

PREDACEOUS BAETIDAE IN MADAGASCAR: AN UNCOMMON AND UNSUSPECTED HIGH DIVERSITY

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ABSTRACT

Mayflies are generally considered as primary consumers; the majority of genera are either filterers or collector-gatherers. Very few feed on invertebrates. Predation can be found in different families, suggesting that the habit evolved independently in major lineages.

Three predaceous genera belonging to the family Baetidae were found in Madagascar. They feed mainly on other mayfly larvae. The diet at different stages was investigated by analysing the gut contents, and comparisons among species were performed. Besides, the study of morphology of mouthparts and legs allows us to propose apomorphies related to the predatory behaviour.

INTRODUCTION

The original nature of Madagascar is demonstrated by the extremely high diversity of some taxa and the absence of others (Paulian, 1996). This originality is the result of several factors. The long isolation of the Malagasy Plate, first from Africa (165 Ma B.P.), then from the subcontinent India (80 Ma B.P.) was the most fundamental event (Battistini, 1996). Major geodynamic events took place during the Eocene (50 Ma B.P.) with the new distribution of continental fragments derived from Gondwanaland. They induced the reorganisation of atmospheric systems and important changes on the Malagasy climate, as well as on its hydrological system (Fröhlich, 1996). As these events took place after the isolation of Madagascar, it allowed the exploitation by the present taxa of new free ecological niches. The absence of predators and more evolved taxa, at different levels of the trophic web, explains the remaining presence or the unusual success of different taxa; for example the absence of Felidae and evolved monkeys allowed the lemurs to survive and diversify (Mittermeier *et al.*, 1994); the rarity of insectivorous fishes (De Rham, 1996) led to the

reduction of predator pressure on the aquatic invertebrate community and allowed the evolution of the flightless mayfly genus *Cheirogenesia* (Ruffieux *et al.*, 1998). On the other hand, Madagascar is constituted by very contrasted climatic areas (tropical rain forest and degraded areas on the Eastern coast; deciduous forest, very dry on the Southern and Western coasts and almost completely degraded into relatively dry grassland on the Highlands); this implies also a high diversity of aquatic environments (Chaperon *et al.*, 1993).

The Baetidae is composed of more than 60 different genera. This is the most cosmopolitan mayfly family with the Leptophlebiidae. It is present on every continent and in every kind of freshwater habitat, from the smallest pond to the waterfall. The baetid diversity is very high in Madagascar. Fifteen genera are actually known, and we estimate that seven others are present but still not mentioned. It means that almost one-third of the world baetid genera are present in Madagascar. Although the present knowledge of Malagasy baetid is still very incomplete, we have evidence that this diversity is not only high at the generic level but also at the specific one.

Most of the baetid genera are considered as collector-gatherers or collector-filterers. They are trophic generalists, extremely facultative in the type of food they consume (Brown, 1961). Among them, only 5 are recognized as carnivorous: *Centroptiloides* Lestage from Africa, *Echinobaetis* Mol from Sulawesi (formerly Celebes), *Harpagobaetis* Mol from Surinam, *Raptobaetopus* Müller-Liebenau from Eurasia and *Barnumus* McCafferty and Lugo-Ortiz from Southern Africa. All these genera are monospecific, except *Raptobaetopus* known by two allopatric species.

Analysis of the gut contents of Malagasy Baetidae allowed the discovery of three further predaceous genera: *Nesoptiloides* Demoulin, *Herbrossus* McCafferty and Lugo-Ortiz and *Guloptiloides* Gattolliat and Sartori. This diversity is unsuspected in comparison to only five other carnivorous genera occurring in the rest of the world. These three genera are strictly endemic to Madagascar. According to our present knowledge, *Nesoptiloides* and *Guloptiloides* are monospecific, *Herbrossus* being represented on the Eastern coast by three species. These three genera are closely related. Actually, the classification of the African Baetidae is still not clearly established. According to Lugo-Ortiz and McCafferty (1998), these three genera belong to the *Centroptiloides* complex, that gathers together all the African carnivorous genera (*Centroptiloides* and *Barnumus*) and also more primitive genera such as *Afroptilum* Gillies and *Dicentroptilum* Wuillot and Gillies. According to Kluge (1997), they belong to the subfamily Afroptilinae.

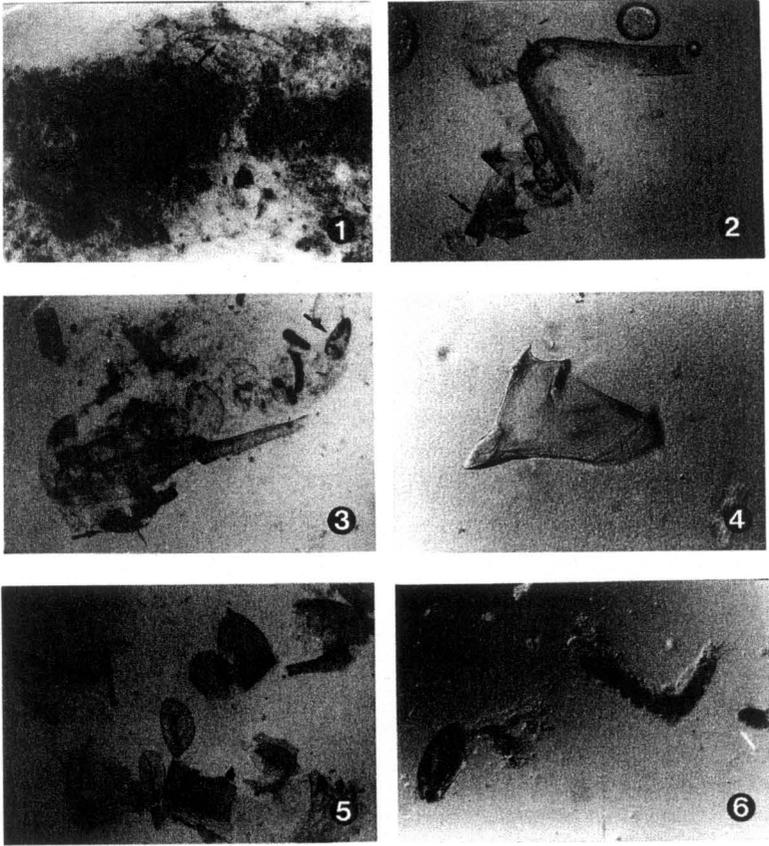
In this work, we want to compare the feeding behaviour between five species: *Herbrossus edmundsorum* McCafferty and Lugo-Ortiz, *H. christinae* Gattolliat and Sartori, *H. elouardi* Gattolliat and Sartori, *Nesoptiloides electroptera* (Demoulin) and *Guloptiloides gargantua* Gattolliat and Sartori. It is generally admitted that changes in mayfly diet occur during the final larval stages, either for higher-quality nutritional requirement or because larger animals can ingest larger particles (Cummins, 1973; Riaño *et al.*, 1997). Thus the diet was also compared among the different larval stages of each species.

We also observed the functional morphological evolution related to this diet. The most important adaptations have been found on the mouthparts and the legs. As the *Centroptiloides* complex presents all types of feeding behaviour, it appears particularly well-adapted to this study, as it offers, at the same locality, primitive and specialised genera.

MATERIAL AND METHODS

This study took place as a part of a general program of the ORSTOM lab: Biodiversity and Biotypology of the Malagasy Freshwaters. In this aim, more than 700 samples were taken in every types of running waters. The larvae as well as the imagoes of Ephemeroptera and Trichoptera were collected.

We chose stations where we possessed a large number of specimens of different stages. Whenever it was possible, we also chose localities where several carnivorous species were



Figs. 1 to 6. Gut contents: 1: second part of the gut content of *H. edmundsorum*, arrow: baetid leg, enlargement x100. 2: first part of the gut content of *H. edmundsorum*, enlargement x40. 3: gut content of *H. christinae* with pieces of *Xyrodromeus*, arrow: chironomid head. 4: gut content of *H. christinae*: mandible of *Xyrodromeus*, enlargement x400. 5: gut content of *N. electroptera*: pieces of *Afropitulum*, enlargement x40. 6: gut content of *N. electroptera*: chironomid, enlargement x100.

present. We sorted the larvae according to features based on size, the degree of development of the forewing pads, and for the female, the degree of maturation of the eggs. We named the last stage LM for Matured Larva, and then we numbered the different stages in decreasing order.

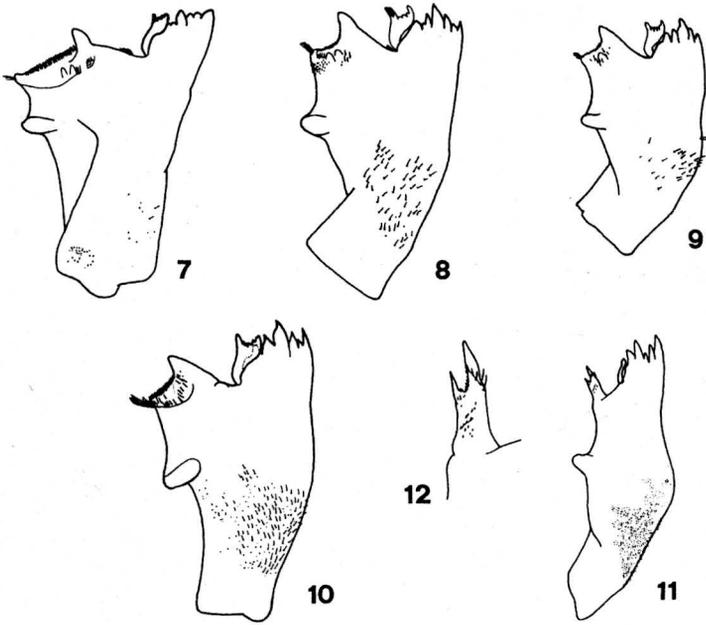
LM stage: larvae with the forewings well-visible inside the pads, the forewing pads reaching at least the anterior margin of the second tergite and eggs well-separated.

LM-1 stage: forewing scarcely distinctive inside of the pads, forewing pad reaching at least the middle of the first tergite and eggs still piled up.

LM-2 stage: forewing pad reaching at least the anterior margin of the first tergite.

LM-3 stage: forewing pad reaching at least the middle of the metathorax.

Because of the differences between male and female, we could not only use size to sort larval stages. We dissected each specimen and extracted the gut. A brief description of its



Figs. 7 to 12. Left mandible: 7: *Afroptilum* sp. 8: *H. elouardi*. 9: *H. christinae*. 10: *N. electropetera*. 11: *G. gargantua*. 12: *G. gargantua*: detail of the mola.

contents was made and the proportions of fine detritus, algae, macrophytes and prey were estimated. These values were relatively rough since we wanted to demonstrate a tendency more than an absolute number. Among the invertebrates, we tried to determinate the prey to the lowest systematic level: at the family for all the insects except to the genus for the Baetidae. The gut contents was mounted on slides in Liquid de Faure.

Mouthparts and legs of each species were mounted in Canadian Balsam after being bathed in a Creosote solution. The different parts were compared between species and genera.

RESULTS

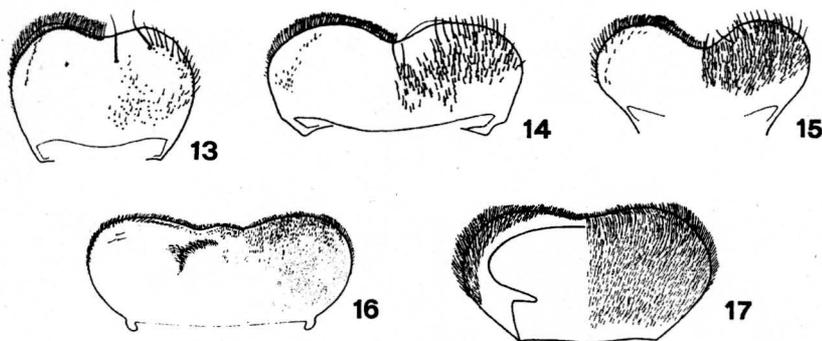
Diet

The three species of *Herbrossus* show different foraging strategies.

H. edmundsorum is detritivore during all the larval stages, except the last one. During this stage, its diet changes abruptly, and it becomes a quasi-strict predator (figs 1,2). The prey are mainly larvae of the baetid genera *Afroptilum* and *Dicentropilum*, and more rarely, Chironomidae larvae (fig. 23).

H. elouardi presents also a transition in the diet. During the young stages, since LM-3, the larvae feed mostly on fine detritus and macrophytes. Until LM-2, the larvae begin to feed on macroinvertebrates, mostly Simuliidae. *H. elouardi* presents a progressive transition from a detritivore to a carnivorous diet. At LM-2, *H. elouardi* feeds quasi-exclusively on Simuliidae. We did not own any data for the LM stage; all our mature specimens presented reduced and empty digestive tracts (fig. 23).

At LM-3, *H. christinae* is already partly carnivorous. Although the invertebrates, predominantly Simuliidae, represent half of the gut contents at LM-2, they are the main energetic



Figs. 13 to 17. Labrum (left ventral, right dorsal): 13: *Afroptilum* sp. 14: *H. elouardi*. 15: *H. christinae*. 16: *N. electropetra*. 17: *G. gargantua*.

source. The proportion of baetid larvae increases since LM-2 and becomes predominant at LM-1 (fig. 23). It is mostly constituted by larvae of the small genus *Xyrodromeus* Lugo-Ortiz and McCafferty (figs 3,4).

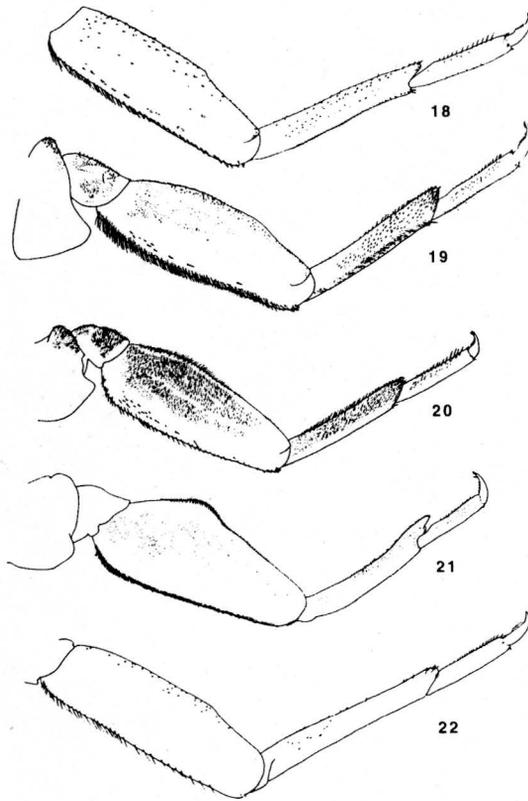
Nesoptiloides electropetra is a strict carnivorous species. Since the earliest stages, its gut contains quasi-exclusively invertebrates (figs 5,6). The size and diversity of the prey evolve between the different stages. At first this species feeds mostly on Diptera larvae (Chironomidae, Simuliidae and Blepharoceridae). Since LM-3, the baetid proportion becomes more and more important, with three genera: *Afroptilum*, *Dicentropilum* and in lesser importance *Xyrodromeus*. At LM-2 and LM-1, the prey are chewed; we found only small particles of cuticles of the same prey instead of whole parts such as legs, head and abdomen.

Little information is available on the diet of *Guloptiloides gargantua*. This species is actually only known at the larval stage by three specimens. Two of them had reduced and empty digestive tracts. Only one had its gut full. Its contents were exclusively baetids of the genus *Afroptilum* (fig. 23). According to the degree of development of the hindwing pads, we assign this larva to LM-3.

Morphological Adaptation

The comparison of the mouthparts of these five species indicated that the mandibles and the labrum are clearly the most adaptable part. The mandibles of *N. electropetra* (fig. 10), *H. edmundsorum* and *H. elouardi* (fig. 8) are the less transformed; they are stouter with more robust incisors, compared to those of *Afroptilum* (fig. 7). The evolution of the mandibles in *H. christinae* (fig. 9) shows a clear adaptation to predation: reduction of the mola and an increase of the lateral margin angulation (Gattolliat and Sartori, 1998). The molars of *G. gargantua* (fig. 12) are transformed into incisors, and the incisors themselves are completely modified for impaling the prey (Gattolliat and Sartori, 2000). This species presents the highest degree of morphological adaptation.

The labrum of the five species is conspicuously wider than long and almost completely covered dorsally with fine setae, which is not the case of those of *Dicentropilum* and especially of *Afroptilum* (fig. 13). The three species of *Herbrossus* have a deep and broad U-shaped anteromedian emargination (fig. 14), most developed in *H. christinae* (fig. 15). The labrum of *G. gargantua* (fig. 16) is three-lobed, but the median lobe is shorter and consequently could function as an anteromedian emargination. The labrum of *N. electropetra* (fig. 17) is by far the most transformed. It is dorsoventrally extremely thick, to some extent comparable to the seal elephant nose.



Figs. 18 to 22. Foreleg: 18: *Afroptilum* sp. 19: *H. elouardi*. 20: *H. christinae*. 21: *N. electroptera*. 22: *G. gargantua*.

The forelegs of the three species of *Herbrossus* (fig. 19) have numerous, acute setae on the femora and tibiae. As for the mandibles, *H. christinae* (fig. 20) shows the most important adaptation with numerous and well-developed setae on both femora and tibiae. Apart from the numerous setae, *N. electroptera* (fig. 21) shows two apomorphies on the forelegs; femora with pronounced ventral convexity and tibiae with a conspicuous ventrodistal process (Demoulin, 1973). The second apomorphy is clearly an adaptation to catching and holding prey. The forelegs of *G. gargantua* (fig. 22) do not show any apomorphy; they are similar to those of *Afroptilum* (fig. 18).

DISCUSSION

Among these five predaceous genera, we found three different strategies.

N. electroptera, *G. gargantua*, and to a lesser extent *H. christinae*, can be considered as strictly carnivorous. Since the earliest stages, they mainly or strictly feed on invertebrates. The only changes are the increase of the size and proportion between Baetidae and Diptera. The earliest stages feed mainly on Diptera, especially on Simuliidae and then switch to Ephemeroptera (mainly on Baetidae) during the next stages. This kind of diet occurs seldom among the carnivorous baetid, most of the genera feeding mainly on Diptera (Chironomidae and Simuliidae). This is the case of *Raptoabaetopus* which is strictly carnivorous, feeding on

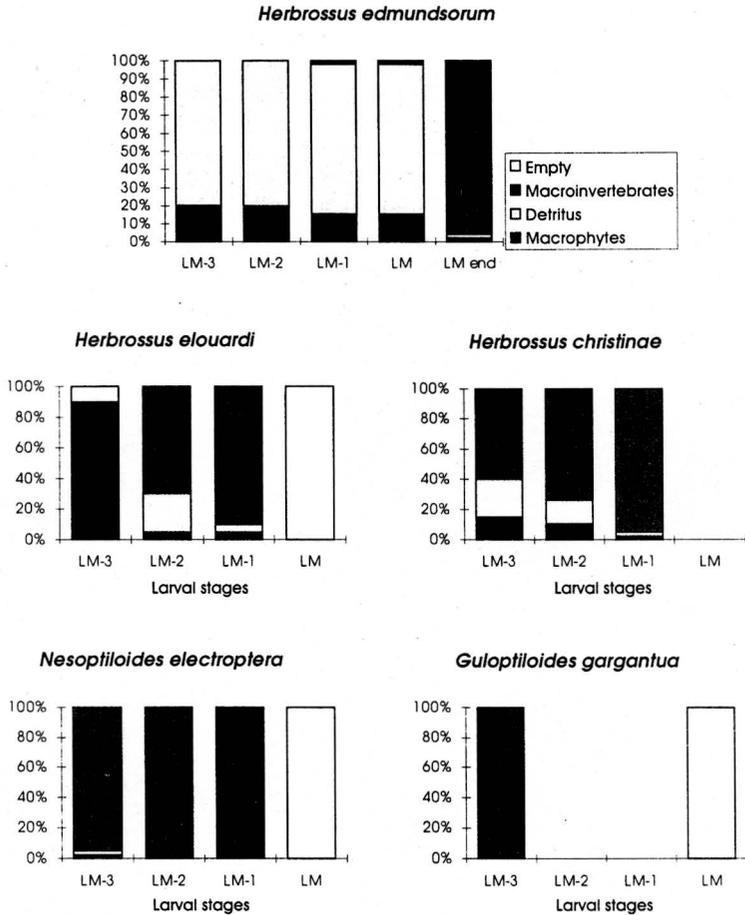


Fig. 23. Diet of the five species. Larval stages: see material and method.

Oligocheta and Diptera (Müller-Liebenau, 1978; Fontaine and Perrin, 1981), and of *Harpagobaetis gulosus* which feeds exclusively on Simuliidae (Mol, 1986). *Echinobaetis phagas* feeds mainly on Baetidae and in a less important proportion on Simuliidae and mayflies from other families (Mol, 1989). *Centroptiloides bifuscata* feeds mainly on Simuliidae and Baetidae. The proportion of Baetidae increases with the size and the larval stage. No filamentous algae were present in the digestive tract and much fine detritus was identifiable as larval remains (Agnew, 1962). This author also suggested that the type of food ingested by *C. bifuscata* depends on the availability and relative abundance of the different prey. He found a more or less direct correlation between the size of the prey eaten and the size of the larva. Prey found in the foregut of *C. bifuscata* seemed to have been little damaged by chewing, although some of the larger larvae appeared to have been merely bitten in half, probably to aid ingestion (Agnew, 1962). These two species, *C. bifuscata* and *E. phagas* appear to be the only species with a diet similar to those of *N. electoptera*, *G. gargantua* and *H. christinae*.

Among the *Centroptiloides* complex, we considered that *Afroptilum* and *Dicentroptilum* are the most primitive species presenting less adaptive structures; the mouthparts and the legs are the most plesiomorphic. In this complex, the mouthparts, particularly the mandibles, show

important morphological adaptations. We can mention the large and robust mandibles with specialised armature of *Edmulmeatus* (Lugo-Ortiz and McCafferty, 1997a) and the bladelike mandibles of *Xyrodromeus* (Lugo-Ortiz and McCafferty, 1997b).

The Malagasy carnivorous species show a number of morphological adaptations. Among them, we can list: the short and broad shape of labrum with numerous sensitive setae, mandibles with stout and acute incisors, the increase of the lateral angulation, the molar reduction and its apical transformation to form a process analogous to the incisors (*G. gargantua*, fig. 23). It had been proposed that these adaptations are apomorphies clearly associated with a predatory behaviour (Lugo-Ortiz and McCafferty, 1998). The degree of specialisation of diet is directly related to the degree of adaptation of the mouthparts; for example the most adapted labrum to maintain the prey is the one of *N. electroptera* (fig. 17) and the most adapted mandibles for impaling are those of *G. gargantua* (fig. 11). *N. electroptera* appears to be the only species which chews the prey at least at the last stages. It means that its mandibles (fig. 10) are not only adapted for impaling, as in *G. gargantua*, but also for chewing.

We can find the same adaptations of the mouthparts among the other carnivorous genera of Baetidae (*Raptobaetopus*, *Harpagobaetis*, *Echinobaetis*, *Centropiloides*), but also among three Northern American predaceous genera of Heptageniidae (McCafferty and Provonsha, 1986).

The forelegs also show significant adaptation for catching, holding and the impaling of the prey. The ventral margin of the femora and tibiae are covered with stout and acute setae. They are especially numerous in *N. electroptera* (fig. 21) and *H. christinae* (fig. 22).

The high degree of development of the femoral ventral convexity and the ventrodistal process of *N. electroptera* represent apomorphic adaptation for catching and impaling the prey. In this way, *N. electroptera* appears to have the most adapted legs for carnivorous behaviour.

H. elouardi changes its diet at the LM-2 stage (fig. 23). During the earliest stage, it can be considered as a collector-shredder, then its diet becomes more and more carnivorous, feeding mostly on Simuliidae. All the mature larvae caught had empty gut. We can presume that it must not be an important change of diet with the previous stage, maybe the proportion of Baetidae would increase. Its mouthparts and legs are less modified, allowing a more omnivorous diet.

H. edmundsorum is the most interesting case. It is a collector-shredder species during all its larval life except the second part of the last stage (fig. 23). The change between fine detritus and macrophytes to invertebrate prey is extremely fast (figs 1,2). It is difficult to find a single explanation for this behavioural change. It is obvious that invertebrates make up an energetic source much more important than detritus and macrophytes. They are the highest quality food because of both high calorific and protein contents (Cummins and Klug, 1979). Proteins represent between 50 and 85% of the total dryweight of mayflies, lipids between 10 to 25% and carbohydrates between 5 and 10% (Meyer, 1990; Ruffieux, 1997). Moreover ingested food is not equal to assimilable food; we can admit that invertebrate are easier ingested than detritus (Hawkins, 1985). This change consequently permits an important input of protein and lipid. The female imagoes need a large amount of energetic reserve for gamete production and compensation flight. But this diet change seems not directly connected with these supplementary energetic needs, since we found the same change of feeding behaviour among male and female mature larvae. It could be a determinant input if we consider that the imagoes do not eat, and permit a longer imaginal life or the attribution of more abundant reserves for flight. If the advantages of this change of diet are quite clear, we do not understand why it does not occur at earlier stages, especially if we consider that there are no morphological changes between the carnivorous and the collector-gather larval stages. The abundance of prey refutes the possible competition between the different stages; moreover, the differences among prey size avoids this competition. It had been demonstrated that addition of invertebrates to the diet of the *Clistronia magnifica* (Trichoptera) at the last stage, highly increases the production of eggs and the rate of development, and decreases the

death rate (Anderson, 1976). The carnivorous diet of *H. edmundsorum* could also be optional, but could highly increase its reproductive success.

We can state that the changes in diet as the larvae are not matched by changes in the mouthparts between the stages. Each species mouthparts are an adaptive compromise to offer the best fitness at all stages. Consequently, we can not deduce from the mouthparts the diet at each stage, but we can formulate a global diet for the entire larval life.

We noticed that four of the five species feed mainly on Baetidae, at least at one stage. The identification at the genus level is relatively easy, but a determination at a species level is impossible as long as the knowledge of the Malagasy Baetidae is so scarce. We found prey of the genera *Afroptilum*, *Dicentropilum* and *Xyrodromeus*. *Afroptilum* and *Dicentropilum* were by far the most abundant in the gut of *G. gargantua*, *H. edmundsorum* and *N. electroptera* (figs 2, 5, 6). *Afroptilum* and *Dicentropilum* were also the most abundant genera in all the prospected stations. The proportion between *Afroptilum* and *Dicentropilum* depended on the localities for the same species at the same larval stage. According to that, we can conclude that these three species are more opportunist than selective in their choice of prey.

Xyrodromeus is dominant in the gut of *H. christinae* (figs 3,4), but is relatively scarce in the gut of other species. This difference can have two explanations. The Malagasy species of *Xyrodromeus* are smaller than those of *Afroptilum* and *Dicentropilum*; in this way, they appear more suitable prey for smaller predator such as *H. christinae*. *Xyrodromeus* present morphological adaptation to the fast flow and its bladelike mandibles seem to indicate that *Xyrodromeus* exploits a different ecological niche than *Afroptilum* and *Dicentropilum*. The study of its gut contents shows this genus feed mostly on macrophytes and algae. As *H. christinae* is sympatric with *H. edmundsorum*, we can admit that both species exploit different ecological niches. Field observations confirm that the niche exploited by *Xyrodromeus* and *H. christinae* is more reduced.

A lot of larvae that are ready to moult are present in the gut contents. This could be explained by the reduced mobility of the larvae during this interstage.

We must note that we found no larva of caddisfly in the gut contents of our five species, even though this order is quite abundant in Eastern coast rivers (Gibon *et al.*, 1996). None of the five species fed on algae at any stage.

We can conclude that the five species show clear adaptations to predaceous behavior. We propose apomorphies directly related to the diet on the labrum, the mandibles and the forelegs. These features are more developed in the species *N. electroptera*, *G. gargantua* and *H. christinae*. It can easily be explained by their quasi-carnivorous diet from the earliest stages. At the opposite, *H. edmundsorum* and *H. elouardi* have less adapted mouthparts; this allows a more omnivorous diet, becoming carnivorous only at the last stages to supply high quality nutritional requirements.

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