

## An overview of the Baetidae of Madagascar

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### Abstract

Until 1995, the knowledge of the Malagasy mayflies was extremely poor. During the last seven years, 25 papers were dedicated to the systematics of the Baetidae, allowing the description of 50 new species and 8 new genera. This fauna now encompasses 22 genera and 54 species.

The level of endemism is quite high (53 of the 54 species and one third of the genera). Malagasy fauna shows extremely strong affinities with the African fauna. Other components, especially Oriental and Oceanian, are negligible. These affinities are in contradiction with the separation history of Gondwana. The most likely explanation to solve this contradiction is that the dispersal power of the Baetidae is greatly underestimated. The study of recent volcanic islands clearly demonstrates that the Baetidae are able to disperse over more than 300 km.

This study must be considered as a first step for understanding the dispersion and colonization of the islands of the western part of the Indian Ocean.

**Keywords:** systematics, fauna, biogeographic affinities, endemism.

### Introduction

With a maximum length of 1600 km and a width of 570 km, Madagascar is the fourth largest island in the world. It is situated in the western part of the Indian Ocean, at a distance of more than 300 km from the African coast. The uniqueness of its fauna does not need to be demonstrated. A global estimation of the proportion of endemic animal taxa indicates that about 90% of the species and 70% of the genera are endemic to Madagascar. However, the interest of the Malagasy fauna is not only due to the uniqueness of the taxa present, but also to the absence of others (such as Felidae, ungulate and primate).

Gondwanaland was originally made up of what is now South America, Africa, India (Deccan Plate), Australia, Antarctica and Madagascar. Madagascar first separated from the African plate (-165 M.y.), then moved to the South (-125 M.y.) where it remained in its current position. The last major event was the separation with the Indian plate (-85 M.y.) (Battistini, 1996; Fröhlich, 1996).

Until recently, the knowledge of the Malagasy mayflies, as well as most other aquatic invertebrates, was extremely poor. The program *Biodiversity and Biotypology of Malagasy Freshwaters*, jointly run by the French ORSTOM and the Malagasy CNRE, began a global survey of the freshwater macroinvertebrates. Sampling, rearing of larvae and light traps were performed in about 650 stations representing near one thousand sampling points (Elouard and Gibon, 2001). This survey involved all the important regions of Madagascar, except a few inaccessible massifs in the North of Madagascar (Sambirano and Tsaratanana massifs) and one of the best preserved primary rainforests (Masoala Peninsula); these unprospected areas probably possess a high degree of endemism. The systematics of the main mayfly families (Baetidae, Caenidae, Ephemeridae, Heptageniidae, Polymitarcyidae, Palingeniidae, Tricorythidae), with the exception of the Leptophlebiidae, was also the subject of detailed studies (Sartori *et al.*, 2000).

### The systematics of the Malagasy Baetidae

The history of studies on the Malagasy mayflies began in quite an unusual way with the description in 1833 by Latreille of a new genus of what was thought to be a Crustacean. This pseudo-crustacean was in fact the type-species of the Prosopistomatidae (*Prosopistoma variegatum* LATREILLE, 1833). The attribution to the right

order and class was only made in 1872 (Joly and Joly, 1872).

The presence of Baetidae in Madagascar was first indicated in 1909 (Ulmer, 1909). Larvae and subimagoes of *Cloeon* were caught in Aloatra Lake. No specific description was performed.

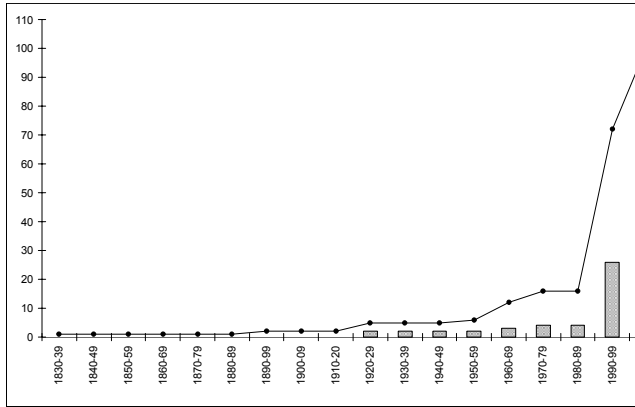


Fig. 1 - Changes in the number of Malagasy species known since 1830: dots: total number of mayfly species; histogram bars: total number of baetid species.

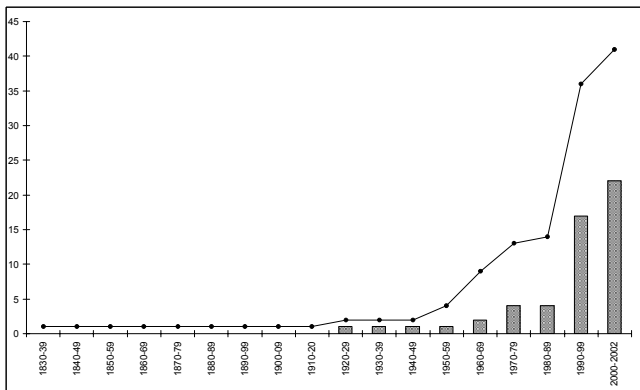


Fig. 2 - Changes in the number of Malagasy genera known since 1830: dots: total number of mayfly genera; histogram bars: total number of baetid genera.

Until the middle of the 1990's, very little work on the systematics of the Malagasy baetids had been done (Figs. 1, 2). Only eight species were described, mainly by Navás (1926; 1930; 1936) and Demoulin (1966; 1973). Among them, only four species belonging to three genera are now considered valid (Lugo-Ortiz and McCafferty, 1998b; Gattolliat and Sartori, 1999b; Gattolliat and Rabeantoandro, 2002). Only since 1997 has the knowledge of the Malagasy Baetidae really increased (Figs 1, 2). Between 1997 and 1999, Lugo-Ortiz and McCafferty published nine papers of systematics describing 4 new genera and 14 new species (Lugo-Ortiz and McCafferty, 1997a, b, c, d; 1998a, b, c; 1999; Lugo-Ortiz *et al.*, 1999).

These descriptions were mainly based on an extremely small number of specimens collected by G.F. and C. Edmunds and F. Emmanuel. During the same period, we also began a systematic and phylogenetic study of the Baetidae, describing 4 new genera and 34 new species (Gattolliat and Sartori, 1998; 1999a, b; 2000a, b; 2001; Gattolliat *et al.*, 1999; Gattolliat, 2000; 2001a, b, c; 2002a, b, c; Gattolliat and Rabeantoandro, 2002).

The Malagasy baetid fauna now encompasses 22 genera and 54 species (Table 1). The knowledge of this family is however not complete: *Afroptilum* and *Dicentropilum*, which are the most abundant genera and potentially quite diversified, are still in great need of a global study.

Despite its small size, Madagascar has the same diversity, at specific and generic level, as a continent (Campbell, 2001; Elouard, 2001; McCafferty, 2001; Pescador *et al.*, 2001; Sartori, 2001; Soldán, 2001).

Table 1 - List of the Malagasy species of Baetidae. In bold: endemic genera.

<i>Afrobaetodes</i> DEMOULIN, 1970	<b><i>Edmulmeatus</i></b> LUGO-ORTIZ & MCCAFFERTY, 1997
<i>Afrobaetodes lenae</i> GATTOLIAT & SARTORI, 1999	<i>Edmulmeatus grandis</i> L.-ORTIZ & MCCAFFERTY, 1997
<i>Afroptiloides</i> GILLIES, 1990	<b><i>Guloptiloides</i></b> GATTOLIAT & SARTORI, 2000
<i>Afroptiloides delphinae</i> GATTOLIAT, 2000	<i>Guloptiloides gargantua</i> GATTOLIAT & SARTORI, 2000
<i>Afroptiloides spinosum</i> GATTOLIAT, 2000	<b><i>Herbrossus</i></b> MCCAFFERTY & LUGO-ORTIZ, 1998
<i>Afroptiloides namorona</i> GATTOLIAT, 2000	<i>Herbrossus christinae</i> GATTOLIAT & SARTORI, 1998
<i>Afroptilum</i> GILLIES, 1990	<i>Herbrossus edmundsorum</i> MCCAFFERTY & L.-ORTIZ, 1998
<i>Afroptilum confusum</i> L.-ORTIZ & MCCAFFERTY, 1998	<i>Herbrossus elouardi</i> GATTOLIAT & SARTORI, 1998
<i>Afroptilum gilberti</i> GATTOLIAT & SARTORI, 1999	<i>Labiobaetis</i> NOVIKOVA & KLUGE, 1987
<i>Afroptilum lepidum</i> L.-ORTIZ & MCCAFFERTY, 1998	<i>Labiobaetis dambrensis</i> GATTOLIAT, 2001
<i>Afroptilum mathildae</i> GATTOLIAT & SARTORI, 1999	<i>Labiobaetis fabulosus</i> L.-ORTIZ & MCCAFFERTY, 1997
<i>Cheleocloeon</i> WUILLOT, 1993	<i>Labiobaetis gilliesi</i> GATTOLIAT, 2001
<i>Cheleocloeon mirandei</i> L.-ORTIZ & MCCAFFERTY, 1997	<i>Labiobaetis longicercus</i> GATTOLIAT, 2001
<i>Cheleocloeon</i> sp. nov.	<i>Labiobaetis nigrocercus</i> GATTOLIAT, 2001
	<i>Labiobaetis plumbago</i> L.-ORTIZ & MCCAFFERTY, 1997

*Cloeodes* TRAVER, 1938

*Cloeodes bicoloratus* GATTOLLIAT, 2001

*Cloeodes freitagae* GATTOLLIAT, 2001

*Cloeodes portabilis* L.-ORTIZ & McCAFFERTY, 1999

*Cloeodes pseudogladus* GATTOLLIAT, 2001

*Cloeon* LEACH, 1815

*Cloeon durani* NAVÁS, 1926

*Cloeon emmanueli* L.-ORTIZ & McCAFFERTY, 1998

*Cloeon smaeleni* LESTAGE, 1924

*Dabulamanzia* LUGO-ORTIZ & McCAFFERTY, 1996

*Dabulamanzia concolorata* GATTOLLIAT, 2000

*Dabulamanzia duci* GATTOLLIAT & ELOUARD, 1999

*Dabulamanzia gladius* GATTOLLIAT, 2000

*Dabulamanzia gigantea* GATTOLLIAT, 2000

*Dabulamanzia improvida* L.-ORTIZ & McCAFFERTY, 1997

*Delouardus* LUGO-ORTIZ & McCAFFERTY, 1999

*Delouardus djabala* L.-ORTIZ & McCAFFERTY, 1999

*Delouardus* sp. nov.

*Demoulinia* GILLIES, 1990

*Demoulinia insularis* L.-ORTIZ & McCAFFERTY, 1998

*Demoulinia* sp. nov.

*Dicentropitulum* WUILLOT & GILLIES, 1994

*Dicentropitulum merina* L.-ORTIZ & McCAFFERTY, 1998

*Echinopus* GATTOLLIAT, 2002

*Echinopus giboni* GATTOLLIAT, 2002

*Echinopus minutus* GATTOLLIAT, 2002

### Biogeographic affinities

Before the separation of Gondwana, Madagascar was situated between the Kenyan coast of Africa and India. According to the low dispersal power of the mayflies, we originally considered that the colonization of the landmass after the break-off was rather unlikely (Sartori *et al.*, 2000). Based on the geological events, the Malagasy fauna should share a low similarity with South America and Africa and a much higher similarity with India and Australia.

All the species, except *Cloeon smaeleni*, are endemic to Madagascar. *C. smaeleni* is one of the most common and widespread in the Afrotropical area; it is also present in the Arabian Peninsula (Gillies, 1985). This wide distribution is probably related with its peculiar ecology (relatively long imaginal stage and oviviparity).

The Malagasy genera of Baetidae present principally two kinds of distribution: nine genera are endemic and ten have a distribution limited to the Afro-Malagasy area (Fig. 3). Only two genera (*Cloeon* and *Labiobaetis*) have an almost cosmopolitan distribution and one genus (*Cloeodes*) is pantropical. The strong affinities with the African fauna are even more evident if we do not consider Madagascar and Africa separately but rather as a single biogeographical

*Labiobaetis punctatus* GATTOLLIAT, 2001

*Labiobaetis vulgaris* GATTOLLIAT, 2001

*Mutelocloeon* GILLIES & ELOUARD, 1990

*Mutelocloeon thomasorum* L.-ORTIZ & McCAFFERTY, 1997

*Nesydemius* LUGO-ORTIZ & McCAFFERTY, 1998

*Nesydemius polhemusorum* L.-ORTIZ & McCAFFERTY, 1998

*Nesoptiloides* DEMOULIN, 1973

*Nesoptiloides electroptera* (DEMOULIN, 1966)

*Pseudopannota* WALTZ & McCAFFERTY, 1987

*Pseudopannota vinckei* (DEMOULIN, 1973)

*Pseudopannota camillae* GATTOLLIAT, 2002

*Rheoptilum* GATTOLLIAT, 2001

*Rheoptilum arni* GATTOLLIAT, 2001

*Rheoptilum lokohensis* GATTOLLIAT, 2001

*Scutoptilum* GATTOLLIAT, 2002

*Scutoptilum verrucosum* GATTOLLIAT, 2002

*Xyrodromeus* LUGO-ORTIZ & McCAFFERTY, 1997

*Xyrodromeus namarona* L.-ORTIZ & McCAFFERTY, 1997

*Xyrodromeus modestus* GATTOLLIAT, 2002

*Xyrodromeus sartorii* GATTOLLIAT, 2002

*Xyrodromeus latipalpus* GATTOLLIAT, 2002

region. Madagascar and Africa possess respectively 40 and 58% of endemic genera, but if we consider them as a single region we have more than 90% of the genera present in Madagascar or in Africa that are endemic to this area.

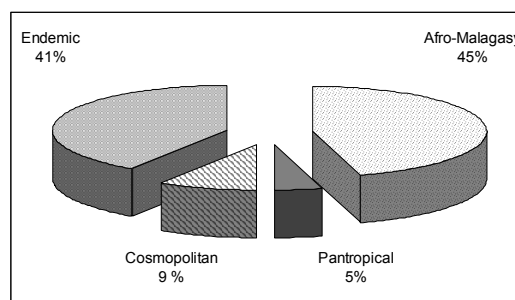


Fig. 3 - Types of distribution of the different Malagasy genera of Baetidae.

Other components, especially Oriental and Oceanian, are negligible. These areas share only a few widespread genera with Madagascar (Fig. 4). It means that these strong African affinities are in contradiction with the geological events, especially the historical sequence of the splitting of Gondwana. The same affinities can be observed in most other families of mayflies except the Palingeniidae and probably the Leptophlebiidae (Sartori *et al.*, 2000).

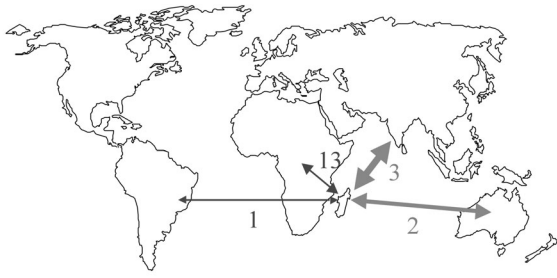


Fig. 4 - Number of genera in common between the different areas: the thickness of arrows indicates the degree of affinity supposed according to the age of the separation (Gondwana break-off).

Three explanations can be put forward to explain these contradictions:

1) The Afro-Malagasy genera had a gondwanan distribution before the separation. They became extinct on all plates except Africa and Madagascar or evolved by anagenesis on these plates.

2) The Afro-Malagasy genera already presented a restricted distribution before the break-off of the Gondwana.

3) The Afro-Malagasy genera originally had a restricted distribution. The actual distribution is the result of colonization events after the separation.

No definite argument can be given to support the first hypothesis. Large extinction can only be proved by the presence of fossils. We have to admit that there are very few baetid fossils compared to other mayfly families. The relatively rapid movement of most plates after separation, especially India, may have caused rapid extinction. The pantropical distribution of *Cloeodes* is certainly due to the widespread distribution of the genus before the break-off. This case must be considered an exception.

The second hypothesis seems rather insufficient to explain the Afro-Malagasy affinities: there is apparently no geological or historical reason why the Afro-Malagasy genera, belonging to different lineages, should be restricted only to these two plates before the separation.

The hypothesis that the dispersal power of the Baetidae has been underestimated is probably the most relevant. The observation of the composition of the baetid fauna of recent volcanic islands confirms the validity of this hypothesis. The Comoros Islands constitute a good study case. They are young volcanic islands (less than 5 millions years) and are at least 300 km from Madagascar and Africa. Three families are present in this archipelago: Leptophlebiidae, Baetidae and

Prosopistomatidae (Starmühlner, 1979). The presence of these families can only be explained by a recent immigration. Consequently, it means that Baetidae are able to disperse over a distance equal to the distance between Africa and Madagascar to colonize a new area. The main difference between Madagascar and the Comoros Islands is the origin of the island. In the case of a large continental island such Madagascar, we can assume that, at the moment of the break-off, the island possessed a fauna as diverse as the one of the main continent. Because most of the ecological niches of the continental island are already occupied, its colonization by new taxa has a rate of success much lower than for an oceanic island.

The composition of the Malagasy fauna is probably the result of a combination of the three hypotheses mentioned above. The colonization of Madagascar by African baetid after the separation is probably the most dominant factor, but it is also the most underestimated or neglected factor in other studies. This hypothesis offers the best explanation for the affinities observed between Africa and Madagascar and also justifies the high similarity of Malagasy and African species.

### The uniqueness of the Malagasy fauna: the endemic genera

One third of the Malagasy genera are endemic. This proportion may seem high. In fact, it is the combined result of two factors: all the generalist genera are not endemic and, on the other hand, the endemic genera present important adaptations. The endemic genera exploit much narrower ecological niches than the non-endemic. We can postulate that there is almost no competition between the endemic and non-endemic genera although they can be found at the same locality. The presence of these genera, resulting from evolution in situ or colonization, has probably not involved major extinction in Madagascar.

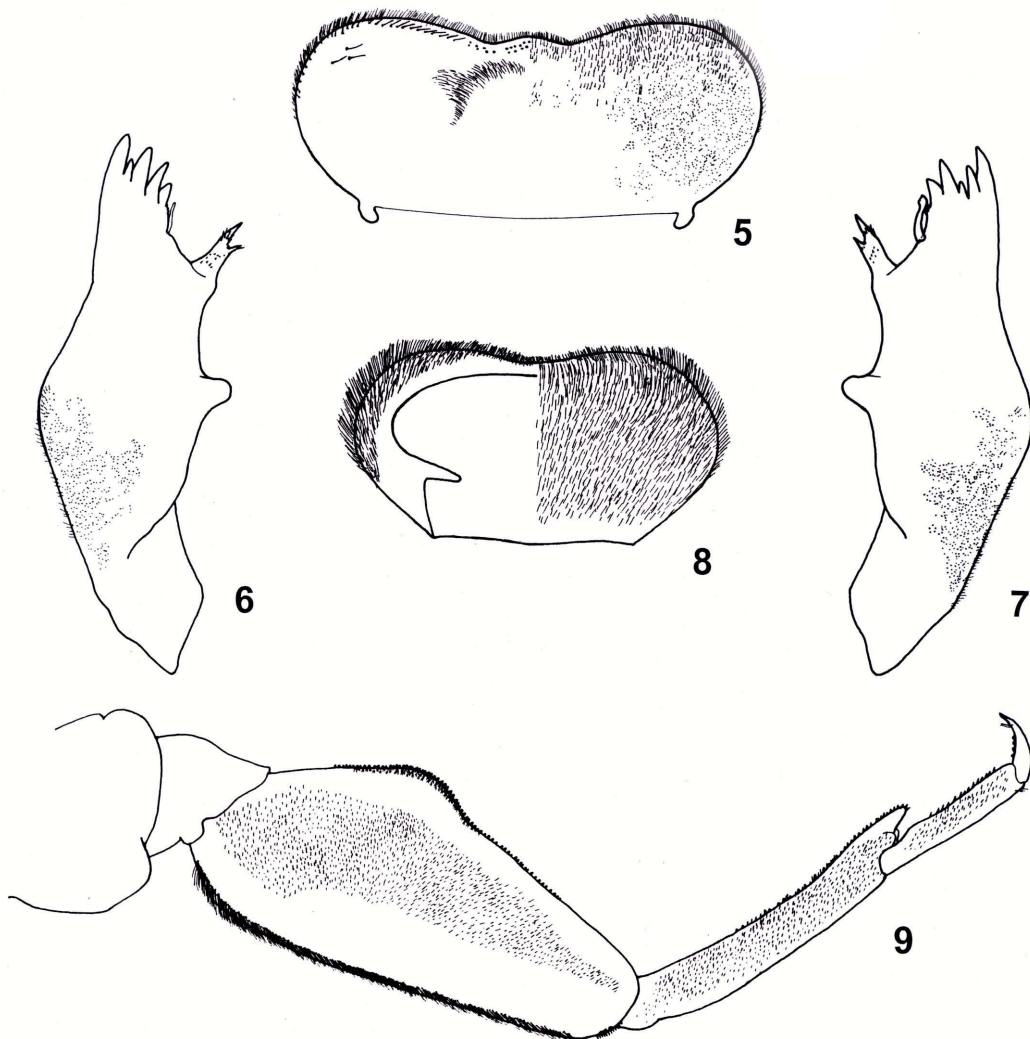
Six endemic genera are monospecific; only two have two species and one has three species. In comparison with non-endemic genera (average of three species per genus), the endemic genera have a low species diversity. The same observation on the difference of diversity between endemic and non-endemic genera can be made in Africa.

The majority of endemic genera have distributions restricted to the Eastern Domain. Except for *Scutoptilum* and *Echinopus*, which have been found in very few localities, they have wide but fragmented distributions in this Domain.

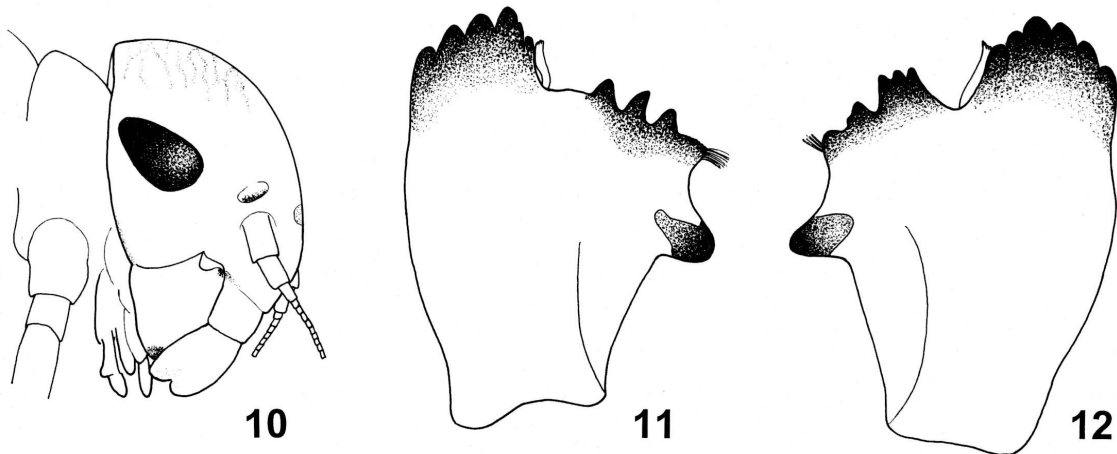
In the localities where they are present, the endemic genera are generally quite abundant; they can even be the most abundant species (*Rheoptilum arni*, *Edmulmeatus grandis*).

Among the adaptations of the endemic genera, the most peculiar and unusual is, without doubt, the carnivorous diet. Most genera of Baetidae are trophic generalists; they are considered as collector-gatherers or collector-filterers. The analysis of the gut content confirmed the carnivorous diet of three recently discovered genera, endemic to Madagascar: *Guloptiloides*, *Herbrossus* and *Nesoptiloides*. A study of their diet and morphological adaptations (Figs. 5-9) was

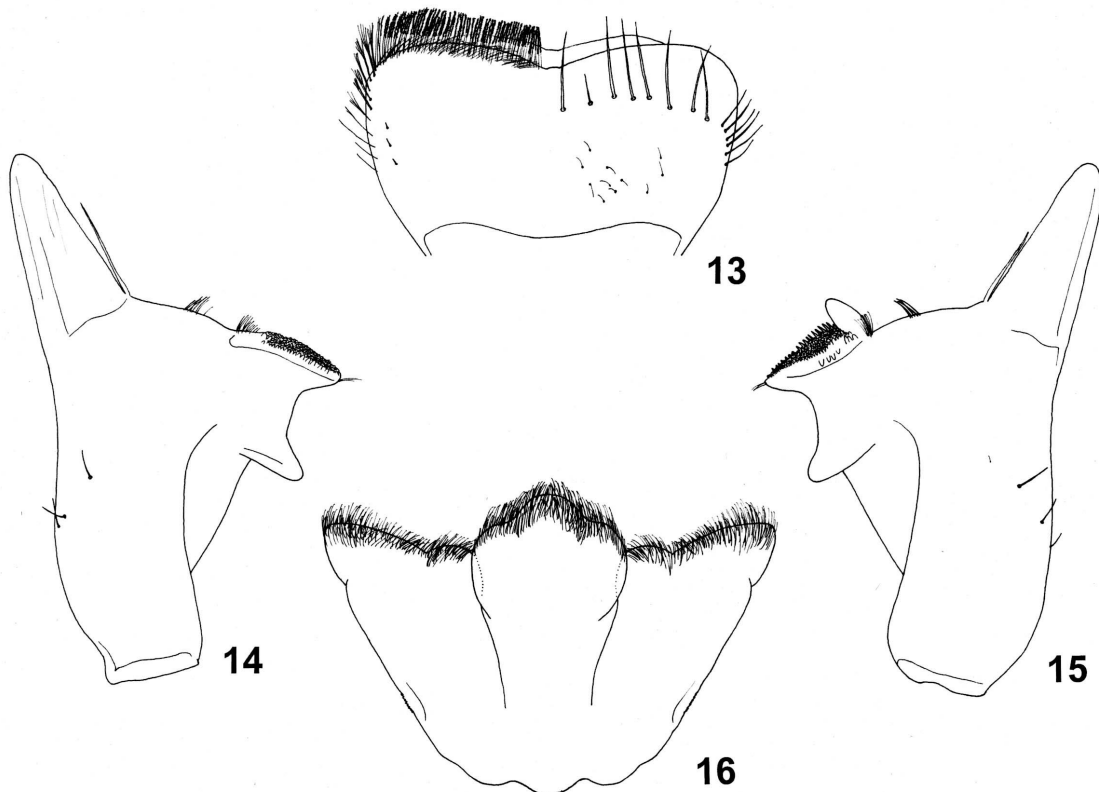
carried out by Gattolliat and Sartori (2001). This diversity is unexpected if we consider that only five carnivorous genera occur in the rest of the world. The larva of *Edmulmeatus grandis* also presents an unusual feeding behaviour (Lugo-Ortiz and McCafferty, 1997a). It feeds only on vascular plants (*Hydrostachis* sp.). The mouthparts, especially the mandibles, are completely modified for chewing the plants (Figs. 10-12). These modifications give its head the appearance of a cricket. In the field, the colouration of the living larva is vivid green due to the ingested chlorophyll.



Figs. 5-9 - Carnivorous genera: *Guloptiloides gargantua* (Figs. 5-7) and *Nesoptiloides electroptera* (Figs. 8, 9): 5 labrum (left: ventral; right: dorsal); 6 right mandible; 7 left mandible; 8 labrum (left: ventral; right: dorsal); 9 foreleg. Figs. 5-7 redrawn from Gattolliat and Sartori, 2000b; Figs. 8 and 9 redrawn from Gattolliat and Sartori, 1999b.



Figs. 10-12 - Herbivorous genus: *Edmulmeatus grandis*: 10 head lateral view; 11 right mandible; 12 left mandible.



Figs. 13-16 - Scraper genus: *Xyrodromeus latipalpus*: 13 labrum (left: ventral; right: dorsal); 14 right mandible; 15 left mandible; 16 hypopharynx. Figs. redrawn from Gattolliat, 2002a.

Adaptations for scraping algae from rocks are quite common in different Malagasy lineages. The mouthparts are the most modified structures for this feeding behaviour: the labrum and the hypopharynx are wide and the incisors of both mandibles are completely or almost completely fused (Figs. 13-16). In the cases of *Xyrodromeus*, *Rheoptilum* and *Scutoptilum* these adaptations are at a generic level (Lugo-Ortiz and McCafferty,

1997c; Gattolliat, 2001b; 2002b); in *Cloeodes* and *Dabulamanzia*, they are present only in one or two species, the others presenting unmodified mouthparts (Gattolliat and Sartori, 2000a; Gattolliat, 2001a). This feeding behaviour is also present in other areas, but it is not as common elsewhere as in Madagascar.

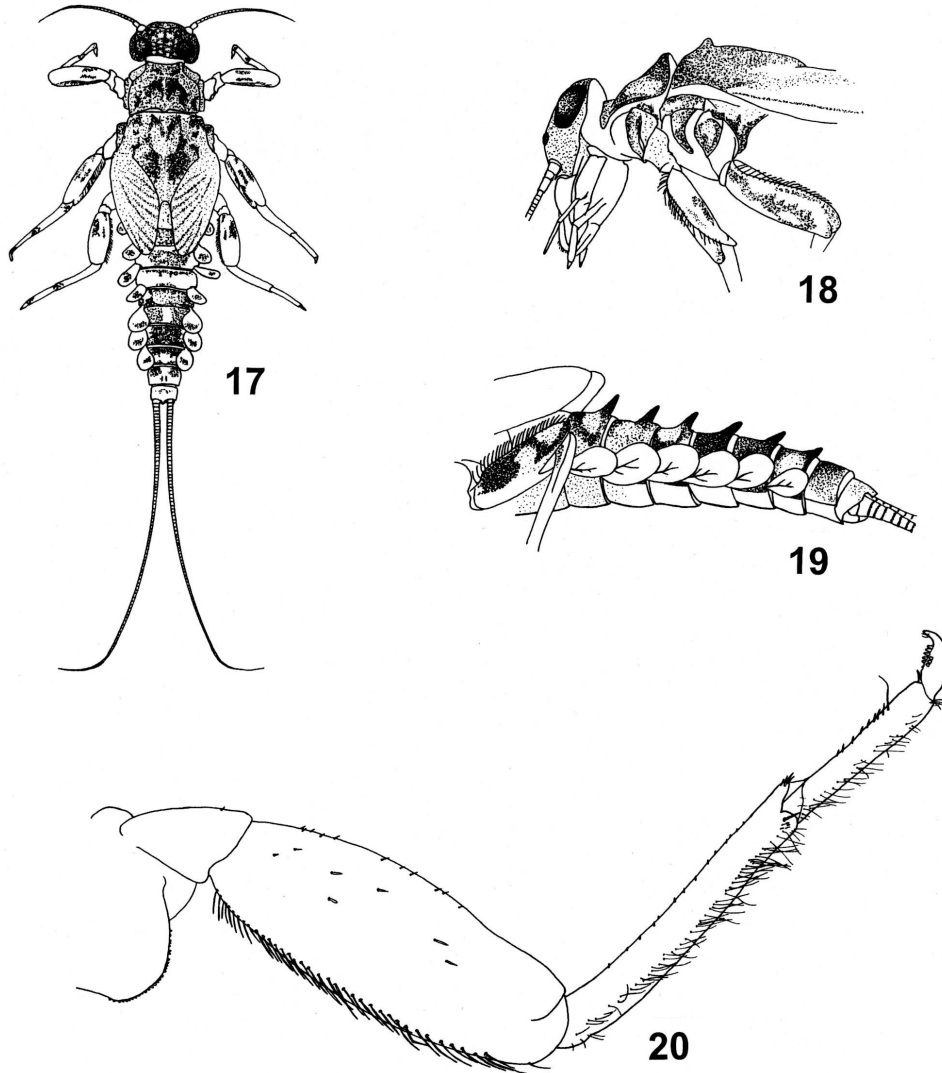
The last modification is the adaptation for the fast flow. This adaptation is present in endemic

(*Rheoptilum* and *Scutoptilum*) and non-endemic genera (*Afrobaetodes* and *Afroptiloides* / *Acanthiops*). It generally implies the reduction of the median caudal filament, long and slender legs with twisted tarsi, dorsal margin of legs with rows of long and fine setae and sometimes apophyses on the thorax and terga (Figs. 17-20). As observed by Gillies (1991), these kinds of adaptations occur independently in different lineages.

### Further perspectives

We now possess a good knowledge of the systematics of the Malagasy baetids. However, some gaps are still present, especially in the two most diverse and abundant genera, *Afroptilum* and *Dicentropilum*. These two genera will be the subject of a complete study later. Some

systematics problems need to be solved. The validity of the genera *Nesydemius* and *Delouardus* is dubious; their cases will require a complete revision or even a true cladistic analysis. The generic attribution of male imagoes with unusual genitalia to the genus *Mutelocloeon* (Lugo-Ortiz and McCafferty, 1997d) also appears doubtful. As the larva is symbiotic with mussels (Gillies and Elouard, 1990) and mussels are missing in Madagascar (Elouard and Gibon, 2001), the genus is also probably absent of Madagascar. We possess some new material; its study will certainly help to correctly place this species. Furthermore, the prolonged dispute over the validity of the genus *Afroptiloides* and its inclusiveness or not in the genus *Acanthiops* needs to be finally resolved.



Figs. 17-20 - Fast-flow adapted genus: *Afroptiloides delphinae* (Fig. 17) and *Afroptiloides spinosum* (Figs. 18-20): 17 *in toto* (dorsal view); 18 head and thorax (lateral view); 19 abdomen (lateral view); 20 foreleg. Figs. redrawn from Gattolliat, 2000.

Despite the gaps mentioned above, the knowledge of the systematics of Baetidae is now sufficient to allow its use for faunistic and ecological studies, especially for problems related to water quality (e.g. impacts of logging activities in the remaining tropical forests).

We now also have the necessary tools for the reconstruction of the phylogeny of the Afro-Malagasy Baetidae. Such a reconstruction will be based on morphological characters. Molecular analysis should be performed to clarify the phylogenetic position of problematic taxa.

By estimating the genetic distance between African and Malagasy species, molecular phylogenetic studies will allow the determination of the significance of historical dispersal of Baetidae between Madagascar and Africa and consequently the relative importance of dispersal and vicariance in the composition of Malagasy fauna. We shall be able to determine the centers of origin of the main lineages and their historical distributions. This study will greatly improve our understanding of the mechanism of dispersion and colonization in the western part of the Indian Ocean.

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