirsch, W. Hennig, and B.B. Rohdendorf, among others. Recent knowledge on compression, but especially on Tertiary and Cretaceous amber fossils, however, has dramatically altered the picture of Diptera evolution (e.g., Kovalev 1981, 1982, 1986, 1987, 1989, 1990; Krzeminski 1985, 1990, 1991, 1992a, b, 1993,

1998; Evenhuis 1994; Blagoderov *et al.* 1993; Blagoderov, 1994; Scherbakov *et al.* 1995; Grimaldi 1989, 1990, 1991, 1999, 2000; Grimaldi & Amorim 1995; Borkent 1995, 1996; Fraser *et al.* 1996; Grimaldi & Cumming 1999; Grimaldi *et al.* 2000; Currie & Grimaldi 2000).

We have moved from a purely descriptive approach of Diptera diversity, dominant some decades ago, to a stage in which phylogenetic methods add to vicariance biogeography and detailed palaeontological information to compose a complex framework for dipteran evolution. What does this general picture show about Diptera diversity in time and space? The picture is far from complete, but it clearly shows an origin of the Diptera late in the Permian or in the Triassic, with an early diversification of the dipterans in the Triassic. Because major clades of Diptera are clearly present in Triassic and Jurassic deposits (see Krzeminski 1992b), it is certain that a number of dipteran species already existed in Pangaea before its geologic break-up. These Pangaeian ancestral species underwent divisions promoted by the sequence of continental disruptions during the Upper Mesozoic, diversifying in each continent in the Tertiary to generate the present diversity of the order.

This view contrasts to the mid-XXth century understanding of the evolution of the recent fauna. A synthesis of this pre-vicariance view of biogeographical evolution can be seen, e.g., in Darlington (1957) and Simpson (1953, 1965). Darlington (1952), in a 4-page article, makes a very nice review of cases of invertebrate transtropical relationships, as well as of circumantarctic disjunctions. Considering the family Paussidae in Coleoptera, he describes in detail the distribution of two main grades in the family. However, when he comes to the discussion of the causes of the patterns he uses a number of arguments to dismiss the connection of these cases of intercontinental disjunctions to the shift of continents. In some parts, his arguments are technically equivocal from an evolutionary point of view, e.g., "So far as I can determine, the South American paussids are not directly related to any other living ones." (Darlington 1952). In other parts, his points are purely rhetoric: "Schuchert (1932) has thought not [of disjunction of marine molluscs to be due to larval dispersion], but his long argument does not seem to me to be very convincing." He also raises some unfocused arguments, "I repeat that it is a fact beyond argument that some living South American invertebrates are related to tropical African forms or to south temperate Australian or South African forms. But these relationships involve only



parts of the South American fauna; the relationships are often general rather than direct; and they can often be explained in several different ways."

Darlington (1965, 1979) to his very end was against the new paradigm –intercontinental disjunction related to plate tectonics–, as were most of the biogeographers of his generation. But tectonic-based biogeographical reconstructions grew slowly and solidly in the last 40 years. Croizat was completely alone in the beginning (e.g., Croizat 1958, 1964), at a time when even geologists were skeptical about continental drift. More recent papers have discussed vicariance from conceptual and methodological view points, and many others have shown congruence between biological disjunction and geological divisions (e.g., Rosen 1976, 1978; Platnick & Nelson 1978; Platnick 1976; Humphries 1982; Humphries & Parenti 1986; Matile 1990; Amorim & Tozoni 1995; Amorim & Pires 1996; Nelson & Ladiges 1996, etc.), but there is still some resistance and/or insufficient understanding.

Data from different sources make it now undeniable that at least part of recent dipteran diversity was already evolving in the Triassic and, hence, at least part of present cases of disjunction are related to tectonics. But a question still remains: how much of it? Or even better, what part of it?

The central point we want to address in this paper is how much had the Diptera diversified in Pangaea. The implications of the answers to this question are manifold. We want to address here, however, a particular one: how to discriminate which major groups of Diptera presently with world-wide distributions have this condition due to ancestral distribution in Pangaea and which achieved this world-wide distribution due to dispersion events between already separated continents. It is beyond the scope of this paper to examine the phylogeny and biogeography of the entire Diptera. Rather, we call attention to the question itself, to some of the data available, to some of the methodological problems to be considered, and to the implications of the answers. This will shed light on the understanding of the temporal and spatial evolution of the Diptera as a whole and to the evolution of families, so particular cases can be properly addressed in the future.

Figure 1
General scheme of Diptera evolution with two hypotheses for degree of Diptera diversification at the beginning of the Jurassic. The "paleontological line" is based on the fossil record and points to a more limited diversification of Diptera at the time of the division of Pangaea. Schizophoran families would not have appeared. The "biogeographical line" is based on cases of intercontinental disjunction and points to a larger diversification at the time of the division of Pangaea. Taxa originated at that time would appear only much later on the fossil record.

Table 1 – Fossil genera of Diptera from Triassic to Eocene. Middle / Upper Jurassic genera are placed under Middle Jurassic; Lower / Middle Jurassic placed under Lower Jurassic. At the Palaeocene / Eocene column, first appears the number of known extinct genera, followed by the number of recent genera known at that period. Eocene data includes the Eocene / Oligocene border. Question marks indicate groups of uncertain affinities.

Family	Triassic	Lower Jurassic	Middle Jurassic	Upper Jurassic	Upper Jurassic / Lower Cretaceous	Lower Cretaceous	Middle Cretaceous	Upper Cretaceous	Palaeocene / Eocene
Not Diptera			<i>Beipiaoptera</i> <i>Sinoptera</i>						
Diptera <i>incertae sedis</i>			<i>Jurafacemargus</i>	<i>Mesobrachyopteryx</i> <i>Pseudoptera</i> <i>Arcus</i> <i>Gansuoptera</i> <i>Sinoptera</i>					
Vladipteridae	<i>Psychotipa</i> <i>Vladiptera</i>								
Grauvogelomorpha									
Grauvogelidae	<i>Grauvogella</i>								
Tipulomorpha									
?Musidoromimidae		<i>Musidoromima</i>							
?Tipulodictyidae		<i>Tipulodictya</i>							
?Eopolyneuridae		<i>Eopolyneura</i> <i>Paropopolyneura</i>							
Diplopolynuridae		<i>Diplopolynura</i>							
Zhangobidae				<i>Ceuthoneura</i> <i>Zhangobia</i>					
Limoniidae	<i>Architipula</i> <i>Mabelyia</i> <i>Gonomusca</i>	<i>Archimesotipula</i> <i>Architipula</i> <i>Dictyotipula</i> <i>Diplarchitipula</i> <i>Dipterodictya</i> <i>Eotipula</i> <i>Haplotipula</i> <i>Leptotipuloides</i> <i>Liastipula</i> <i>Mesotipula</i> <i>Mikrotipula</i> <i>Ozotipula</i>	<i>Architipula</i> <i>Eotipulina</i> <i>Eotipuloptera</i> <i>Hottipula</i>	<i>Architipula</i> <i>Prearchitipula</i> <i>Xutipula</i> <i>Tipania</i>	<i>Cretolimonia</i> <i>Eotipulina</i> <i>Nemusia</i>	<i>Architipula</i> <i>Limonia</i>		<i>Helius</i> <i>Limonia</i> <i>Macalpinia</i> <i>Trichoneura</i> <i>Dicranoptycha</i> <i>Gynoptisina</i>	14+29
Gracilitipulidae				<i>Gracilitipula</i>					
Tipulidae								<i>Tipula</i>	0+4
Cylindrotomidae									1+1
Bibionomorpha									
Procramp-tonomyiidae	<i>Yala</i>		<i>Procramp-tonomyia</i>						
Boholdyidae		<i>Boholdya</i>		<i>Boholdya</i>	<i>Daiamyia</i>				
Pachyneuridae				<i>Tega</i>		<i>Pivaz</i>			
Vimbrhyphidae	<i>Vimbrhyphus</i>								
Protorhyphidae		<i>Archirhyphus</i> <i>Heterorhyphus</i> <i>Protorhyphus</i>	<i>Protorhyphus</i>	<i>Archirhyphus</i> <i>Brachyopteryx</i>	<i>Protorhyphus</i>				
Siberhyphidae			<i>Siberhyphus</i>						
Anisopodidae		<i>Mesorhyphus</i>	<i>Sinorhyphus</i>	<i>Megarhyphus</i> <i>Mesobrachyopteryx</i>	<i>Megarhyphus</i> <i>Mesorhyphus</i> <i>Pachyrhyphus</i>	<i>Mycetobia</i> <i>Obliogaster</i> <i>Thiras</i>		<i>Mycetobia</i>	0+2
Crosaphididae	<i>Crosaphis</i>								
Bibionidae		<i>Penthetria</i>		<i>Mesopteciella</i>				<i>Plecia</i>	2+4
Sciiridae									0+9
Cecidomyiidae					<i>Carotricha</i>			<i>Cretocatocha</i> <i>Cretocordylomyia</i> <i>Cretomiazor</i> <i>Cretowimmerzia</i>	2+31
Plecofungivoridae		<i>Archihesperimus</i> <i>Archiplecofungivora</i> <i>Bryanka</i> <i>Matifia</i> <i>Plecofungivora</i> <i>Plecofungivorella</i> <i>Prohesperius</i> <i>Rhaetofungivora</i> <i>Rohdendorfomyella</i>	<i>Archiplecofungivora</i> <i>Bryanka</i> <i>Eohesperimus</i> <i>Fungivorplecia</i> <i>Fungivorplecia</i> <i>Gilfaroviana</i> <i>Krasnoyarskia</i> <i>Plecofungivora</i> <i>Plecofungivorella</i> <i>Willibrongia</i> <i>Fera</i>	<i>Bryanka</i> <i>Eohesperimus</i> <i>Fungivorites</i> <i>Mesopteciifungivora</i> <i>Paraplecofungivora</i> <i>Plecofungivora</i> <i>Plecofungivorella</i> <i>Prohesperimus</i>	<i>Bryanka</i> <i>Plecofungivorella</i>				
Archizelmiridae				<i>Archizelmira</i>					
Antefungivoridae		<i>Pleciomima</i>	<i>Antefungivora</i> <i>Mimallactoneura</i> <i>Sciaronima</i>	<i>Antefungivora</i> <i>Antipamedia</i> <i>Aaromima</i> <i>Baishulingella</i> <i>Lycorimimodes</i> <i>Mimallactoneura</i> <i>Paralycorimimodes</i> <i>Pleciomima</i> <i>Sciaronima</i>	<i>Lycorimimodes</i> <i>Pleciomima</i> <i>Sciaronima</i>				
Tipuloplectidae				<i>Tipuloplectia</i>					
Protoligoneuridae		<i>Protoligoneura</i>							
Palaeopteciidae		<i>Palaeoptecia</i>							
Mycetophiliformia genera <i>incertae sedis</i>				<i>Parazygia</i>	<i>Eomycetophila</i>				
Propteciidae		<i>Archipleciomima</i> <i>Dynopolynura</i> <i>Mesoptecia</i>	<i>Paraoligus</i> <i>Pleciopsis</i> <i>Sinoptecia</i>	<i>Heiplectecia</i> <i>Mesoptecia</i> <i>Pseudoptecia</i>		<i>Simulidius?</i>			

Table 1. (continued)

		<i>Palurohesperinus</i> <i>Phragmologoneura</i> <i>Proallactoneura</i> <i>Protoplecia</i> <i>Rhaetofungivorella</i>	<i>Sanoplecia</i>						
Protobibionidae				<i>Protobibio</i>					
Parapleciidae			<i>Paraplecia</i>						
Mesosciophilidae			<i>Mesosciophila</i>	<i>Mesosciophila</i> <i>Mesosciophilodes</i> <i>Eobolusina</i>		<i>Mesosciophilopsis</i>			
Paraxomyiidae			<i>Arcus</i>	<i>Paraxomyia</i>					
Bolitophilidae						<i>Morgas</i>			0+2
Ditomyiidae									0+2
Diadocididae									0+1
Keroplastidae							<i>Schwaeteromyia</i>		2+7
Lygistorrhinidae									1+0
Mycetophilidae		<i>Prodocia</i>		<i>Sciophilopsis</i>		<i>Sciophila</i> <i>Thimna</i> <i>Cecidomyia?</i>			14+32
Culicomorpha									
Culicomorpha incertae sedis			<i>Leptoplecia</i>						
Dixidae									0+2
Dizamimidae				<i>Dizamima</i>					
Chaoboridae			<i>Chironomoptera</i> <i>Eucorethrina</i> <i>Helobrenia</i> <i>Hysocorethra</i> <i>Praechaoborus</i>	<i>Chironomoptera</i> <i>Mesochaoborus</i>	<i>Astrocorethra</i> <i>Chironomoptera</i>	<i>Astrocorethra</i> <i>Chironomoptera</i>	<i>Chironomoptera</i>		1+2
Rhaetomyiidae		<i>Rhaetomyia</i>	<i>Rhaetomyia</i>						
Asiochaoboridae				<i>Asiochaoborus</i> <i>Chaoboreopsis</i> <i>Sinochaoborus</i> <i>Sinochaoborus</i>					
Culicidae		<i>Amianta?</i> <i>Anphiprosopa?</i> <i>Culicocler?</i> <i>Empidocampe?</i> <i>Propexis</i> <i>Rhopalucocler?</i>				<i>Asioculicu?</i>			0+3
Thaumaleidae					<i>Mesothaumalea</i>				
Simuliidae		<i>Simulimeta?</i>		<i>"Simulites"</i> <i>brevisetris</i> <i>Mesarsimulium</i>	<i>Kovalevomyia</i>	<i>Balsomyia</i> <i>Gydarina</i>			0+2
Ceratopogonidae							<i>Atriculoides</i> <i>Astroconops</i> <i>Brachypogon</i> <i>Ceratopogon</i> <i>Culicoides</i> <i>Leptocnops</i> <i>Leptohela</i> <i>Protocalicoides</i> <i>Lasiobela cretaea</i> <i>Lasiobela globosa</i> <i>Dasybela tyrrelli</i>		6+18
Serendipidae				<i>Serendipa</i> <i>Thawinterdipes</i>					
Protendipidae		<i>Pritcotendipes</i>		<i>Pritcotendipes</i> <i>Protendipes</i>					
Mesophantasmidae				<i>Mesophantasma</i>					
Chironomidae	<i>Aenne</i>	<i>Juraplecia</i> <i>Podonomus</i> <i>Aenne</i>	<i>Jurochilus</i> <i>Mallonia</i> <i>Mogronomus</i> <i>Oryctochilus</i> <i>Podonomus</i> <i>Tophocladus</i> <i>Ulaia</i> <i>Ulaimalia</i> <i>Ulaimallonia</i> <i>Ulaimalloniella</i> <i>"Tanypodites"</i> <i>garchonensis</i>	<i>Coelochironomus</i> <i>Manlayomyia</i> <i>Orua</i> <i>Oryctochilus</i> <i>Simvryctochilus</i> <i>Tendipopsis</i> <i>Tuactum</i> <i>Vidua</i> <i>Eopodonomus?</i> <i>Pachyroryncha?</i>	<i>Gurvanomyia</i> <i>Manlayomyia</i>	<i>Chironomopsis</i> <i>Libanochlites</i> <i>Shiblastia</i> <i>Switta</i> <i>Asaba?</i> <i>Bibionites?</i> <i>Dara</i>	<i>Cretodiamesa</i> <i>Electrotenia</i> <i>Metricnemus</i> <i>Spantotoma</i> <i>Chironomites?</i>		3+6
Sinotendipidae		<i>Sinotendipes</i>							
Luampingiidae			<i>Luampingites</i>						
Psychodomorpha									
Tanyderophryneidae				<i>Tanyderophryne</i>					
Limnorhynchidae			<i>Limnorhynchus</i>						
Ellidae					<i>Ellia</i> <i>Polyanka</i>	<i>Ellia</i>			
Blephariceridae									2+0
Tanyderidae			<i>Praemacrophile</i>	<i>Protanyderus</i> <i>"Tanyderites"</i> <i>admirandus</i>	<i>Protanyderus</i>				0+1

Table 1. (continued)

Perissomatidae			<i>Palaeoperissomma</i>	<i>Palaeoperissomma</i>	<i>Garvaniella</i>			
Psychodidae			<i>Eoperioma</i>	<i>Mesopsychoda</i>		<i>Phlebotomites</i>		3+6
Trichoceridae		<i>Eotrichocera</i>	<i>Molotrichocera</i> <i>Trichocera</i>	<i>Mesotrichocera</i> "Trichonomites" <i>apollinaris</i>		<i>Paleotrichocera</i>		0+1
Protocatapsidae		<i>Mesocatapse</i>		<i>Protocatapse</i>				
Scatopsidae								0+4
Canthylosceldidae			<i>Prohyperoscelis</i>			<i>Symenon</i>		
Psychoptera			<i>Psychoptera</i>			<i>Psychoptera</i> <i>mesozoica</i>		1+0
Ansorgidae				<i>Ansorgia</i>				
Eoptychopteridae	gen. sp.	<i>Eollembyia</i> <i>Eoptychoptera</i> <i>Eoptychoptera</i> <i>Architendipes</i> <i>Cremoptychoptera</i>	<i>Cremoptychoptera</i> <i>Eoptychoptera</i> <i>Eoptychoptera</i> <i>Proptychoptera</i> <i>Proptychoptera</i>	<i>Eoptychoptera</i> <i>Eoptychoptera</i> <i>Proptychoptera</i> <i>Proptychoptera</i> <i>Cremoptychoptera</i> <i>Nedoptychoptera</i>	<i>Bolbaia</i>	<i>Cremoptychoptera</i> <i>Eoptychoptera</i> <i>Proptychoptera</i> <i>Proptychoptera</i> <i>Proptychoptera</i> <i>Daptychoptera</i>		
Brachycera								
Stratiomyomorpha								
Cratomyiidae						<i>Cratomyia</i>		
Xylomyiidae				<i>Archisobia</i>				0+1
Eostratiomyiidae				<i>Eostratiomyia</i>				
Stratiomyidae							<i>Cretaceogaster</i>	3+3
Oligophryneidae		<i>Oligophryne</i>						
Xylophagomorpha								
Xylophagidae								2+1
Rachiceridae								3+1
Vermileonomorpha								
Vermileonidae								1+0
Tabanomorpha								
Rhagionidae			<i>Ija</i> <i>Jurabrachyceron</i> <i>Kubekovia</i> <i>Palaeobolbomyia</i> <i>Palaeobrachyceron</i>	<i>Archihagio</i> <i>Mesorhagiofhyne</i> <i>Mesostratiomyia</i> <i>Palaeostratiomyia</i> <i>Rhagiofhyne</i> <i>Scolrhagio</i> <i>Stratiomyopsis</i> <i>Symphoromyia</i> <i>Protarhagio?</i>	<i>Arthroteles</i>	<i>Atheromorpha</i> <i>Mongolomyia</i> <i>Ptilonia</i> <i>Ptilonites</i> <i>cretaceus</i>	<i>Zaria</i>	0+2
Alinidae	<i>Alinka</i>							
Athericidae								
Tabanidae								0+1
Tabanoidea Ls.						<i>Baryana</i> <i>Stulmar</i>		0+1
Eomyiidae				<i>Eomyia</i>				
Protobracheridae		<i>Protobrachyceron</i>						
Nemestrinoidea								
Acroceridae				<i>Archocyrtus</i>				4+1
Nemestrinidae				<i>Archinemestrus</i> <i>Eohirmonera</i> <i>Prohirmonera</i> <i>Protonemestrus</i> <i>Sironemestrus</i> <i>Rhagionemestrus?</i>				
Asiloidea								
Bombyliidae								4+2
Therevidae								2+2
Asilidae							<i>Araripogon</i>	2+4
Eremochetidae				<i>Eremochaeta</i> <i>Pareremochaeta</i> <i>Archisargus</i>		<i>Disap</i> <i>Eremochaetosoma</i>		
Protomphralidae				<i>Protomphrale</i> <i>Mesomphrale?</i>				
Mythicomyiidae			<i>Palaeoplatygygus</i>				<i>Procyrtosis</i> <i>Proplatygygus</i>	2+1
Empidoidea								
Protempididae				<i>Protempis</i>				
Rhagionempididae			<i>Palaeoptiolina</i> <i>Ussatchovia</i>	<i>Probolomyia</i> <i>Rhagionempis</i>	<i>Sheviaptera?</i>			
Empididae				<i>Empida?</i> <i>Haemona</i>		<i>Microphorites</i> <i>Trichinites</i>	<i>Apalocnemus</i> <i>Archichrysotus</i> <i>Archiplatypus</i> <i>Cretamicrophorus</i> <i>Cretoplathypus</i> <i>Ecomocycromyia</i> <i>Pseudocarterus</i> <i>Retinitus</i>	10+22
Dolichopodidae						<i>Sympicrites</i>		6+16
Cyclorrhapha								
Platypteroidea						<i>Lonchopterites</i>		
Lonchopteridae								0+1
Platypteroidea				<i>Lithoptera</i>				1+1

Table 1. (continued)

				<i>Mesopetia</i> <i>Palaeopetia</i> <i>Pseudopetia</i> <i>Sinoletia</i>					
Sciadoceridae						<i>Archicelada</i> <i>Archiphora</i>			0+1
Ironomyiidae								<i>Cretomyia</i>	
Phoridae								<i>Dolrnhphora</i> <i>Metopina</i> <i>Prioriphora</i> <i>Sclatophora</i>	6+8
Syrphoidea									
Pipunculidae									2+3
Syrphidae									11+9
Acalyptratae									
Nerioidea									
Cypselosomatidae									1+0
Microporidae									1+0
Diopsoidea									
Megamerinidae									1+0
Diopsidae									1+1
Conoidea									
Conopidae									2+0
Tephritoidea									
Richardiidae									1+0
Fallopteridae									3+0
Lauxanioidea									
Lauxaniidae									2+1
Chamaemyiidae									1+0
Scyomyzoidea									
Dryomyzidae									2+0
Sciomyzidae									4+1
Sepsidae									1+0
Opomyzoidea									
Clusiidae									2+0
Acartophthalmidae									1+0
Odiinidae									1+0
Agromyzidae									3+0
Anthomyzidae									1+0
Aulacigasteridae									1+0
Neurochaetidae									1+0
Pseudopomyzidae									1+0
Astelidae									1+0
Carnoidea									
Carnidae									1+0
Milichidae									1+1
Chloropidae									2+2
Cryptochetidae									1+0
Sphaeroceroidea									
Heleomyzidae									3+2
Sphaeroceridae									0+2
Camillidae									1+0
Drosophilidae									1+0
Diaetidae									1+0
Eghydridae									0+1
Pillidae									1+0
Pronotioptilidae									1+0
Chyromyidae									1+0
Calyptratae									
Hippoboscoidea									
Muscoscoidea									
Scatophagidae									0+1
Anthomyiidae									0+1
Muscidae									1+0
Oestroidea									
Calliphoridae?								<i>Cretiformia</i>	
Sarcophagidae									0+1
Tachinidae									3+0
Oestridae									1+2
Eophlebotomyiidae									1+0
Unplaced Brachycera	<i>Agmatozoan</i> <i>Campesinix</i> <i>Chorolimonobia</i> <i>Dimeretes</i> <i>Epimetophora</i> <i>Griphocanion</i> <i>Liassomypha</i> <i>Oocephalina</i> <i>Platyconion</i>	<i>Mesosolva</i> <i>Protolva</i>		<i>Palaeophora</i> <i>Mecowera</i> <i>Psychodites</i> <i>Remalia</i> <i>Tipularia</i>					1+0

Phylogenetic information

The last 15 years has shown more intense work on the problem of Diptera phylogeny than in many decades before. The "strict consensus" of the phylogenies proposed to date, however, results in a large, uninformative polytomy at the base of the Diptera (Yeates & Wiegmann 1999). This could give the impression that we know less now than Willi Hennig, which is false. Congruence between different sources of information confirm the monophyly of a number of groups and clarifies the relationships among some taxa. This is relevant here, since the implications of fossil data depends on the phylogeny accepted.

Hennig (1968) published a frequently overlooked paper, in which he addressed the question of basal relationships in the Diptera, indicating for the first time that the "Nematocera" are not monophyletic. His conclusions pointed to the relationships among five main stems: (Tipulomorpha + (Psychodomorpha + (Culicomorpha + (Bibionomorpha + Brachycera))). Hennig (1973) reviewed some of his earlier positions and added considerable information to the understanding of Diptera evolution.

Rohdendorf (1974), with a non-phylogenetic approach, and Griffiths (1972), strictly working under a phylogenetic perspective with the Cyclorrhapha, proposed phylogenies which were alternatives to Hennig's points of view. A complete phylogenetic study of the Diptera appeared more recently in Volume 3 of the *Manual of the Nearctic Diptera*—with the chapters by Wood and Borkent (1989), dealing with basal dipteran relationships, Woodley (1989), who worked out the basal brachyceran phylogeny, and McAlpine (1989) with a phylogenetic study of the Cyclorrhapha. This was followed by a number of articles published in the last ten years: Griffiths (1990, 1994), Courtney (1990, 1991), Oosterbroek & Theowald (1991), Wood (1991), Sinclair (1992), Krzeminski (1992b), Amorim & Carvalho (1992), Amorim (1993), Sinclair *et al.* (1993), Blaschke-Berthold (1994), Oosterbroek & Courtney (1995), Cumming *et al.* (1995), Michelsen (1996), Friedrich & Tautz (1997), and Saether (2000).

Trying to solve the problem of the basal levels of the dipteran phylogeny, Amorim *et al.* (submitted) added thorax sclerite characters. In general terms, their results agree with Wood & Borkent (1989), although significant differences are seen for the position of some families. Mazzarolo & Amorim (2000) also tried to synthesize the opinions of different authors about basal Brachycera phylogeny. For the Cyclorrhapha, the positions of Griffiths (1972), Hennig (1973), and McAlpine (1989) disagree significantly on the pro-

blem of the monophyly of the Acalyptratae and about the position of many Acalyptratae families. Figure 1 has a phylogenetic system for the Diptera as a whole to serve as a working base for some of the discussions here. The phylogeny considers positions accepted by most, but not all authors in the literature. Disagreements about details in the phylogeny, however, would do not interfere with the main conclusions drawn ahead.

Palaeontological information

The growth of our knowledge of the Diptera in Mesozoic deposits in the last 50 years is amazing. We will not review here Diptera palaeontological literature (see Evenhuis 1994; Krzeminski & Evenhuis 2000), but mainly the implications of the accumulated data for the understanding of Diptera evolution.

An extensive contribution was given by the Russian palaeontologist Boris Rohdendorf, although many of his wing drawings (and consequently his systematic conclusions) were not accurate and he did not employ a consistent phylogenetic method. Hennig (1954) synthesized the available Mesozoic fossil Diptera information, trying to put together palaeontology and phylogeny. The number of fossil dipterans known at the time was limited compared to what is now known; also the phylogenetic system he proposed suffered a number of changes in the last 30 years. Nevertheless, the paper created a new model on how to integrate both sources of information.

More recently, Krzeminski (1992b) and Krzeminski & Evenhuis (2000) published a synthesis of the knowledge of the Triassic and Jurassic Diptera. They reinforce the idea that the Permian genus *Permotipula* is not directly related to the Diptera, so the oldest fossils assigned to the dipterans without dispute would be Triassic. It must be noted, however, that if there was a mecopteran diversification in the Permian and that if the Permian Permochoristidae are the possible sister group of the recent Diptera, it would be out of question that the origin of the Diptera as a clade is in the Permian — the age of the origin of the Diptera would be given by its sistergroup. The basal diversification of Diptera would more probably have begun in the Triassic.

The dipteran diversity in the Triassic now known includes: (1) the genera *Psychotipa* and *Vladiptera*, of the family Vladipteridae; (2) the genus *Grauvogelia*; (3) the genus *Nadiptera*; (4) the genera *Architipula*, *Mabelysia* and *Gonomusca* (Tipulomorpha: Limoniidae); (5) one described species of *Crosaphis* (Bibionomorpha: Anisopodoidea) from Australia, along with another undescribed species from Virginia;

(4) one species of *Yala* (Bibionomorpha: Procramp-tonomyiidae); (5) one incomplete specimen assigned to the family Eoptychopteridae (Psycho-domorpha: Eoptychopteroidea); and (6) one species of *Alinka*, in a monotypic extinct family Alinkidae assigned to the Brachycera Tabanoidea. The position of Alinkidae in the Brachycera, however, is doubtful and it may be related to the Cramptonomyiiformia.

Lower Jurassic fossils add a number of stems to this early Diptera radiation. Some of the families described for this period seem to be extinct (but see the discussion on the methodological constraints, below). In the Tipulomorpha are included the families Diplopolynuridae, Tipulodactylidae, Eopolyneuridae, Musidoromimidae, Gracilitipulidae, Zhango-biidae. In the Bibionomorpha there are Jurassic records for the families Procramp-tonomyiidae, Boholdoyidae, Protorhyphidae, Anisopodidae, Mycetobiidae, Bibionidae, Siberhyphidae, Pleciofungivoridae, Archizelmiridae, Antefungivoridae, Tipulopleciidae, Paraxymyiidae, Protoligoenuridae, Palaeopleciidae, Eopleciidae, Protopleciidae, Protobibionidae, Parapleciidae, Mesosciophilidae, and Mycetophilidae.

In the Culicomorpha, the families Dixamimidae, Chaoboridae, Asiochaoboridae, Rhaetomyiidae, Limnorhyphidae, Simuliidae, Architendipedidae, Serendipidae, Prototendipedidae, Mesophantasmidae, Chironomidae, Sinotendipedidae, Luanpingitidae, and possibly Culicidae already appear in the Jurassic. Some Culicidae have been assigned to Triassic deposits (Lambrecht, 1980), but without further information (see Evenhuis 1994). Also a number of Lower Jurassic culicid genera described from immatures are still questionably associated with the family (Evenhuis 1994).

The Psychodomorpha records in the Jurassic include Tanyderidae, Perissomatidae, Psychodidae, Trichoceridae, Protoscatopsidae, Canthyloscelidae, Ptychopteridae, Ansorgidae, and Eoptychopteridae. As discussed elsewhere (Amorim *et al.* in press), the monophyly of the Psychodomorpha is still a problem, since there is disagreement between authors concerning the families included in this taxon.

The Jurassic brachycerans are clearly less diverse, but they are already present in the fossil record. This includes the Xylomyidae, Eostratiomyiidae, and Oligophryneidae (of the Stratiomyomorpha), Rhagionidae (which are quite diverse at that time), Eomyiidae, and Protobrachyceridae (of the Tabanomorpha), Acroceridae, Nemestrinidae, the families Eremochetidae, Protomphralidae, and Mythicomyiidae of the Asiloidea, and an early divergence of the Empidoidea, with the families Protempididae, Rhagioempididae, and Empididae. The only con-

firmed Jurassic cyclorrhaphans to date belong to the Platypezidae.

The Jurassic/Cretaceous border is particularly relevant in this discussion because of the division of Pangaea. It certainly took some time for the separation between Gondwanaland and Laurasia to be completed, after its beginning in the Lower Jurassic about 180 m.y. ago, and it will mark the isolation of the main faunas. Cretaceous dipteran diversity seems to be higher than in previous periods (see Grimaldi 1990). A number of Limoniidae genera (including recent ones) are already present in the Cretaceous, as well as species assigned to the recent genus *Tipula* (which is still a catchall genus). In the Bibionomorpha, the families Pachyneuridae, Protorhyphidae, Olbiogastridae, Mycetobiidae, Protopleciidae, Pleciofungivoridae, Bibionidae, Antefungivoridae, Archizelmiridae, Cecidomyiidae, Bolitophilidae, Keroplatidae, and Mycetophilidae are present in the Cretaceous. In the Culicomorpha, Chaoboridae, Thaumaleidae, Simuliidae, Mesotendipedidae, Ceratopogonidae, Chironomidae, and possibly the Culicidae are known from Cretaceous deposits. In the Psychodomorpha, Cretaceous deposits show species of Psychodidae, Trichoceridae, Canthyloscelidae, Scatopsidae, Ptychopteridae, and Eoptychopteridae.

In the Brachycera a number of families are recognised in the Cretaceous, including the Cratomyiidae and Stratiomyidae (of the Stratiomyomorpha), Rhagionidae (of the Tabanomorpha), Asilidae, Therevidae, Eremochetidae, and Mythicomyiidae (of the Asiloidea), Bombyliidae (of the Bombyloidea), Empididae (of the Empidoidea), Ironomyiidae, Sciadoceridae, and Phoridae (of the Platypezoidea), Pipunculidae and Syrphidae (of the Syrphoidea), Milichidae (of the Acalyptratae) and Calliphoridae (of the Calyptratae). The confirmation of an undescribed Lower Cretaceous Acalyptratae of Australia (Jell & Duncan 1986: 49G,H, 50E,F) would be particularly relevant in this discussion.

Next in the fossil record appear some Upper Tertiary compression fossils and the highly diversified and rather abundant Baltic amber fossils from the Eocene/Miocene border. Most of the recent families of Diptera, including the Acalyptratae, are known at this time, even though some represent basal genera of their respective families (Grimaldi & Cumming 1999).

There are only four Triassic deposits known to contain Diptera: a Lower Triassic in France, a Middle / Upper Triassic in Ferganskaya, Tajikistan, and two Upper Triassic, one in Queensland, Australia, and the other in North Carolina/Virginia, USA. The Issyk-Kul' deposit in Kyrgyzstan, was previously believed to

be from the Upper Triassic, but is now assigned to the Lower Jurassic. The dipteran specimens recovered from these deposits are still few and mostly undescribed.

In North America, there is a single Jurassic deposit known from the Callovian (Middle Jurassic) in Utah (USA), with a limited number of species described. Jurassic deposits in Eurasia are relatively more abundant, with 14 Lower Jurassic sites, 32 Middle Jurassic or Middle / Upper Jurassic sites, and 30 Upper Jurassic or Upper Jurassic / Lower Cretaceous deposits. Although Jurassic sites are more abundant in Europe and Asia, the number of species adequately described in the literature and taxonomically well placed is still low. Boris Rohdendorf and A. Bode (see Evenhuis, 1994), for example, produced a considerable contribution to palaeontology describing Jurassic fossils, but their wing drawings are not reliable and revisions of most of their types is needed. The later contribution of Kalugina & Kovalev (1985) is superb in quality.

Cretaceous compression deposits with dipteran fossils are completely absent in North America. There are four Lower Cretaceous compression deposits in Europe and nine in Asia, and only three Upper Cretaceous deposits in Asia. On the other hand, Africa, Australia, India and South America each have a single Mesozoic deposit of compression fossils including dipterans, the former an Upper Cretaceous deposit, the latter three from the Lower Cretaceous. The Santana Formation is now beginning to become well known (see Grimaldi 1990), and important material has been described from Moonwarra, Australia, but still very few specimens are known from the other three deposits.

Cretaceous amber deposits are now being systematically studied. There are two Lower Cretaceous amber deposits known, one from Djezziz, Lebanon, and the other from Salzburg, Austria. Upper Cretaceous deposits are more numerous, with 16 deposits in different countries—three in France, two in Canada, four in USA (Arkansas, New Jersey, two in Alaska), five in Russia, one in Spain, and the Burmese deposit, until recently assigned to the Palaeocene. Considering the amount of morphological, systematic, temporal, and biogeographical information brought out in the last ten years with the description of the dipterans in Cretaceous amber deposits (and still much is to be published), it is possible to anticipate that significant evolutionary conclusions will amount in the next few coming years. *Mycetobia*, for example, was completely unknown from the Cretaceous in the published literature until recently, but the study of Cretaceous amber fossils added one new species from New Jersey, two

from Lebanon, one from Spain, one from Russia, and one from Burma. In other words, a genus considered absent in the Cretaceous is now known to have been widespread, differentiated, and considerably diversified in the late Mesozoic.

Some additional comments shall be made on the process of accumulation of palaeontological information. Looking back we can visualise the large steps taken with the income of new sources of palaeontological data. Rohdendorf's studies of Jurassic Russian deposits corresponded to a revolution in relation to the early XXth century palaeodipterology. Even though not abundant, Triassic deposits of Australia and Virginia substantially increased our knowledge of the basal Diptera radiation. The Baltic amber dipteran fauna, yet to be more extensively studied, brought enormous light to Early Tertiary diversity, and Dominican Republic amber showed how much of the present fauna was already differentiated at the Oligocene / Miocene border. The impact brought by knowledge of Cretaceous amber dipterans, however, seems to be one of the most important ever, because of the age and the state of preservation of the specimens.

Biogeographic information

In the first years after vicariance biogeography became known into English, a rather large number of papers were published (Nelson 1973; Croizat, Nelson & Rosen 1974; Rosen 1976; Rosen 1978; Platnick & Nelson 1978; Humphries 1981, 1982, 1983; Nelson & Platnick 1981; Croizat 1982; Craw 1982, 1983; Craw & Weston 1984; Platnick & Nelson 1984). Later on, the rate of publications in biogeography was somewhat reduced. This may be due to two different causes: (1) the difficulty in finding additional reliable algorithms for biogeographical analyses, since early mathematical biogeographical methods seemed to fail as adequate tools for biogeography; and (2) the difficulty in finding reliable cladograms to support biogeographical analyses.

Albeit some problems with details of the method, congruence between the biogeographical patterns of different groups has been found for intercontinental relationships, as well as for disjunctions within major biogeographical regions. The classic work of Brundin (1966) was not a vicariance biogeography study, but some of his biogeographical patterns for the Chironomidae were shown to be congruent with the data for other groups, e.g., Rosen (1976, 1978), Platnick (1976), Brooks *et al.* (1981), Humphries (1981, 1982), Bandoni & Brooks (1987), Matile (1990), Amorim & Haenni (1992), Amorim & Tozoni (1995), Amorim & Pires (1996), etc. For a

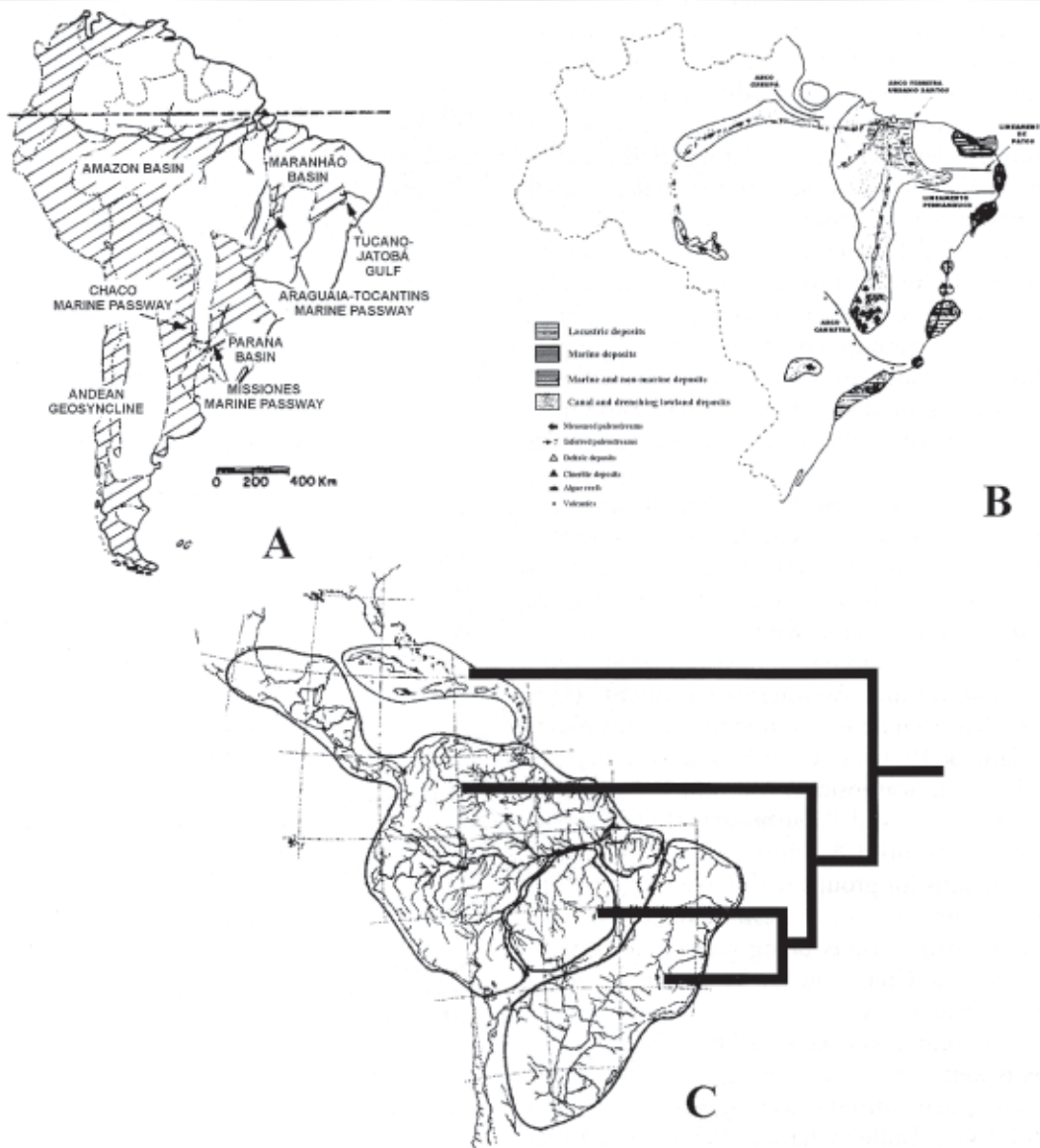


Figure 2
 Congruence between South American geological events in the Devonian (A) and Cretaceous (B) and a biological area cladogram for tropical groups of the Neotropical region (C). The area cladogram was constructed considering different groups of insects and vertebrates (see Amorim & Pires 1996; Amorim 2001). The limits of the areas and the sequence of divisions is congruent with the geological reconstruction of main events of marine transgressions during the Cretaceous. The congruence gives support to hypotheses of Mesozoic diversification of different genera and families of Diptera.

number of groups, it seems undeniable that biogeographical disjunctions between continents was caused by plate tectonics. Vicariance biogeography studies for intracontinental disjunctions are less numerous. For the Neotropical Region, studies of different groups of animals have shown congruence among biogeographical components in tropical – e.g., Sciaridae, Ditomyiidae (Diptera) (Amorim 1987; Amorim & Pires 1996), Pentatomidae (Hemiptera) (Grazia,

1997; Campos 1999), Apidae (Hymenoptera) (Camargo 1996), Callitrichidae (Primates) (Amorim & Pires 1996)– and temperate areas (Morrone 1993; Morrone *et al.* 1994). Nevertheless, modern dispersionists still resist these conclusions (see Nelson & Ladiges 2000).

The intercontinental disjunctions in Diptera are better known for more basal groups, such as Anisopodidae, Ditomyiidae, and Scatopsidae. In these

cases, not only are the intercontinental patterns considerably congruent with tectonics (see Amorim & Pires 1996, Amorim 2001), but the biogeographical area cladogram of the Neotropical subdivisions is chorologically and chronologically congruent with the Cretaceous-Tertiary geological history of the continent (figure 2). The question here is whether or not typical Gondwanan or Laurasian disjunction patterns can also be traced for higher groups of Diptera. In Diptera there are hundreds of taxa, of different ranks, that are disjunct between biogeographical regions. However, because monophyly of these taxa is questionable, this per se does not constitute evidence for or against vicariance or dispersion, so focus should be given to taxa for which there are phylogenetic studies available.

Many cases of Nearctic/Palaearctic disjunctions may well be explained by recent dispersion. The well demonstrated cases of Holarctic disjunctions associated with tectonics show Eastern North America connected to Europe, and Western North America connected to Asia, congruent to the prior connections in the Euramerica and Asiamerica continents (Cox 1974). This has been demonstrated for the Laroniinae spiders (Platnick 1976), but can be also seen, e.g., in *Scatopse* (Diptera, Scatopsidae; Amorim 1982) and in the genera *Symmerus* and *Psilosymmerus* (Ditomyiidae; Munroe 1974; Amorim & Pires 1996). When there are no cladograms for groups with Holarctic distribution, however, no assumptions can be made whatsoever about the disjunctions being generated by vicariance in the Late Cretaceous or by dispersion along the Tertiary/Quaternary.

A tectonic connection between Africa, Madagascar, and India is well known and some groups show a distribution congruent with this tectonic event. Archbold et al. (1982) and Audley-Charles (1984) argued that Southeast Asia was geologically part of Gondwanaland, which may find support in the distribution of some taxa (see Amorim & Pires 1996), but this is still in dispute. Regardless, different groups of Diptera show taxa with an Afrotropical / Oriental distribution. Among basal dipterans, this can be seen, for example, in the genera *Eogaster* (Anisopodidae) and *Mesochria* (Mycetobiidae) (Amorim & Tozoni 1995). A more extensive Gondwanan biogeographical pattern connecting the Neotropical, Afrotropical, Oriental, and Australian regions can be seen in the (*Mesochria* + *Neomesochria*) clade of the Mycetobiidae, in the (*Eogaster* + *Austrogaster* + *Olbiogaster*) clade of the Olbiogastridae, in the (*Nervijuncta* + *Calliceratomyia* + *Rhipidita*) and the (*Australosymmerus* l.s. + *Melosymmerus*) clades of the Ditomyiidae (Amorim & Tozoni 1995; Amorim & Pires 1996).

More clear evidence of disjunction caused by tec-

Table 2 – Possible cases of circumantarctic relationships based on taxon distribution, but for which there is no detailed phylogenetic analysis. Some of these cases may be false indications of ancestral circumantarctic relationships, since the taxa upon which they are based are not monophyletic. But also, numerous other cases may exist that have not been included because there is no formal taxon gathering the Australian/New Zealand to the Chilean/Argentinian representatives.

Abbreviations: AUS, Australasian Region; Aus, Australia; NZ, New Zealand; NC, New Caledonia; LH, Lord Howe; PNG, Papua/New Guinea; Indon, Indonesia; NEO, Neotropical; Arg, Argentina; SEBrazil, Southeast Brazil; Ecu, Ecuador; AFR, Afrotropical; SAfr, South Africa.

Tipulidae	<i>Leptotarsus</i>	Aus / Chile
	<i>Sribadocera</i>	PNG, Indon / Chile
	<i>Limonia</i> (<i>Zelandoglochina</i>)	NZ / Chile / Arg
	<i>Tonnoiroomyia</i>	Aus / Chile / Arg
	<i>Gynoplistia</i> (<i>Ginoplistia</i>)	NZ / Aus / NC / Indon / PNG / LH / Chile / Arg
	<i>Paralimnophila</i> (<i>Paralimnophila</i>)	NC / Aus / NZ / Chile / Arg
	<i>Amphineura</i> (<i>Amphineura</i>)	Aus / NZ / Indon / Chile
	<i>Aphrophila</i>	NZ / Chile
Culicomorpha		
Thaumaleidae	<i>Austrothaumalea</i>	Aus / NZ / Chile / Arg
Ceratopogonidae	<i>Macrurohelea</i>	Aus / Chile / Arg
Simuliidae	<i>Austrosimulium</i>	Aus / NZ / Chile / Arg
Bibionomorpha		
Bolitophiliidae	<i>Heterotricha</i>	Aus / Chile / Arg / SEBrazil / SAfr
	<i>Colonomyia</i>	Aus / Chile
Ditomyiidae	<i>Nervijuncta</i>	NZ / Chile / SEBrazil
	<i>Australosymmerus</i> +	Aus / NZ / Chile
Psychodomorpha		
Canthylloscelidae	<i>Canthylloscelis</i>	Aus / NZ
Scatopsidae	<i>Diamphidicus</i>	Aus / Chile
Perissommatidae	<i>Perissomma</i>	Aus / Chile
Blephariceridae	<i>Edwardsina</i>	Aus / Chile / Arg
	(<i>Apistomyiini</i> + <i>Paltostomatini</i>)	NEO / AFR / AUS / NZ / NC
Brachycera		
Stratiomyomorpha		
Stratiomyidae	<i>Hylorops</i>	Aus / Chile
	<i>Benhamyia</i>	NZ / Chile
	<i>Antissa</i>	Aus / Chile / SEBrazil
Tabanomorpha		
Tabanidae	<i>Scaptia</i>	Aus / Chile
	<i>Dasybasis</i>	Aus / Chile
Pelecorhynchidae	<i>Pelecorhynchus</i>	Aus / Chile
Athericidae	<i>Dasyomma</i>	Aus / Chile / Arg
Rhagionidae	<i>Austroleptis</i>	Aus / Chile / Arg
	<i>Atherinomorpha</i>	Aus / Chile / Arg / SAfr
Nemestrionoidea		
Mydidae	Diochlistinae	Aus / Chile
Nemestrinidae	<i>Trichophthalma</i>	Aus / Chile / Argentina
Empidoidea		
Empididae	<i>Ceratomerus</i>	NZ / Aus / Chile
	<i>Homalocnemis</i>	Afr / NZ / Chile
Cyclorrhapha		
Lonchopteroidea		
Acalypterae		
Sciadoceridae	(<i>Sciadocera</i> + <i>Archiphona</i>)	Aus / Chile
Ephidridae	<i>Eleleides</i>	NEO / AUS / ORI
	<i>Ephydrella</i>	NZ / Aus / Brazil
	<i>Gymnopiella</i>	AUS / AFR
	<i>Hostes</i>	AUS / AFR
Canacidae	<i>Isocanace</i>	AUS / AFR
Helcomyzidae	<i>Paractora</i>	Mcquarie I. / Chile / Arg / Malvinas I.
Teratomyzidae	<i>Teratoptera</i>	Chile / SEBrazil / Ecu / Aus / NG / Philippines / China / Nepal

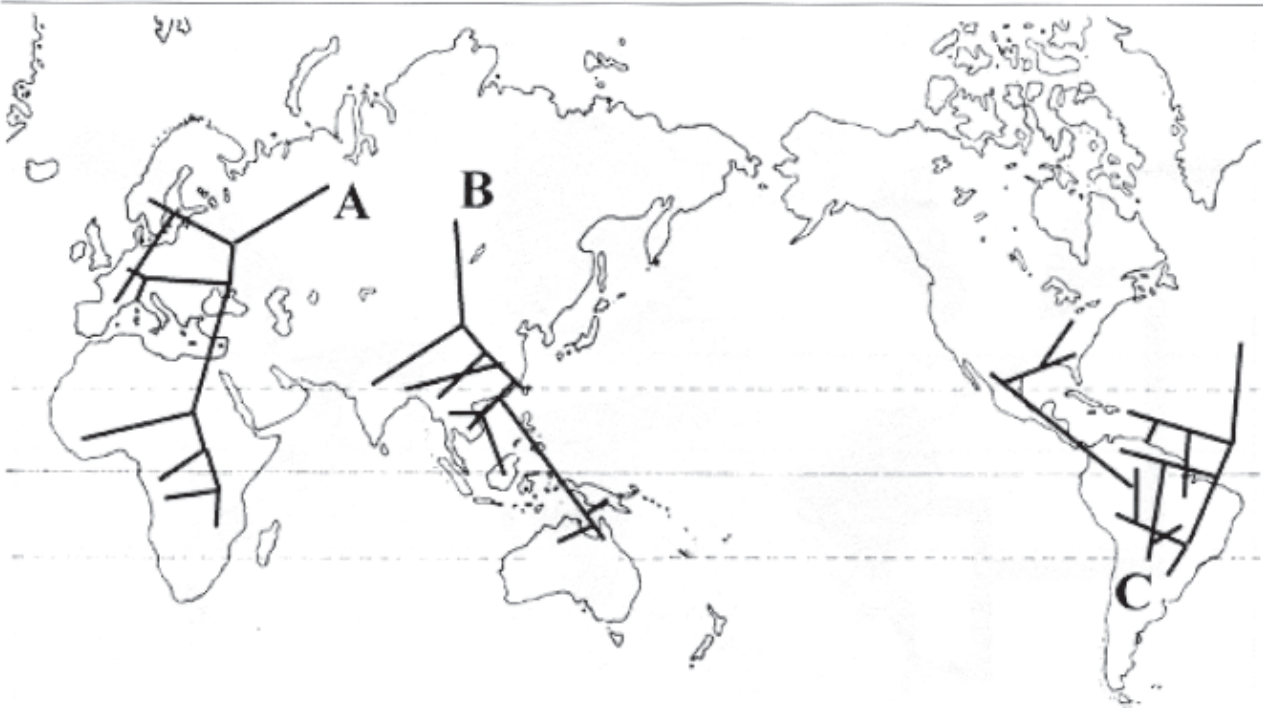


Figure 3
Typical biogeographical patterns of dispersion between continents. Connections between groups are not congruent with plate tectonics.

tonics, however, comes from taxa with circumantarctic disjunction. Darlington (1952) tried to explain these patterns on the basis of early dispersion from north to south, followed by extinction of northern representatives without leaving fossil evidence behind. Short after, Hennig (1960) tried to explain this kind of distribution by dispersion across Antarctica using his concepts of phylogenetic biogeography. Vicariance biogeography, however, has shown that detailed biogeographical congruence among different groups has an insignificant probability to occur by chance (Rosen 1978; Platnick & Nelson 1978). Consequently, circumantarctic distributions, especially considering the distances involved, are particularly important evidence of vicariance related to tectonics.

As mentioned above, the number of analyses of circumantarctic patterns in Diptera with the support of phylogenetic data is still small. Brundin (1966) has shown some cases of circumantarctic disjunction in the Chironomidae. Changes in details of Brundin's (1966) original phylogeny did not alter the biogeographic interpretation. Cranston & Naumann (1991) reconsider southern Gondwanaland palaeoenvironments and southern hemisphere biogeography. In the Scatopsidae, *Diamphidicus* shows this similar pattern (Amorim 1989). In the Canthyloscelidae, this distri-

bution is seen in *Canthyloscelis* (Hennig 1960). In the Ditomyiidae, this pattern is found in *Nervijuncta* and in the monophyletic group of genera including *Australosymmerus* (Munroe 1974; Amorim & Pires 1996). In the Bolitophilidae, *Heterotricha*, *Ohakunea*, and *Colonomyia* (Mycetophiliformia genera of doubtful position) this pattern is also present. All these cases give support to the idea of a dipteran Gondwanan fauna fragmented by tectonics.

An additional relevant case is that of genus *Brachypremna* (Tipulidae). This genus has a particularly speciose monophyletic subgroup in tropical areas of the Neotropical region, with its sister clade composed of a pair of Australian species. The next more basal clade is a Baltic amber species of the genus (Krzeminski 1996). This is especially significant. First, there is a direct connection between the Neotropical and Australian regions, which could be associated with tectonics. Second, the sister stem of the Gondwanan clade with tropical distribution is in the Baltic Eocene / Oligocene amber (Collucci 1999). That is, the Baltic amber fauna may represent at least for some groups the continuation of an earlier Cretaceous fauna of tropical environment in Laurasia, now in large scale extinct in the northern hemisphere, but largely represented in the Gondwanan continents.

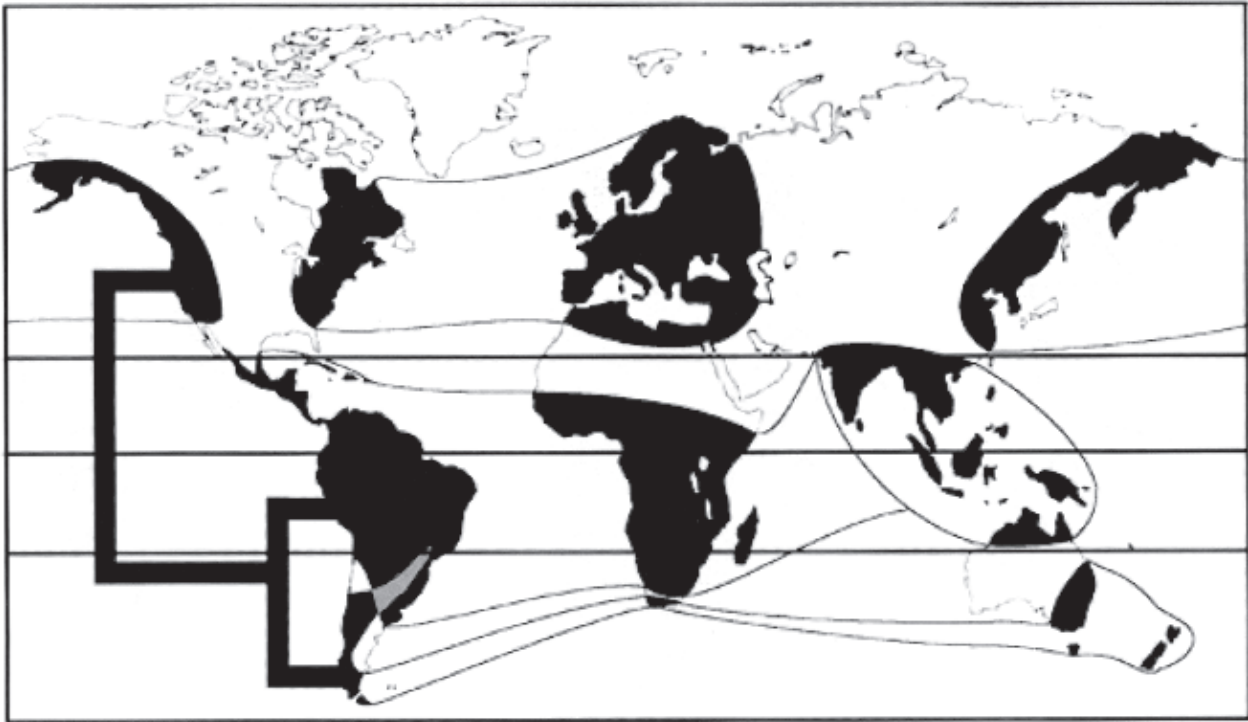


Figure 4

Typical biogeographical patterns of disjunction due to tectonics. Tropical groups in the Neotropical region (B-E) connect to Afro-Oriental (A) sister groups, while temperate Neotropical groups connect to groups in southern Africa, southeastern Australia and New Zealand. Nearctic and Palaearctic groups connect each other.

There are numerous other cases of Diptera distribution that have not been formally treated in a phylogenetic perspective, but that suggest circumantarctic relationships. Table 2 lists demonstrated and possible cases of Gondwanan components based on taxon distribution. Of particular relevance in the higher Diptera we should note the cases of the pair of sister genera (*Sciadocera* + *Archiphora*) in the Sciadoceridae, species in the Teratomyzidae genus *Teratoptera*, and species of *Dryomyza* (Dryomyzidae). The implications of these cases will be discussed below.

The biogeographic pattern of cases of intercontinental dispersion are quite easy to recognize. Either with one or more cases of continental invasion, the set of descendants of the original invader ancestor would be a member of a group at least partially diversified in the "center of origin", that is, the continent from which the ancestor came. The expected biogeographical pattern in cases of intercontinental disjunction due to dispersion (fig. 3) is different from the patterns resulting from tectonics (fig. 4).

Methodological Constraints

1. Paraphyletic taxa and deficient phylogenetic knowledge

Born under an essentialistic paradigm in the XVIIIth

century, formal taxonomy moved on to an evolutionary perspective only more than a century later, and to a phylogenetic perspective two centuries later. Even after the origin of the phylogenetic method (Hennig 1950), quite a lot of taxonomy still used a non-phylogenetic praxis. Taking together the number of essentialistic taxa and the intrinsic difficulties of phylogenetic reconstructions, we can have a glimpse of the problem of drawing conclusions directly from formal classifications.

Diptera is most certainly the group that has been more extensively studied under a phylogenetic perspective among all groups of organisms. Dipteran families may be reasonably accepted as monophyletic, but the same cannot be said about subfamilies, tribes, and genera.

The situation of fossil taxa is even more critical. The number of genera and families proposed before the development (or without the use) of a phylogenetic method is quite high. Most of these groups have never been revised. Also, taxonomic concepts and practices in traditional palaeontology – which add to difficulties of working with fossils – conflict with the idea of a phylogenetic background in classification. Thus, inferences depending on the monophyly of fossil taxa in classifications should be made very carefully.

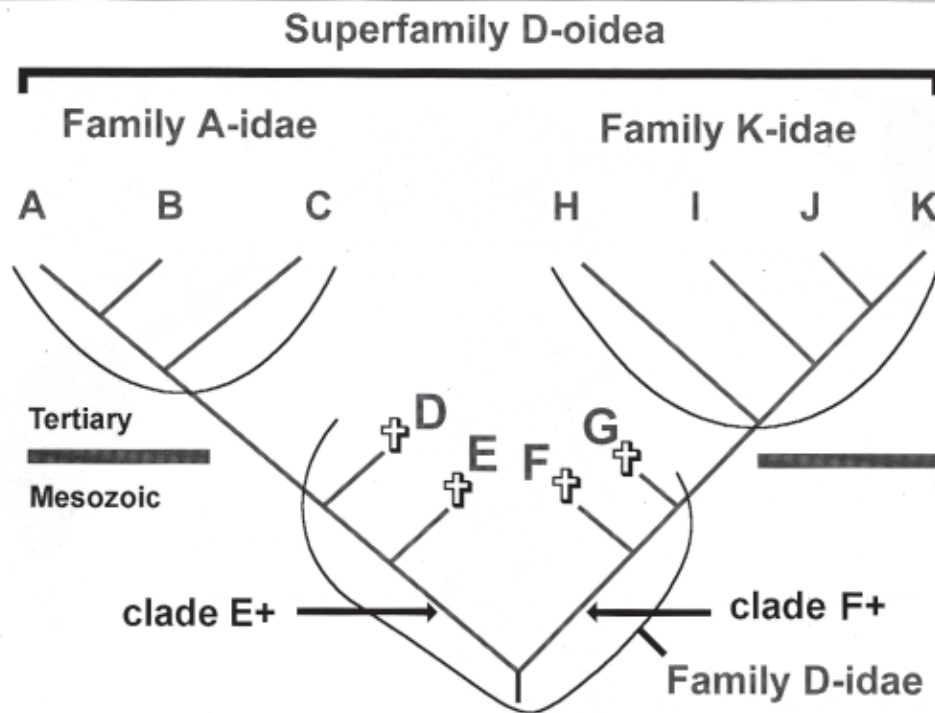


Figure 5

Paraphyletic taxa hide evolutionary information. A hypothetical example of a non-phylogenetic classification affecting the understanding of the evolution of groups with fossil and recent representatives. Two recent taxa are given family level, separated from a paraphyletic family gathering Mesozoic extinct genera. D and E are actually related to family A-idae, while F and G are related to family K-idae. There is a false idea that families A-idae and K-idae are Tertiary, while the Mesozoic family would be extinct. Actually, both families descend from clades originated in the Mesozoic, and only clades of generic level have undergone extinction.

The problem with non-monophyletic taxa are manifold. Paraphyletic taxa may be useful for nomenclatural purposes, if useful at all. However, from an evolutionary perspective, they put together taxa that are not most closely related and separate closely related groups. Figure 5 is a hypothetical example. In an essentialistic classification, superfamily D-oidea is assumed to have three families, one extinct and two extant; families A-idae and K-idae would appear not to have originated before the Tertiary, while family D-idae would be considered to have originated and undergone extinction in the Mesozoic. These are false evolutionary inferences. The closest clade to A-idae is genus D and K-idae is the closest clade to genus G, but both these genera belong to "D-idae", i.e., no phylogenetic connection including D or G whatsoever could exclude either A-idae or K-idae. In other words, there is no historical or evolutionary entity of itself that could be referred to as "D-idae".

Temporal inferences from this classification would be equally false. D-idae is not a Mesozoic taxon (especially because there is no historical entity like D-idae

in nature), and A-idae and K-idae are not Tertiary taxa. In fact, the Mesozoic taxa in this example are D-oidea, genera D, E, F, and G, and clades C⁺ (=A-idae) and H⁺ (=K-idae). D-oidea has only two main clades –E⁺ (which includes A-idae) and F⁺ (which includes K-idae), both originating back into the Mesozoic.

A good example of the distortions of a system including fossils which is non-phylogenetic and separated from the recent classification can be seen in the Sciaroidea (Bibionomorpha). Almost 60 genera of 11 "extinct" families have been described from the Jurassic and Cretaceous (see Table 1): Pleciofungivoridae, Archizelmiridae, Antefungivoridae, Tipulopleciidae, Protoligoneuridae, Palaeopleciidae, Protopleciidae, Protobibionidae, Parapleciidae, Mesosciophilidae, and Paraxymyiidae. Of these families, only Protopleciidae and Mesosciophilidae can be argued as monophyletic, but of questionable position in relation to the recent families. Of the other nine families, six are monotypic and the other three gather genera on the basis of plesiomorphy. On the other hand, the list of fossils from the Mesozoic included in

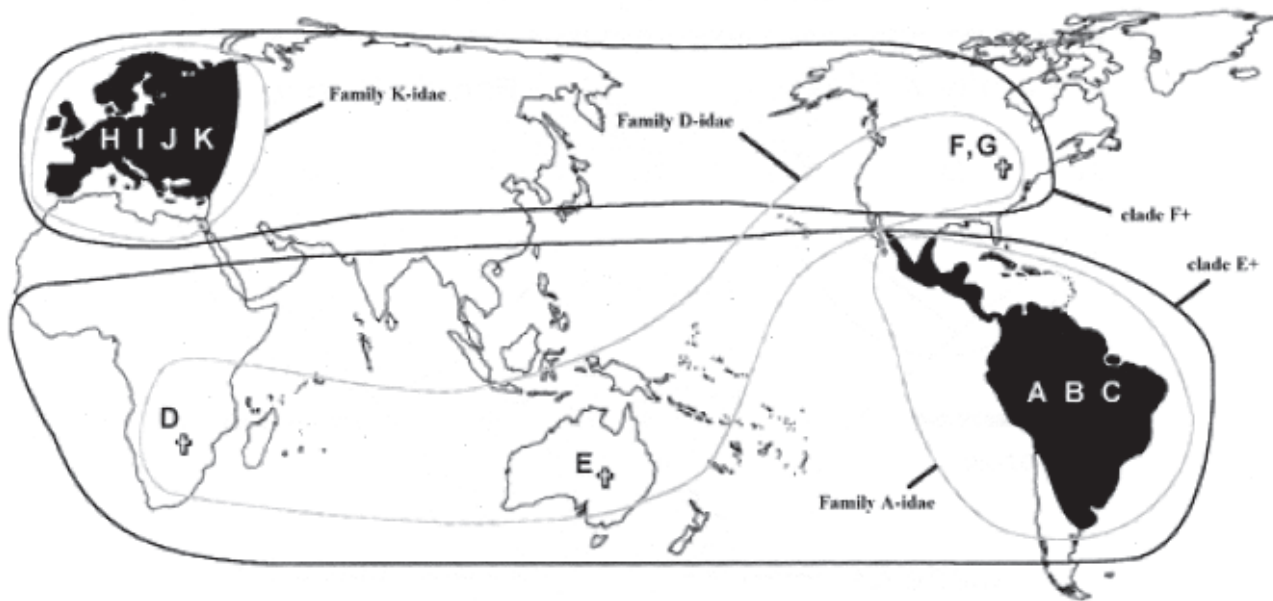


Figure 6

Paraphyletic taxa hide biogeographic information. Same example of Figure 5, from a biogeographical point of view. The paraphyletic family D-idae gives the impression of an ancient group with an odd ancient distribution, from which recent taxa have originated by dispersion. Actually, the distribution of both larger clades, (E+D+A-idae) and (F+G+H-idae), is congruent with plate tectonics.

the group includes only five extinct and two recent genera that have been assigned to four of the eight recent families of the Sciaroidea. This picture gives an impression of an "early, extinct" fauna of Sciaroidea, replaced by a "more recent, Tertiary diversification of the group". This is an artifact resulting from an artificial classification. Most of the Mesozoic "extinct families" correspond to basal members of recent families of Sciaroidea. So there was probably no intense Mesozoic family extinction in this group, nor an intense Tertiary family and generic diversification.

From a biogeographical point of view distortions are no less important. Consider in figure 6 the distributions of the taxa in the example of figure 5. A-idae is Neotropical, K-idae is Palaearctic, and "D-idae" has representatives in Africa, Australia, and North America. From a classification without phylogenetic basis, this would be considered a case of Tertiary invasion of subgroups of this "D-idae" ancestor to new continents after Gondwanaland was already separated from Laurasia. However, considering the phylogenetic relationships in the group, it is actually a very obvious case of tectonic disjunction of a Pangaeic ancestor (fig. 6).

The conclusion is that paraphyletic taxa are not only useless for evolutionary analyses, but they also induce false inferences. Because taxa in traditional classifications do not come with labels saying whether

or not they are monophyletic, we have to be especially careful about inferences based on taxa of doubtful monophyly.

Also, the lack of phylogenetic knowledge has direct and indirect effects on evolutionary interpretations. From a biogeographical perspective, there is a loss of biogeographic information with unresolved phylogenies. Figure 7 shows the loss of biogeographical information for intercontinental relationships when a detailed phylogeny is reduced to a list of included taxa. The phylogenetic relationships among the groups of genera would allow the recovery of the full biogeographic history of the group.

Lack of phylogenetic knowledge also interferes with assumptions about the age of a group, independently of biogeographical reconstructions. Incompleteness of fossil specimens and insufficient phylogenetic reconstruction (when present at all) strongly tend to displace fossil taxa to higher levels of generality, where they are referred to as *incertae sedis*. Displacement of fossil positions to the base result in parallel displacement of age information, so the higher clades are not recognized at their true, older age (fig. 8).

The Triassic Queensland fossil *Crosaphis* is a good example here. Originally described as a homopteran, it was moved by Kovalev (1983) to a family of its own in the Diptera, supposed to be close to the Anisopodidae

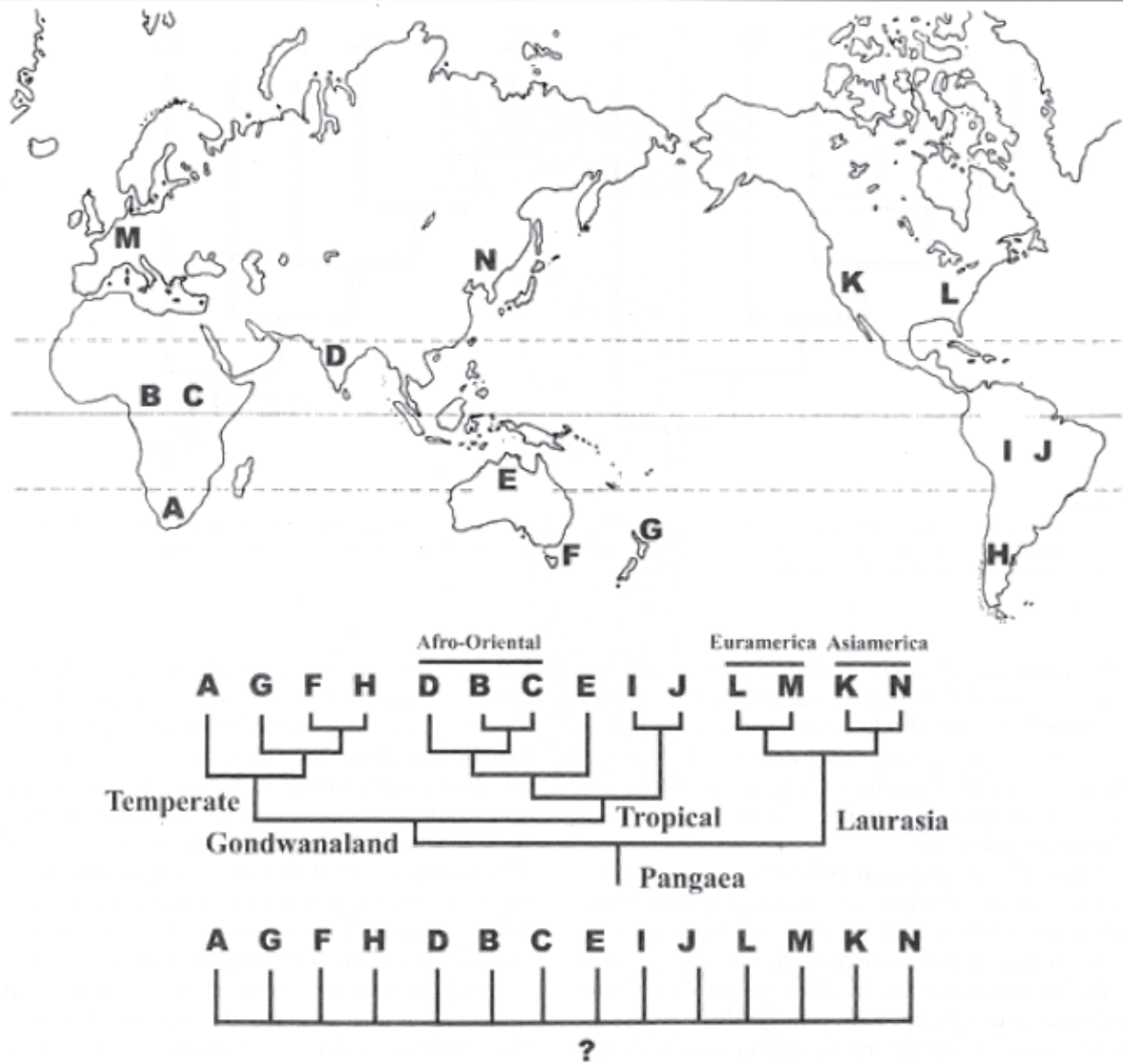


Figure 7
Absence of phylogenetic reconstructions hides biogeographic information. If the phylogenetic relationships among the genera spread in the world was known, congruence with plate tectonics would be recognized.

l.s. This indicates a Triassic origin for the Anisopodoidea, that would be in accordance with the age of Vimrhyphidae (Scherbakov *et al.* 1995), a basal clade of the group. However, Amorim & Tozoni (1995) showed that *Crosaphis* would fit high up in the phylogeny of the Anisopodoidea, as the sister group of the (*Mycetobia* + *Mesochria* + *Neomesochria*) clade. Consequently, the minimum age attributed to the Mycetobiidae, Eocene/Oligocene, based on Baltic amber fossils, is automatically moved to the Triassic, indicated by its sister group Crosaphididae.

2. Minimum age for clades given by the fossil record

The next question is, how much can we trust the fossil record as an indicator of age of origin of clades? If we look back 50 years, it becomes very clear how the fossil record-based picture of the age of groups has changed. It is well known that fossils indicate only minimum ages of taxa. The fact that a member of a clade is known to occur in a certain deposit indicates that the clade already existed at that time, but does not deny it existed before. Nevertheless, as per tradition, fossils have been extensively used as a source of infe-

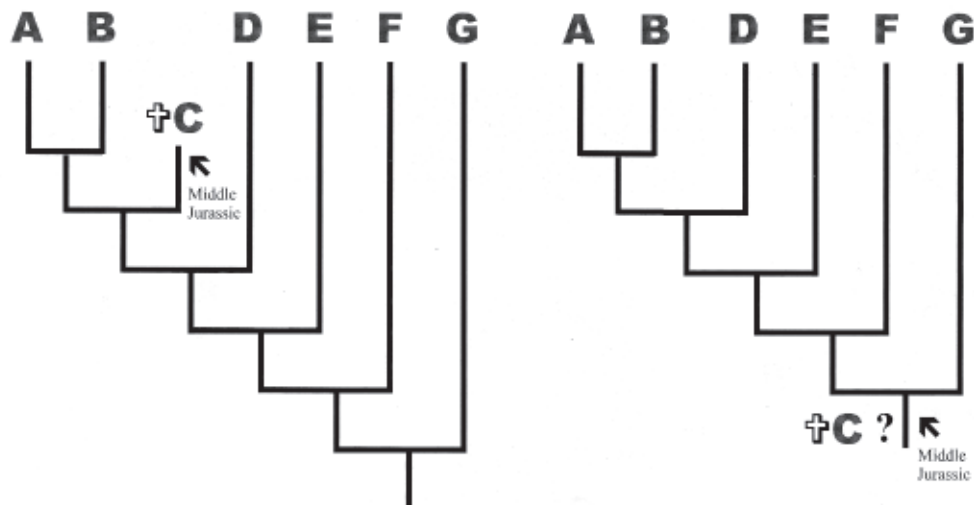


Figure 8

Absence of precise phylogenetic information on fossils generates the false hypotheses of young age of taxa. If the precise position of the extinct Middle Jurassic genus C was known, the age of the stem (A + B) would be correctly understood as Middle Jurassic. If genus C is considered *incertae sedis* at the base of the group, Middle Jurassic would be shifted to the base of the group.

rence about age of origin of clades, even to calibrate molecular clocks! Assumed age of large groups of organisms has only slowly moved back to the past as new fossil deposits have been discovered. Some of these new fossil findings have a huge impact because of previous conservative assumptions about the evolution of animals and plants.

From a biogeographical point of view, the result is that the “center of origin” of certain groups have “travelled around the world”, as older and older fossils of these groups have been discovered. For a long period in the last two centuries, the oldest fossils of vertebrate and invertebrate groups were younger than the separation between the continents, so present worldwide distributions of these groups have been insistently proposed to have occurred by dispersion over fixed continents.

León Croizat’s conclusions (e.g., Croizat 1964) for the origin of a number of taxa based on a vicariant method pointed to a much older age than previous inferences based on the fossil record. This was probably one of the main reasons causing George G. Simpson and Philip J. Darlington Jr. to strongly ignore Croizat’s concepts, methods and, especially, his reconstructions. The resistance to vicariant biogeography reconstructions still persists, as shown by Nelson & Ladiges (2000).

The general picture given by the traditional perspective is that “some groups” (like Diptera itself and a few of its basal clades) are indeed old (i.e., Pangaean),

but “present diversity” evolved more recently, in the Tertiary. However, the growth of our palaeontological knowledge and the correction of the Diptera system based on phylogenetic studies (see previous section) has shown more and more “recent” groups to be present in the Cretaceous, and that many groups probably were already differentiated in the Triassic/Jurassic. This change in our evolutionary view of Diptera illustrates the general problem of developing assumptions using negative fossil evidence. We shall obviously avoid the problems of making statements for which we do not have evidence. However, the point here is that quite a lot of inferences have been proposed accepting that negative evidence as evidence of absence. The result is that we are always surprised by the shift of the origin of taxonomic groups further into the past.

A final point to be considered here is that the closer we are from the origin of a group, the less will be the diversity in that group (and possibly lesser taxonomic dominance of the group in the environment). At the extreme there is a single species (the ancestral species itself) representing the clade. This means that close to the time of origin of a group, the probability of finding fossil specimens of the group will be correspondingly lower, i.e., the total number of fossilised specimens of the stem group of a clade is certainly smaller than when there is already some diversification. Also, the species may not even present the full set of synapomorphies that characterise the clade, so additional problems of misidentification may apply. The

chance of sampling the true origin of any clade is low and this must be taken into account when preparing evolutionary reconstructions.

The nature of vicariant biogeographical evidence, on the other hand, points to the time of the very origin of clades. Consequently it is highly unlikely to find fossil evidence that strictly supports biogeographical evidence.

3. Fossil deposit bias

The number of Mesozoic fossil deposits (old enough to be relevant in a discussion of the evolution of the major clades of Diptera) is still quite low. The limited number of deposits corresponds itself to a sampling limitation of the early Diptera fauna. However, additional problems apply. First, a considerable part of the Jurassic compression deposits are restricted to Russia. Chinese Jurassic dipteran fossils which were reported recently in the literature have brought new insight to Jurassic Diptera diversity. From Gondwanan terranes, however, there are no Jurassic deposits and there are only four known Cretaceous deposits. This means that there is a huge predominance of Laurasian fossils in our present view of the evolution of basal Diptera.

Moreover, Mesozoic amber deposits come from conifer resin, which indirectly means a particular kind of environment. Hence, Cretaceous amber samples a fauna from a particular kind of biogeographic domain. It is not easy to foresee the implications of this fact. It is possible that in some degree these environments may correspond to temperate areas or areas with temperate climate, so tropical Cretaceous dipteran faunas will probably not be sampled in amber. This may explain why there are representatives of a single subfamily of Ceratopogonidae (Leptoconopinae; Borkent 1996) and of Scatopsidae (Ectaeiinae; unpublished data) in Cretaceous amber from all sources.

This kind of sampling problem may be seen by comparing the Baltic amber fauna with the recent Palaearctic fauna. Baltic amber diversity seems to be to a certain extent more similar to the fauna of recent warmer areas than to the recent temperate fauna. This also applies, e.g., to the Quilchena Early Eocene fossil deposits in Canada (Archibald & Mathewes 2000). Additions to the Mesozoic Diptera knowledge, by the Santana Formation (see Grimaldi 1990; Mazzarolo & Amorim 2000) also gives a measurement of the possible deviation.

The conclusion is that deposits and modes of fossilisation represent themselves a bias, in terms of a restricted sample of available diversity in the world at that time. This restriction applies to geographical areas, but also to kinds of environment and even kinds of bio-

logy. Our reconstruction should also take this into account.

Significance of the data available for the reconstruction of Diptera evolution

While assessing the age of Diptera groups, palaeontology and biogeography correspond to two sources of evidence with incongruent results –this is a rule for any group. We dealt above with the different reasons that make palaeontological estimations more conservative than biogeographical estimations. Fossil deposit discovery and the description of discovered material occur slowly. Moreover merely giving names to fossil taxa is not quite a contribution to understanding evolution. Not only good descriptions are fundamental, but a precise association of the fossils to the biological system as a whole is indispensable, so as to give names evolutionary meaning. Vicariant biogeographical methods, on the other hand, show where intercontinental congruent patterns are best interpreted by vicariance due to tectonics. The age of origin of groups proposed based on this kind of reconstruction is much older than that indicated by palaeontological evidence. Data available about the evolution of Diptera unfortunately is not enough to answer most of the questions posed here. Some of the known cases of biogeographical patterns congruent with Pangaea geology include Mesozoic fossils, so they do not constitute conflicting sources of evidence about the evolution of groups –e.g., Scatopsoidea (Amorim 1982, 2000), Anisopodoidea (Amorim & Tozoni 1996) and Mycetophiloidea (Matile 1990).

The more complicated cases, however, are those at the “apex” of the phylogeny of different large dipteran clades. This does not concern only the so-called higher Diptera, but actually all major lineages supposed to be Pangaeic. How advanced was the evolution of the Tipulomorpha in Pangaea? How advanced was the evolution of the Psychodomorpha in Pangaea? How advanced was the evolution of the Asiloidea in Pangaea? And the more difficult question, how advanced was the evolution of the Schizophora in Pangaea?

The number of taxa known from the Triassic fossil record is still limited. A number of basal Diptera and even basal Brachycera are known from the Lower Jurassic. The Empidoidea are known to be differentiated in some clades by Middle Jurassic, so this would be indirect support for a Pangaeic origin of the Cyclorrhapha because of their sister group relationship. There are some genera from the Upper Jurassic assigned to the Platypezidae, so it would not be too far from the division of Pangaea to say that the fossil record would support its Pangaeic origin.

Cretaceous fossils are more abundant and include the Lonchoceridae, Ironomyiidae, Sciadoceridae, Phoridae, Syrphidae, and a few undetermined Schizophora, but the latter three are known only from the Upper Cretaceous. The identification of an acalyptrate from the Lower Cretaceous of Australia (Jell & Duncan 1986, figs. 49G,H, 50E,F) is still to be confirmed.

This means that the fossil record is insufficient to support an origin of Acalyptratae families before the division of Pangaea. Biogeography, on the other hand, shows some cases that are quite congruent with other patterns related to tectonics, particularly the distribution of Helcomyzidae and Teratomyzidae. This conflict is shown in figure 1, which has two lines, corresponding to alternative hypotheses of the time of division of Pangaea in the phylogeny of the Diptera. The lower line is a palaeontological-based hypothesis and cuts the phylogeny of the Diptera more to the base. The evolution of Diptera in Pangaea, in this case, would have not advanced too much. The upper line is a biogeographical-based hypothesis and cuts the phylogeny of the Diptera more to the apex, and most families would have already differentiated. The true line may also be somewhere in-between.

This is still an open field. Phylogenetic studies of acalyptrate families may show in the future a number of undetected cases of intercontinental disjunction associated with tectonics or, on the contrary, that these few cases are taxonomic artifacts and the correct relationships of the groups will dismiss vicariance as the cause of disjunction. If we consider that the methodological constraints all artificially push actual age of the clades towards the present, it is possible that schizophoran families arose back in the age of Pangaea.

The purpose of this paper is not to prove or dismiss either hypotheses. Besides considering a number of methodological questions, it intends to show that the answer to the question posed here is relevant in terms of understanding Diptera evolution. If the early diversification of the Acalyptratae occurred before the separation between Laurasia and Gondwanaland, most of its genera would have slowly evolved in the environments where they occur now. If Acalyptratae diversification took place more recently, after the continents were already separated, then the worldwide distribution of families and even genera would be due to a huge process of dispersion in the terms posed by ear-

lier biogeographers. The Schizophora would be either Laurasian or Gondwanan and families and genera would have adapted to the new environments after dispersion to the new continents.

Diptera evolution in Pangaea developed only to a certain extent, so some level of intercontinental dispersion is necessary to explain present worldwide distribution patterns of higher dipteran clades. The question is which of the faunal elements in each continent were there since continents were connected, and which arrived afterwards. Note that the same problem applies to other groups of animals and plants. In early times of paleontology and biogeography, every recent group was supposed to have invaded southern continents coming from northern centers of origin (see Croizat, Nelson & Rosen 1974). There is a debate about which mammal clades were differentiated in the Lower Jurassic, so it should be possible to recognise also ancient and recent groups of mammals in each continent. Possibly, the presence of armadillos in Texas, for example, as well as large cats in South America, are due to dispersion; marsupials in Australia are accepted as ancient; but monkey disjunction being due to vicariance or dispersion remains disputed.

A discussion of the subject in the future, however, should focus on the proper use of the data available. The use of phylogenetic tools to analyze the amount of new Mesozoic amber and compression fossils available is indispensable. And to draw conclusions from well made biogeographic analyses, even if without fossil support, is also desirable. The cases of inferences on basal groups of Diptera based on biogeographic analyses that later found good evidence in the fossil record should strongly encourage this approach and resulting conclusions.

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