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BIOGEOGRAPHY OF MALAGASY MAYFLIES (INSECTA, EPHEMEROPTERA): PRELIMINARY RESULTS

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ABSTRACT.- Mayflies (Ephemeroptera) are among the oldest known flying insects. They are strictly freshwater inhabitants with weak dispersal abilities, thus an interesting group for biogeographical studies. At the beginning of the 1990s, only twenty species were known in Madagascar. Since then, extensive studies by the LRSAE at over 660 different localities (more than 850 sampling points) led to the identification of at least 200 species, all endemic, and belonging to more than 40 genera and 11 families. The distribution of the investigated families is discussed herein. One family, the Palingeniidae, is not present in continental Africa. The absence from Madagascar of some other families is also analysed. The generic endemism rate is about 50% and can be in part explained by radiations of some taxa after the breakoff with Gondwana. These adaptations were made possible by the lack of competitors in most of the running waters. Comparisons are made between African and Malagasy faunas. The main distribution patterns found in Malagasy mayflies are illustrated.

KEY-WORDS.- Ephemeroptera, Mayflies, Madagascar, Biogeography

RESUME.- Les Ephéméroptères constituent un ancien ordre d'insectes exclusivement dulçaquicoles, à pouvoir de dispersion restreint. De ce fait, ils constituent un groupe de choix pour des études de biogéographie. Jusqu'au début des années 1990, seule une vingtaine d'espèces étaient connues de la Grande Île. Depuis, les recherches menées par le LRSAE sur près de 660 stations différentes, représentant plus de 850 points de prélèvements, ont permis la capture et l'identification d'au moins 200 espèces exclusivement endémiques appartenant à plus de 40 genres et à 11 familles. La distribution des familles rencontrées est discutée. Une seule d'entre elles (Palingeniidae) n'est pas présente en Afrique continentale. L'absence de certaines autres à Madagascar est également analysée. Le taux d'endémisme générique s'élève à près de 50% et peut être expliqué en partie par des adaptations postérieures à la séparation du Gondwana, rendues possible par l'absence de compétiteurs dans les milieux colonisés. Des comparaisons sont faites entre les genres endémiques et communs des faunes africaine et malgache. Les principaux types de distribution rencontrés chez les éphémères malgaches sont illustrés par quelques exemples.

MOTS-CLES.- Ephemeroptera, Ephémères, Madagascar, Biogéographie

INTRODUCTION

Mayflies (Ephemeroptera) are the most primitive order of living winged insects. Larvae colonise all types of freshwaters, from brooks and springs to large rivers, ponds and lakes. Although the adult stage is extremely short (generally less than one day), the larval growth may last from a few weeks until two or three years, mainly depending on water temperature and food availability (See Brittain 1982 for a review).

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As a result of their short adult life, mayflies' dispersal power is generally rather weak, and they represent a good group for biogeographical analyses.

The Madagascar mayfly fauna was almost unknown until the beginning of the 1990s. Less than 20 species were recorded by different authors such as Latreille (1833), Navas (1926) or Demoulin (1973). The start of the program « Biodiversity and biotypology of Malagasy running waters » led to the creation of the Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE) in 1991, jointly between the French ORSTOM (now IRD) and the Malagasy CNRE, and gave a new boost to aquatic insect research on the island.

Our actual knowledge of the Malagasy mayfly fauna, although quite incomplete at the specific level, allows us to present some preliminary results and answer the following questions: What are the affinities and originality of supraspecific taxa, and which other faunas are they linked to ?

MATERIAL AND METHODS

The results presented here are almost exclusively based on the numerous collections of the LRSAE and the Museum of Zoology in Lausanne. From 1991 until 1999, more than 850 samplings, rearing of larvae and light traps, were performed, covering the main geographical areas (Fig. 1).

RESULTS

Our investigations led to the discovery of at least 200 species belonging to more than 40 genera (Tab. I). Among the 28 actually recognised families worldwide, 11 are present in Madagascar.

Leptophlebiidae

This world-wide family is the most diversified on Madagascar. Unfortunately, this is the one, at the moment, for which detailed data are still missing (work in progress by Prof. W.L. Peters, Tallahassee, and Dr J.-M. Elouard, Montpellier). Anyway, it appears that all genera are endemic and present definite transantarctic relationships. Based on Pescador and Peters (1980) and Peters (comm. pers.), the South America - Australia - New Zealand *Hapsiphlebia / Atalophlebia, Penaphlebia,* and *Meridialaris / Atalophlebioides* lineages occur on Madagascar. Further, on the basis of on Towns and Peters (1996), the New Zealand *Tepakia - Isothraulus* lineage is also present.

Baetidae

This cosmopolite family is highly diversified with almost 20 genera, roughly half of those actually known (excluding the Leptophlebiidae). At least six of them are endemic. Most of the genera present on Madagascar are also found exclusively on continental Africa. The case of *Cloeodes*, a pantropical genus (Fig. 2) is rather rare among mayflies (Waltz & McCafferty 1994; Lugo-Ortiz *et al.* 1999). The recent discovery of a single population of the genus *Afrobaetodes* was rather surprising (Gattolliat & Sartori 1999) but confirm the strong relationships between African and Malagasy Baetidae.

Heptageniidae

This widely distributed family is less diversified than in other parts of the World (North America, Asia, Europe) with 3 genera known also from Africa and Asia.

Thalerosphyrus is widespread in Southeast Asia, whereas its presence in continental Africa (Soldan 1977) or even in the Near East (Jensen 1972) needs further investigations.

Oligoneuriidae

The related family Oligoneuriidae is represented by two genera. *Elassoneuria* is widespread in Africa, as in Madagascar, and is represented by two subgenera. Another undescribed genus seems to have a very restricted distribution, and has been found only in the Mangoro River.

Polymitarcyidae

The single endemic genus *Proboscidoplocia* is present in Madagascar. It includes among the largest species of mayflies of the world (Elouard & Sartori 1997).

Ephemeridae

One genus belongs to this family, *Eatonica.* Common in Africa where it colonises large rivers (Fig. 3). This genus has on Madagascar a distribution restricted to the highlands brooks (Elouard *et al.* 1998).

Palingeniidae

A single endemic genus occurs on Madagascar, the flightless *Cheirogenesia*. This is the only case of brachyptery ever found in mayflies, and the consequences of this unique phenomenon have been recently published (Ruffieux *et al.* 1998). This family is the only one that is not present in continental Africa (Fig. 4), but possesses representatives throughout Asia and Europe.

Ephemerellidae

This is the rarest family in Madagascar, with species restricted to the coldest watercourses in mountain areas. The same situation happens with representatives of the order Plecoptera. The two known genera, *Manohyphella* and an undescribed new genus, are endemic and closely related to the ancient Asiatic *Teloganella* lineage.

Tricorythidae

The study of this family brought a lot of surprises. Previously, four genera were known, mainly in Africa, Southeast Asia and South America. Three additional new endemics *Madecassorythus, Spinirythus* and *Ranorythus* were identified on Madagascar, and represent the most plesiotypic forms of the family (Elouard & Oliarinony 1997; Oliarinony & Elouard 1998a, b). *Tricorythus* is present in Africa and Southeast Asia.

Caenidae

This family is represented by three genera. Besides the cosmopolite *Caenis*, the two others are endemic and also rather plesiotypic; *Madecocercus* and an undescribed new genus appear to belong to the old brachycercine rather than to the caenine lineage (Malzacher 1995; M. Sartori & J.-M. Elouard, unpubl. results).

Prosopistomatidae

This monogeneric family is one of the most evolved. *Prosopistoma* has a broad distribution in the world, and as for other genera, its expansion seems to have been made possible through the drifting of the Indian plate (Fig. 5) with subsequent colonisation of southeast Asia and northern Australia.

None of these families is endemic to Madagascar. The Palingeniidae is the only one present in Madagascar but missing in Africa. A striking feature is that representatives of the superfamily Siphlonuroidea are lacking in Africa and Madagascar though some southern Hemisphere families are known as transantarctic elements, such as Ameletopsidae, Nesameletidae or Onisigastridae (Kluge *et al.* 1995).

Among more than 40 genera actually known in Madagascar, half of them are endemic. As seen previously, the proportion of endemism greatly fluctuates between families.

DISCUSSION

There is a consensus now among scientists concerning the geological events that happened for the Malagasy plate. First, the separation from Africa about 140 M.y. BP, then a subsequent breakoff from Antarctica-Australia 110 M.y. BP, and finally the separation from India 80 M.y. BP, leading to the colliding of the Dekkan plate with Asia 50 M.y. BP. (Fröhlich 1996).

Mayflies are the most primitive living winged insects. Their origin goes back to the Carboniferous. Moreover, they exhibit a low vagility and the larvae are strictly associated with freshwaters, mainly running waters. These two features discriminate them from Odonata for instance, another old group of flying insects, that has good dispersal abilities and colonises mainly standing waters, and exhibits a lower proportion of endemism.

The hypothesis that mayflies colonised landmasses such as Madagascar after the breakoff of Gondwana is unlikely. As a result of the actual presence of highly evolved genera in Madagascar, such as *Prosopistoma*, we can state that most of the actual mayfly lineages were already present before the Gondwana breakoff. A similar situation seems to happen with primitive flightless insects and other soil arthropods (Betsch & Cassagnau 1996).

The similarity between the African and Malagasy mayfly faunas is evident. Oriental and Oceanian components are less prevailing. As stated by Paulian (1996), this situation seems in contradiction with the here above mentioned geomorphologic events. This is the case in different lineages such as the ephemerid *Eatonica*, the oligoneuriid *Elassoneuria* or the great majority of the baetid genera. Noteworthy is the fact that these taxa are found nowhere else in the world.

The ancient connection of Madagascar with Australia, New Zealand and South America is attested by the actual presence of leptophlebiid lineages such as the *Atalophlebioides*. The recent discovery of an *Atalophlebioides* precursor dated about 130 M.y. BP in Lebanon (McCafferty 1997) suggest that this lineage was also present in Africa, but later went extinct on that continent. Whereas mayfly faunas of Australia, New Zealand and temperate South America are similar (Peters & Campbell 1991), only two genera are in common to Madagascar and South America; the pantropical *Cloeodes* and the cosmopolite *Caenis*. No Siphlonuroidea, one of the early radiation of the order, are present in Madagascar, nor in Africa, Sri Lanka, and south India, whereas transantarctic lineages have spread through Australia, New Zealand and southern South America. We agree with Edmunds (1972) suggesting that they become extinct, having no cool refuge for survival.

The actual distribution of the Palingeniidae indicates that this family arose when Madagascar and India were still together, leading to an important radiation through Asia after the Dekkan plate collided with Asia. The fact that the Malagasy genus *Cheirogenesia* is the sister-group of all other palingeniid mayflies gives strong support to this hypothesis. In that sense, we do not agree with Edmunds (1975) suggesting that this dispersal dates back to the Pangea with extinction in Africa. Due to the peculiar habitat of the larvae (silt burrowers) we do not believe that extinction was the driving force in Africa (and also South America), where this kind of biotope is abundant, and where these insects had probably no competitors.

Edmunds (1979) pointed out the significance of drifting India to the Oriental fauna and the subsequent spread to other parts of Eurasia. Many examples are known now involving different lineages (Prosopistomatidae, Tricorythidae, and Heptageniidae for instance).

The long isolation of Madagascar led to the exclusively endemic species found nowadays. The lack of diversity in other lineages, such as carnivorous Plecoptera and fishes, allow quiet rapid speciation processes, as it has been shown with the flightless genus *Cheirogenesia* (Ruffieux *et al.* 1998). These factors also induced important shifts in feeding behaviour, leading to the unusual presence of at least three carnivorous baetid genera in Madagascar, whereas only five others are known from other areas of the world (Gattolliat & Sartori in press b).

Finally, if our starting hypothesis is correct, i.e. the actual distribution of mayflies reflects the situation prior to the Gondwana breakoff, we can only be much surprised by the strong relationships still existing between elements that were separated more than 120 M.y. BP. This is the case for instance within baetid genera such as *Afroptilum*, *Afrobaetodes* or *Dabulamanzia*.

Concerning the endemic genera, we are in need of phylogenetic analyses. No doubt that they will bring shed interesting light on this so peculiar mayfly fauna.

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Table I. List of the families and genera actually recorded on Madagascar.

FAMILIES & *Genera* [1]	Distribution [2]	References [3]
LEPTOPHLEBIIDAE [4]	C	
Nesophlebia Peters & Edmunds, 1964	M	Demoulin, 1973
Petersophlebia Demoulin, 1973	M	Demoulin, 1973
Polythelais Demoulin, 1973	M	Demoulin, 1973
BAETIDAE	C	
Afrobaetodes Demoulin, 1970	Af	Gattolliat & Sartori, 1999b
Afroptiloides Gillies, 1990	Af	Gattolliat, unpubl. results
Afroptilum Gillies, 1990	Af	Gattolliat et al., 1999
Bugilliesia Lugo-Ortiz & McCafferty, 1998	Af	Gattolliat, unpubl. results
Cheleocloeon Wuillot, 1993	Af	Lugo-Ortiz & McCafferty, 1997c
Cloeodes Traver, 1938	SA, NA, Af, As	Lugo-Ortiz et al., 1999
Cloeon Leach 1815	Af, Eu, As, Aus	Gattolliat, unpubl. results
Dabulamanzia Lugo-Ortiz & McCafferty, 1996	Af	Gattolliat & Sartori, in press c
Dicentroptilum Wuillot & Gillies, 1994	Af	Lugo-Ortiz & McCafferty, 1998
Edmulmeatus Lugo-Ortiz & McCafferty, 1997	M	Lugo-Ortiz & McCafferty, 1997a
Guloptiloides Gattolliat & Sartori in press	M	Gattolliat & Sartori, in press a
Herbrossus McCafferty & Lugo-Ortiz, 1998	M	Gattolliat & Sartori, 1998
Labiobaetis Novikova & Kluge 1987	Af, Eu, NA	Lugo-Ortiz & McCafferty, 1997d
Mutelocloeon Gillies & Elouard, 1990	Af	Lugo-Ortiz & McCafferty, 1997c
Nesoptiloides Demoulin, 1973	M	Gattolliat & Sartori, 1999a
Pseudopannota Waltz & McCafferty, 1987	Af	Demoulin, 1973
Xyrodromeus Lugo-Ortiz & McCafferty, 1997	Af	Lugo-Ortiz & McCafferty, 1997b
Gen. nov. 1	M	Gattolliat, unpubl. results
Gen. nov. 2	M	Gattolliat, unpubl. results
HEPTAGENIIDAE	C except Aus	
Afronurus Lestage, 1924	Af, As	Sartori & Elouard, 1996
Compsoneuria Eaton, 1881	Af, As	Sartori, unpubl. results
Thalerosphyrus Eaton, 1881	Af, As	Sartori & Elouard, 1996
OLIGONEURIIDAE	C	
Elassoneuria Eaton, 1881	Af	Elouard, unpubl. results
Gen. nov.	M	Elouard, unpubl. results
EPHEMERIDAE	C except Aus	
Eatonica Navas, 1913	Af	Elouard et al., 1998
POLYMITARCYIDAE	C except Aus	
Proboscidoplocia Demoulin, 1966	M	Elouard & Sartori, 1997
PALINGENIIDAE	As, Eu	
Cheirogenesia Demoulin, 1952	M	Sartori & Elouard, 1999
EPHEMERELLIDAE	C	
Manohyphella Allen, 1973	M	Elouard, unpubl. results
Gen. nov.	M	Elouard, unpubl. results
TRICORYTHIDAE	Af, As, SA	
Madecassorythus Elouard & Oliarinony, 1997	M	Elouard & Oliarinony, 1997
Ranorythus Oliarinony & Elouard, 1998	M	Oliarinony & Elouard, 1998a
Spinirythus Oliarinony & Elouard, 1998	M	Oliarinony & Elouard, 1998b
Tricorythus Eaton, 1868	Af, As	Oliarinony et al., 1998
CAENIDAE	C	
Caenis Stephens, 1835	C	Malzacher, 1995
Madecocercus Malzacher, 1995	M	Malzacher, 1995
Gen. nov.	M	Sartori, unpubl. results
PROSOPISTOMATIDAE	Af, As, Aus, Eu	
Prosopistoma Latreille, 1833	Af, As, Aus, Eu	Elouard, unpubl. results

[1] Endemic genera are in bold
[2] Following abbreviations are used: M: endemic to Madagascar; Af: Africa; As: Asia; Aus: Australia, C: Cosmopolite; Eu: Europe, NA: North America; SA South America
[3] Only for the genera account
[4] But see text for further comments

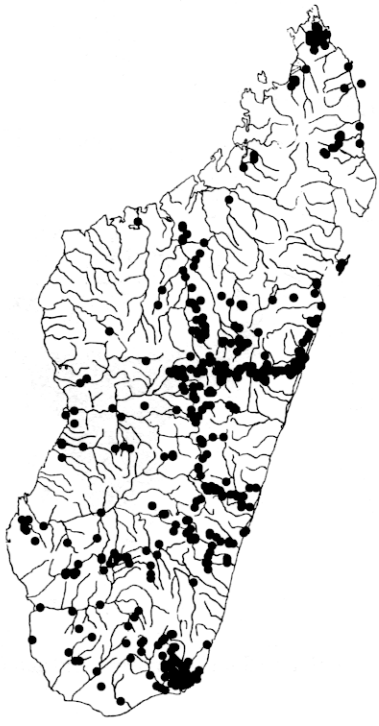

Fig. 1. Map of the sampling stations in Madagascar.

Fig. 2. Distribution of the pantropical baetid genus *Cloeodes* Traver. Actual records are in black, potential distribution in grey.

Fig. 3. Distribution of the Ethiopian ephemererid genus *Eatonica* Navás.

Fig. 4. Distribution of the family Palingeniidae.

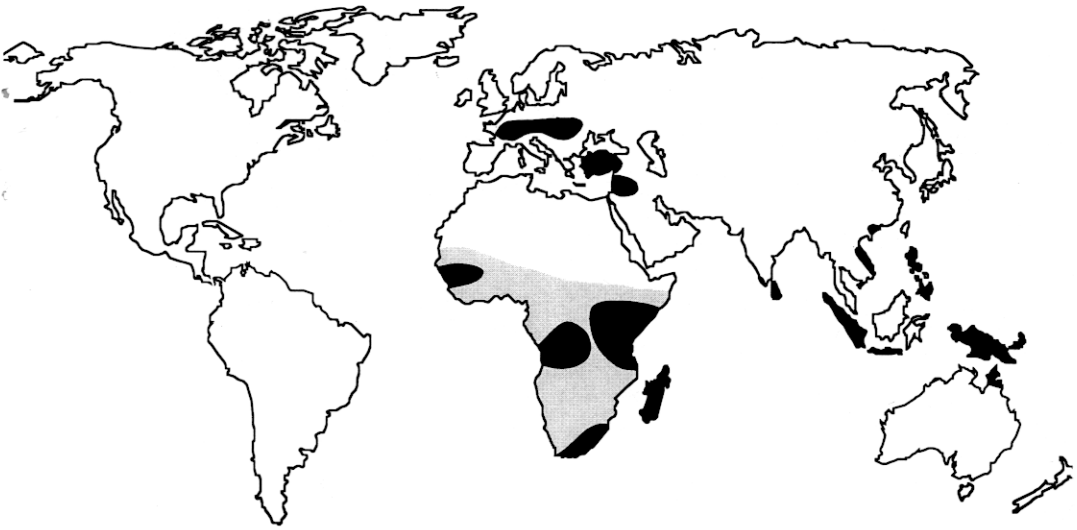

Fig. 5. Distribution of the family Prosopistomatidae.