Africa and its Ephemeroptera: Remarks from a biogeographical view

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Abstract

The author looks at the African continent from a biogeographical as well as from a geological perspective. In biogeographical respects, the African continent today is divided into two parts: south of the Sahara we find a fauna realm of its own kind, the Afrotropic, whereas Mediterranean North Africa has to be considered a part of the Palaearctic and thus the Holarctic.

In former time Africa was a part of Gondwanaland. Before the Gondwana breakoff at the turn between the Jura and the Cretaceous period, i.e. approximately 150 to 100 million years ago what is now West Africa and South Africa formed one land mass. For example, the Niger River formed the upper reaches of the Amazon River while the Amazon River still drained into the Pacific Ocean. The distribution of certain freshwater taxa, for instance of some fish families, seems to reflect the formerly close connection between Africa and South America. Africa has also a close relationship to Madagascar and India, which is also a reflection of the earth's geological history. The author is looking for parallels with the Ephemeroptera respectively tries to characterise the composition of the African Ephemeroptera fauna.

Keywords: Ephemeroptera, biogeography, Africa.

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The African Ephemeroptera fauna reflects the geographic history of this continent. This paper attempts to review the past 150 million years, considering the changing positions of the continents. The continental drift theory (Wegener, 1915), although originally denied, is now a widely accepted concept. It is in the light of this theory that the current distribution of the African mayfly fauna is considered. The changes over time of the continental landmasses can be viewed on the following website: http://www.odsn.de/odsn/services/paleomap/paleomap.html

150 Ma (Fig. 1) the continental plates were still mostly connected, and formed only two supercontinents: Laurasia and Gondwana. South America and Africa were in such a position that the rivers Niger and Amazon still formed a uniform river system (Grabert, 1991). This original river used to flood into the Pacific in the area of today's Ecuador. This was possible, since the Andes had not been folded up to mountains at this time. Then the supercontinents broke. The single continental plates drifted apart, and with and on them their fauna and flora.

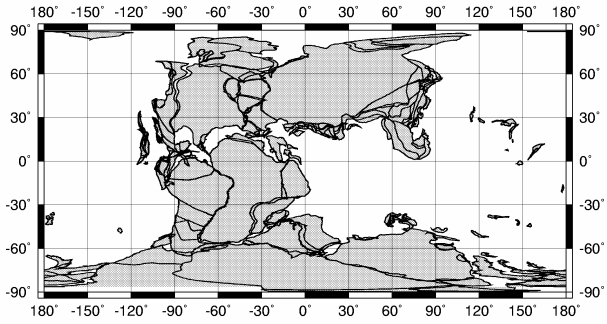
100 Ma (Fig. 2) the Gondwana broke apart, later Laurasia. The Australian plate separated before the placental mammals and true freshwater fish taxa had evolved with the consequence that in Australia autochthone freshwater fish are missing.

South America and Africa separated later, referring to the freshwater fish it means that the families Characidae and Cichlidae show a Neotropic-Afrotropical area disjunction. It is to consider whether a similar disjunction exists in the Ephemeroptera.

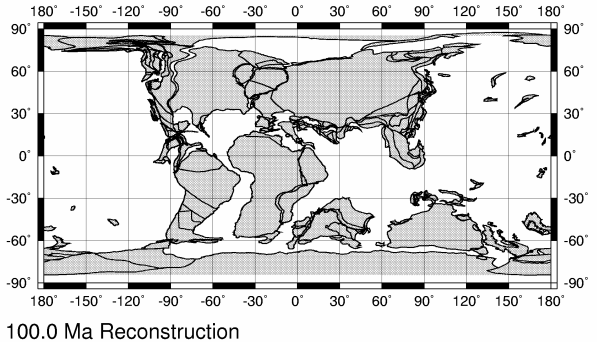
At this time Laurasia was still mostly connected. That explains the circumboreal distribution of many taxa, even at the genus and species level.

The position of the continental plates 50 Ma (Fig. 3) allows a better view of today's fauna realms than their present position does. The Oriental plate for example had not hit the Palaearctic Asia at this time. Like a huge Noah's Arc it carried with it a terrestrial and freshwater fauna, which -from its origins- shows very close connections to Africa and Madagascar.

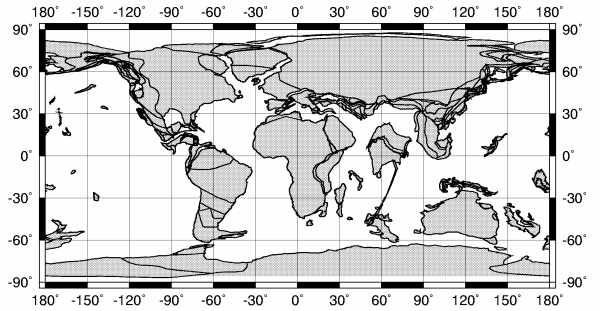
This also applies to the Ephemeroptera (Edmunds, 1979). Peters (1980a, 1997) linked the distribution of the Leptophlebiidae to the ancient Gondwanian land mass. Recently Sartori *et al.* (2000) have considered this by taking a closer look at the Madagascan Ephemeroptera.



150.0 Ma Reconstruction
Fig. 1



100.0 Ma Reconstruction
Fig. 2



50.0 Ma Reconstruction
Fig. 3

Based on these concepts, this paper attempts to give an overview of the biogeography of the African mayfly fauna. Much of the taxonomy is based on Hubbard's world catalogue (1990) without consideration of the Pannota classification by McCafferty and Wang (2000).

Still the knowledge concerning Africa's Ephemeroptera is not yet complete. The only and latest complete work on the families genera and species has been written by Demoulin (1970) over thirty years ago.

The fundamental research about the African mayflies have done Lestage (1919), Barnard (1932), Kimmins (1956 ff), Agnew (1961 ff), and in particular Gillies (1954 up to 1999). In the last decade the number of papers about newly established genera of the Baetidae has rapidly increased, especially by Lugo-Ortiz and McCafferty (1996 ff) and Waltz and McCafferty (1987 ff). This shows that there is a lot of more detailed research to be done. On the family level the composition of Africa's mayflies should be completed:

In Table 1 the 23 orbis terrarum known families with 31 subfamilies are listed. Concerning their assumed origin and also recent distribution they are assigned to the two supercontinents Gondwana and Laurasia. As expected the true Laurasian families do not occur in Africa (as Ametropodidae, Arthropleidae, Behningiidae, Neoephemeridae). It strikes that the number of the Gondwanian families is not as high as one could expect in accordance with earth history. Since Africa represents the central plate of the Gondwanaland and has not changed its equatorial position as much as the other big fragments. Still i.e. the Ameletopsidae, Oniscigastridae, Coloburiscinae, Euthyplociinae, Melanemerellinae and Leptohyphidae are missing.

Africa accommodates 12 families with 14 subfamilies, where the Gondwanian element predominates clearly. Remarkable is the absence of the Palingeniidae, because their closest occurrence is already in Asia minor (genus *Palingenia)* and Madagascar (genus *Cheirogenesia*).

Nowadays Africa is zoogeographically divided in two: the Mediterranean North belongs to the Palaearctic, whereas the part South of the Sahara forms a different fauna realm, the Afrotropic, including the Southern part of the Arabian peninsula, Madagascar, the Seychelles and the Mascarene.

The Palaearctic Africa (Table 2) has a clearly Laurasian mayfly fauna., since it differs hardly from the Southern European one on the family, genus and partly species level; it is only not as rich. Afrotropical elements hardly occur. For the freshwater fauna, and thus the Ephemeroptera , the Sahara should be an insuperable barrier. But the Nile River is flowing from the Afrotropic to the Palaearctic Mediterranean, what should have caused passive drift, respectively active drift compensation by its inhabitants. Still no noticeable faunal interchange has happened.

In contrast to the northern part the African mayflies South of the Sahara consist mainly of taxa of Gondwanian origin (Table 3). Mostly the supraspecies groups follow Kluge (www). Moreover the tropical Africa shows an extremely independent mayfly fauna with an endemic taxa rate of 50 % on genus level.

Table 1 - Families of Ephemeroptera *orbis terrarum*

	occurrence in Africa: yes/no	origin / geographical distribution: Hol = Holarctic Nea = Nearctic Pal = Palaearctic Af = Africa, As = Asien, Aus = Australia E = Europe Mad = Madagascar NA = North America, NZ = New Zealand SA = South America (CA = Central America only)	
Ameletopsidae			
Ameletopsinae	no	Gondwana (SA, Aus, NZ)	
Chiloporterinae	no	Gondwana (SA)	
Ametropodidae	no		Laurasia (Hol)
Baetidae	yes	Gondwana	Laurasia
Siphlaenigmatidae	no	Gondwana (NZ)	
Oniscigastridae	no	Gondwana (SA, NZ)	
Siphlonuridae			
Acanthametropodinae	no		Laurasia (Hol)
Metretopodinae	no		Laurasia (Hol)
Rallidentinae	no	Gondwana (NZ)	
Siphlonurinae	no	Gondwana (3 genera)	Laurasia (6 genera)
Oligoneuriidae			
Chromarcyinae	no	Gondwana (As)	
Coloburiscinae	no	Gondwana (SA, Aus, NZ)	
Isonychiinae	no		Laurasia
Oligoneuriinae	yes	Gondwana (7 genera)	Laurasia (4 genera)
Arthropleidae	no		Laurasia (Hol)
Heptageniidae			
Anepeorinae	no		Laurasia (NeA, As)
Heptageniinae	yes	Gondwana (5 genera)	Laurasia (29 genera)
Leptophlebiidae			
Atalophlebiinae	yes	Gondwana (96 genera)	Laurasia (5 genera)
Leptophlebiinae	yes		Laurasia
Behningiidae	no		Laurasia
Ephemeridae			
Ephemerinae	yes	Gondwana (4 genera)	Laurasia (4 genera)
Ichthyobothinae	no	Gondwana (NZ)	
Palingeniidae			
Palingeniinae	no	Gondwana (Mad, As)	Laurasia (Pal)
Pentageniinae	no		Laurasia (Nea)
Polymitarcyidae			
Polymitarcyinae	yes	Gondwana	Laurasia (Hol)
Campsurinae	no	Gondwana (SA)	Laurasia (Nea)
Asthenopodinae	yes	Gondwana (Af, SA, As)	
Euthyplociinae	no	Gondwana (Mad, SA, As)	
Exeuthyplociinae	yes	Gondwana (Af)	
Potamanthidae	yes	Gondwana	Laurasia (mostly Pal)
Ephemerellidae			
Ephemerellinae	yes		Laurasia (Hol)
Melanemerellinae	no	Gondwana (SA)	
Teloganodidae			
Austremerellinae	no	Gondwana (As, Aus)	
Teloganodinae	yes	Gondwana (Af, As)	
Leptohyphidae	no	Gondwana (SA)	
Tricorythidae			
Dicercomyzinae	yes	Gondwana (Af)	
Ephemerythinae	yes	Gondwana (Af)	
Machadorythinae	yes	Gondwana (Af, SA)	
Tricorythinae	yes	Gondwana (Af, Mad, As)	
Neoephemeridae	no		Laurasia (Hol)
Caenidae	yes	Gondwana (13 genera)	Laurasia (4 genera)
Baetiscidae	no		Laurasia (Nea)
Prosopistomatidae	yes	Gondwana (Af, Mad, As, Aus)	Laurasia (Pal)

Table 2 - Ephemeroptera families and genera in the Palaearctic Africa

Baetidae:	*Acentrella* BENGTSSON, 1912		
	Afroptilum GILLIES, 1990		(Afrotrop. element)
	Baetis LEACH, 1815		
		subgen. *Baetis* LEACH, 1815	
		alpinus gr.	
		pavidus gr.	
		rhodani gr.	
		subgen. *Labiobaetis* NOVIKOVA & KLUGE, 1987	
		(incl. *Cymulabaetis* McCAFFERTY & WALTZ, 1995)	
		atrebatinus gr.	
		subgen. *Nigrobaetis* KAZLAUSKAS, 1987	
		(incl. *Alainites* WALTZ & McCAFFERTY, 1994)	
		gracilis gr.	
		muticus gr.	
		niger gr.	
	Centroptilum EATON, 1869		
	Cheleocloeon WUILLOT & GILLIES, 1993		(Afrotrop. Element)
	Cloeon LEACH, 1815		
	Procloeon BENGTSSON, 1915		
Leptophlebiidae:			
	Atalophlebiinae:		
	Choroterpes EATON, 1881		
		subgen. *Choroterpes* EATON, 1881	
		Euthraulus BARNARD, 1932	
	Leptophlebiinae:		
	Habrophlebia EATON, 1881		
	Paraleptophlebia LESTAGE, 1917		
Heptageniidae:	*Ecdyonurus* EATON, 1868		
	aurantiacus gr.		
	Rhithrogena EATON, 1881		
	germanica gr.		
	Thalerosphyrus EATON, 1881		(Afrotrop. element)
Oligoneuriidae:	*Oligoneuriella* ULMER, 1924		
	Oligoneuriopsis CRASS, 1947		(Afrotrop. element)
Polymitarcyidae:	*Ephoron* WILLIAMSON, 1802		
Ephemeridae:	*Ephemera* LINNAEUS, 1758		
Potamanthidae:	*Potamanthus* PICTET, 1843		
Ephemerellidae:	*Serratella* EDMUNDS, 1959		
Caenidae:	*Brachycercus* CURTIS, 1834		
	Caenis STEPHENS, 1835		
	luctuosa gr.		
	pusilla gr.		
Prosopistomatidae:	*Prosopistoma* LATREILLE, 1833		

Remarkable is the high generic diversity of the Baetidae and the Caenidae in the Afrotropic. In contrast there are comparatively few genera of the Heptageniidae and especially of the Gondwanian Atalophlebiinae.

Especially characteristic for the Afrotropical part of the continent are the following endemic subfamilies: The Exeuthyplociinae with its genera *Afroplocia* and *Exeuthyplocia,* the Dicercomyzinae with its genus *Dicercomyzon* and the Ephemerythinae with its genus *Ephemerythus.*

Another distinctive feature of the Tricorythidae reflects the common history of the Niger and Amazon River: The Machadorythinae are showing a classical Ethiopian-Neotropical area disjunction with the Ethiopian genus *Machadorythus* Demoulin, 1959, and its Neotropical pendant *Coryphorus* Peters, 1981. It seems to be probably the only Ethiopian-Neotropical one among the mayflies.

While there are clear results on family level, number and definition of the Afrotropical mayfly genera will still be subject to modification. Also on species level the knowledge is incomplete. The same goes even more for the distribution of the taxa throughout Africa.

Due to the mostly isolated position of the eight African ranges of mountains as well as the five big river systems it is very difficult to collect in all regions and to compare faunistically.

Table 3 - Ephemeroptera families and genera in Afrotropical Africa (e = endemic taxon).

Baetidae:	*Acanthiops* WALTZ & McCAFFERTY, 1987	(e)
	= *Afroptiloides* GILLIES,1990	
	= *Platycloeon* GILLIES & WUILLOT, 1997	
	Acentrella BENGTSSON, 1912	
	incl. *Tanzaniella* GILLIES, 1991	(e)
	Afrobaetodes DEMOULIN, 1970	
	Afroptilum GILLIES, 1990	
	incl. *Dabulamanzia* LUGO-ORTIZ & McCAFF., 1998	
	incl. *Maliqua* LUGO-ORTIZ & McCAFF., 1997	(e)
	incl. *Micksiops* McCAFFERTY, LUGO-ORTIZ & BARBER-JAMES, 1997	(e)
	Baetis LEACH, 1815	
	subg. *Baetis* LEACH, 1815	
	subg. *Labiobaetis* NOVIKOVA & KLUGE, 1987	
	subg. *Nigrobaetis* KAZLAUSKAS, 1987	
	Barnumus McCAFFERTY & LUGO-ORTIZ, 1998	(e)
	Centroptiloides LESTAGE, 1918	
	Centroptilum EATON, 1869	
	Cheleocloeon WUILLOT & GILLIES, 1993	
	Cloeodes TRAVER, 1938	
	= *Centroptella* BRAASCH & SOLDAN, 1980	
	Cloeon LEACH, 1815	
	Crassabwa LUGO-ORTIZ & McCAFFERTY, 1996	(e)
	Demoreptus LUGO-ORTIZ & McCAFFERTY, 1997	(e)
	Demoulinia GILLIES, 1990	(e)
	Dicentroptilum WUILLOT & GILLIES, 1994	
	Glossidion LUGO-ORTIZ & McCAFFERTY, 1998	(e)
	Ophelmatostoma WALTZ & McCAFFERTY, 1987	(e)
	Peuhlella LUGO-ORTIZ & McCAFFERTY, 1998	(e)
	Procloeon BENGTSSON, 1915	
	Pseudocentroptiloides JACOB, 1986	
	incl. *Potamocloeon* G ILLIES, 1990	(e)
	(*Pseudocloeon* KLAPALEK, 1905)	
	teste SARTORI the genus should be restricted to the type species (and consequently is not present in Africa)	
	Pseudopannota WALTZ & McCAFFERTY, 1987	
	Rhithrocloeon GILLIES, 1985	(e)
	incl. *Bugilliesia* LUGO-ORTIZ & McCAFFERTY, 1998	
	incl. *Kivua* McCAFF. & LUGO-ORTIZ, 1996	(e)
	incl. Mutelocloeon GILLIES & ELOUARD, 1990	
	Susua LUGO-ORTIZ & McCAFFERTY, 1998	(e)
	Thraulobaetodes ELOUARD & HIDEUX, 1991	(e)
	Xyrodromeus LUGO-ORTIZ & McCAFFERTY, 1998	
Oligoneuriidae:	*Elassoneuria* EATON, 1881	
	Oligoneuriopsis CRASS, 1947	(e)
Heptageniidae:	*Afronurus* LESTAGE, 1924	
	Compsoneuria EATON, 1881	
	= *Compsoneuriella* ULMER, 1939	
	= *Notonurus* CRASS, 1947	
	Thalerosphyrus EATON, 1881	
Leptophlebiidae:		
Atalophlebiinae:	*Adenophlebia* EATON, 1881	(e)
	Adenophlebiodes ULMER, 1924	(e)
	subg. *Adenophlebiodes* ULMER, 1924	(e)
	subg. *Hyalophlebia* DEMOULIN, 1955	(e)
	Aprionyx BARNARD, 1940	(e)
	Castanophlebia BARNARD, 1932	(e)
	Choroterpes EATON, 1881	
	subg. *Choroterpes* EATON, 1881	
	subg. *Euthraulus* BARNARD, 1932	
	Fulleta NAVAS, 1930	(e)
	Fulletomimus DEMOULIN, 1956	(e)
	Thraulus EATON, 1881	

Ephemeridae:		*Afromera* DEMOULIN, 1955	(e)
		Eatonica NAVAS, 1913	
		Ephemera LINNAEUS, 1758	
Polymitarcyidae:			
Polymitarcyinae:		*Ephoron* WILLIAMSON, 1802	
Asthenopodinae:		*Povilla* NAVAS, 1912	
Exeuthyplociinae:	(e)	*Afroplocia* LESTAGE, 1939	(e)
		Exeuthyplocia LESTAGE, 1918	(e)
Teloganodidae:		*Ephemerellina* LESTAGE, 1924	
		Lestagella DEMOULIN, 1970	(e)
		Lithogloea BARNARD,1932	(e)
		Nadinetella McCAFFERTY & WANG, 1998	(e)
Tricorythidae:			
Tricorythinae:		*Tricorythus* EATON, 1868	
Dicercomyzinae:	(e)	*Dicercomyzon* DEMOULIN, 1954	(e)
Machadorythinae:		*Machadorythus* DEMOULIN, 1959	(e)
Ephemerythinae:	(e)	*Ephemerythus* GILLIES; 1960	(e)
Caenidae:		*Afrocaenis* GILLIES, 1982	(e)
		Afrocercus MALZACHER, 1987	(e)
		Barnardara McCAFFERTY & PROVONSHA, 1995	(e)
		Caenis STEPHENS, 1835	
		? = *Austrocaenis* BARNARD, 1932	
		= *Caenodes* ULMER, 1924	
		= *Caenomedea* THEW, 1960	
		Caenopsella GILLIES, 1977	(e)
		Clypeocaenis SOLDÁN, 1978	
Prosopistomatidae:		*Prosopistoma* LATREILLE, 1833	

Moreover the political and social conditions in Black Africa do not allow a systematic sampling. It seems that with its hard conditions Africa used to be and will be also concerning mayflies a "black box".

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