

A SYNOPSIS OF THE AFROTROPICAL TRICORYTHIDAE

Helen M. Barber-James

Department of Freshwater Invertebrates, Albany Museum, Grahamstown 6139, South Africa and the Entomology Department, Rhodes University, Grahamstown

Abstract

The Tricorythidae of the Afrotropical Region is currently composed of five described genera, three of which are thought to be restricted to Madagascar (*Madecassorythus* Elouard and Olliarioniny, *Ranorythus* Olliarioniny and Elouard, and *Spinirythus* Olliarioniny and Elouard), one which is restricted to Africa (*Dicercomyzon* Demoulin), and one which is thought to be distributed on both landmasses (*Tricorythus* Eaton). Based on sexual dimorphism, manifest in the relative eye size of mature male and female nymphs and adults and on the structure of the genitalia of adult males, it is proposed that there are two additional genera in Africa, as yet undescribed. One of these genera is represented by a species currently placed in *Tricorythus* (*T. discolor* [Burmeister]). Several other undescribed species within South Africa have been identified as belonging to the group. A second lineage is represented by *Tricorythus tinctus* Kimmins, from Uganda, the only currently described species. There are also several more undescribed species of this group widespread in Africa.

Key words: Africa; Madagascar; Afrotropical; Tricorythidae; Ephemeroptera; mayfly.

Introduction

Currently, ten African species are placed in the genus *Tricorythus*, all described as adults, but with only three also known in the nymphal stage. A further nine species of *Tricorythus* are described from Madagascar (Olliarioniny et al. 1998b), all described as adults. Only one species, *Tricorythus tinctus* Kimmins 1956 has a sound nymphal–adult association (Corbet 1960). For *Tricorythus discolor* (Burmeister) 1839, the nymph was described nearly 100 years later (Barnard 1932). Barnard (1932) also described adult *Tricorythus reticulatus* with Crass (1947) describing the presumed nymph.

Little is known of the other six so-called *Tricorythus* species from Africa, each of which have been scantily illustrated and described, often from female subimagos (Ulmer 1916, 1930; Navás 1936). Even the type species, *T. varicauda* Eaton (1868), is not adequately described. Demoulin (1954b) summarized all that was known about the Tricorythidae at that time. Material of each of these species needs to be examined and nymphal–adult associations made from collections of fresh material.

The taxa being considered in this paper are distributed within the Afrotropical region. This is defined by Crosskey and White (1977) to include Africa south of the Sahara Desert, conveniently delimited by the 254 mm (10 inches) rainfall isohyets (Fig.1), and the Malagasy region. Although Egypt falls out of this region, it is included in this paper as the type species of *Tricorythus* was collected there. This is interesting as it represents the northern-most distribution of the family Tricorythidae, as defined by McCafferty and Wang (2000). The presence of the genus in Egypt suggests possible colonization by the Egyptian species via the Nile and suggests the type species is not the ancestral species. Other members of the family are known from Asia (Ulmer 1913; Sroka and Soldán, these proceedings), suggesting a Gondwanan origin of the family. The currently known genera of Afrotropical Tricorythidae are summarized in Table 1.



Figure 1. The Afrotropical region.

Table 1. Summary of current genera in the Tricorythidae of the Afrotropical region.

Genus	No. of species	Distribution
<i>Madecassorythus</i> Elouard and Oliarioniny, 1997	4 spp	Madagascar
<i>Spinirythus</i> Oliarioniny and Elouard, 1998	3 spp	Madagascar
<i>Ranorythus</i> Oliarioniny and Elouard, 1997	2 spp	Madagascar
<i>Tricorythus</i> Eaton, 1868	19 spp	Madagascar and Africa
<i>Dicercomyzon</i> Demoulin, 1954a	4 spp	Africa

Historical Background to Classification of Afrotropical Tricorythidae

Eaton (1868) placed *Tricorythus varicauda* from Egypt, (originally described by Pictet [1843] as *Caenis*), into his newly created genus *Tricorythus* as the type species for the genus. Only the adult male was described and this was done in inadequate detail. Before the family Tricorythidae was erected, Burmeister (1839) described three species, which he placed in the genus *Oxygypha* (two of these were subsequently placed in *Caenis* by Jacob [1974]). Burmeister's (1839) third *Oxygypha* species, *O. discolor*, was placed in *Tricorythus* by Eaton (1884), after having undergone a series of generic name changes prior to this (Appendix A). Burmeister's poor description was of a female subimago, with the only locality information given as the Cape of Good Hope. Eaton (1884) evidently re-examined Burmeister's material, giving a slightly expanded description of the dry female subimago. Esben-Petersen (1913) described a male of *T. discolor* from Tulbagh (western Cape) and two female subimagos from M'fongosi, Zululand, which he assumed belonged to the same species. Ulmer (1921) further expanded the description of the female from Burmeister's material. Lestage (1924) stated that Ulmer's description agreed with the attributes of *T. discolor* as described by Esben-Petersen (1913). Esben-Petersen (1920) briefly described another unnamed species, again a female subimago, from the Free State, which he maintained was different to *T. discolor*. Lestage (1924) suggested that Esben-Petersen's (1920) female subimago needed to be reassessed in the light of Ulmer's (1921) elaboration on the known information for *T. discolor*, though nothing further was concluded.

The first *Tricorythus* nymph described was *T. discolor*, from the western Cape by Barnard (1932), who redescribed both sexes of the adult at the same time as describing the nymph. Lestage (1942) noted the similarity between Barnard's nymph and the nymph of the Javanese *T. jacobsoni* described by Ulmer (1939), except for the absence of maxillary palps in *T. jacobsoni*. Recent reexamination of Barnard's material indicates that *T. discolor* is not a *Tricorythus* at all, but represents an undescribed genus, many specimens of which have been collected from all over

southern Africa since then. This will be discussed further in a section below. Sroka and Soldán (these proceedings) have erected a new genus to accommodate *T. jacobsoni* and have described a further six new species within that genus from Asia.

Barnard (1932) described a female subimago as *Tricorythus reticulatus*, basing the description on the irregular network of veins in the wings. The type of this is a shrivelled female subimago on a pin. Crass (1947) described a male that he thought was *Tricorythus reticulatus*, though in little detail, and tentatively designated an unassociated nymphal exuvium as representing the nymph. These were from the Lions River, in KwaZulu-Natal, an area approximately five degrees of latitude north of the site where Barnard's adult was collected (east of Swellendam, in the Western Cape). There is nothing to indicate that Crass' material is related to that described by Barnard. There is no record of where Crass' material was lodged, and it is not amongst the material housed at the Natal Museum or Albany Museum, so there are no types to compare with. However, material from the Mooi River, geographically close to the Lions River, fits his description and has allowed closer observation of this species.

Navás (1936) erected the genus *Neurocaenis* (basing this on a female subimaginal specimen, and placed within the family Caenidae at that stage) to accommodate certain African species with a particular kind of wing venation. He decided this wing venation was distinct from what had been described as typical *Tricorythus* wing venation. *Tricorythus fuscata* was the type species for *Neurocaenis*. A further five African species were included in *Neurocaenis* (Appendix 1) as was the Oriental species *T. jacobsoni*. After examining nine new species of *Tricorythus* from Madagascar, Olliarinony et al. (1998b) found the venation was intermediate between that described for *Neurocaenis* and *Tricorythus* and thus decided on the synonymy of the two genera, with the name *Tricorythus* taking precedence due to seniority.

The genus *Dicercomyzon* Demoulin (1954a) has a less complex history than *Tricorythus*. It was first described and named on its very characteristic nymphal stage (Demoulin 1954a) and the first adults were described by Kimmins (1957). These have quite distinct male genitalia with less distinct wing venation.

Madecassorythus (Elouard and Olliarionony 1997) was first described from adult material with nymphs subsequently described by Olliarinony et al. (2000). As nymphs, specimens of *Madecassorythus* are very similar to those of *Tricorythus*. The differences lie more clearly with the adults, particularly in the structure of male genitalia. *Madecassorythus* (Fig. 2B) has completely divided penes and long auxiliary processes (terminology used by McCafferty and Wang (2000)—also referred to as gonostyles by Elouard and Olliarionony (1997). *Tricorythus* on the other hand (Figs. 2G and H) has fused penes and no auxiliary processes. McCafferty and Wang (2000) suggested that *Madecassorythus* and *Dicercomyzon* belong together in a subfamily Dicercomyzoninae based on similarities in the male genitalia (Figs. 2A and B), but the description of *Madecassorythus* nymphs by Olliarinony et al. (2000) suggests a closer association of *Madecassorythus* with *Tricorythus*.

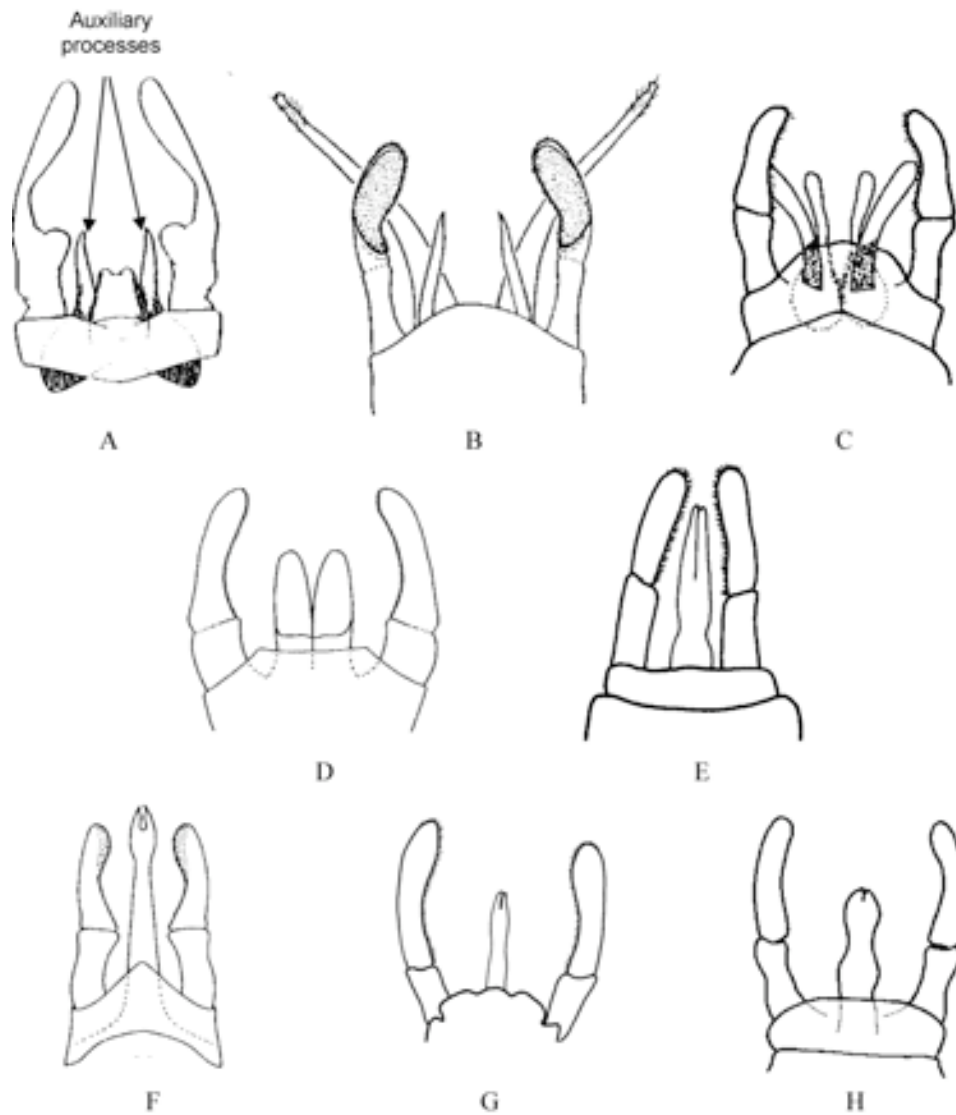


Figure 2. Male genitalia representing each genus of the Tricorythidae. (A) *Dicercomyzon* (redrawn from Kimmins 1957). (B) *Madecassorythus* (redrawn from Elouard and Oliarinony 1997). (C) *Spiniyrythus* (redrawn from Oliarinony 1998). (D) *Ranorythus* (redrawn from Oliarinony and Elouard 1997). (E) *T. discolor* group (material from Mukhutswi stream, Mpumalanga, South Africa). (F) *T. tinctus* group (material from the Sabie River, Kruger National Park, South Africa). (G) *T. reticulatus* (material from Mooi River, KwaZulu-Natal). (H) *Tricorythus ambinintsoae* (Madagascan sp.) (redrawn from Oliarinony et al. 1998b).

Ranorythus (Oliarinony and Elouard 1997) and *Spinirythus* (Oliarinony and Elouard 1998, in Oliarinony et al. 1998a) have only been formally described in the adult stage. The species in each of these two genera have distinctive male genitalia. Like *Madecassorythus*, *Spinirythus* has divided penes and auxiliary processes (Fig. 2C). *Ranorythus* however, has broad, partially fused penes and no auxiliary processes (Fig. 2D). The nymphs of the species in these two genera have been documented by Oliarinony (1998). The general nymphal form and mouthparts showing a remarkable resemblance to those of the other African and Malagasy Tricorythidae, except for *Dicercomyzon*.

A member of the genus *Tricorythafer* (Lestage 1942), originally described from the Congo by Needham (1920) as *Caensopsis futigans*, was included in the Tricorythidae by Demoulin and Edmunds (1954). McCafferty and Wang (2000) synonymised *Tricorythafer* with *Tricorythodes* Ulmer, placing these in the family Leptohyphidae. This family is considered to have a Nearctic and Neotropical distribution. Thus the generic and family placement of Needham's species "*futigans*" is unclear and will be treated in a separate paper after examination of the type material.

The current genera and species of Afrotropical Tricorythidae are summarized in Appendix A, which includes synonyms and known distributional ranges.

Observations from Recent Studies

Currently grouped within the genus *Tricorythus*, there is a distinct lineage of which only one species, *T. tinctus* Kimmins (1956), has to date been described from Uganda. Both the adult and nymph (the latter described by Corbet [1960]) of this species are known. There are several other undescribed species that clearly belong to this group. These are widely distributed in Africa from the Ivory Coast (Elouard, *personal communications*) and the Congo (Demoulin 1957), and several collected more recently from the Kabompo River (Zambia), Cunene River (Namibia) and tributaries of the Limpopo River system (South Africa). This group of species is clearly different to those described as *Tricorythus* s.s., and deserves to be elevated to a generic ranking. The distinctive characters include the greatly produced incisors on the mandibles (Fig. 3) and the male genitalia (Fig. 2F), which have penes slightly longer than the claspers, fused from the base for about four-fifths of their length. These are consistent characters in all of the new species examined, though nymphal-adult associations are not known for all species. There are clear specific differences between the species from each area. The actual description of this new genus and each new species will be done in a future paper.

There is a second African group, also currently placed within the group traditionally called *Tricorythus*. The species in this group have clear sexual dimorphism, with males smaller than females, and with eyes much bigger than in the female (Fig. 4A). This characteristic is clearly visible in both the nymphs and adults.



Figure 3. Dorsal view of left and right mandibles of a species contained in the genus the “*tinctus*” group. Material from the Sabie River, Kruger National Park, South Africa.

Reexamination of some of the material used by Barnard (1932) in his expanded description of *T. discolor* has revealed that those specimens also have such dimorphism, suggesting that *T. discolor* is in fact not a member of *Tricorythus* after all. In *Tricorythus*, the males and females have similarly small eyes as have members of the *T. tinctus* group (Fig. 5). However, the sexual dimorphism with large eyes in the male is also seen in the genera *Ranorythus* and *Spinirythus* (Figs. 4B, C). Interestingly, it has also been noted in a new genus described from Asia (Sroka and Soldán, these proceedings). The African specimens with these characteristics need to be placed in a genus of their own, leaving *T. reticulatus* as the only southern African *Tricorythus* species, together with the remaining species from further north in Africa (Appendix A).

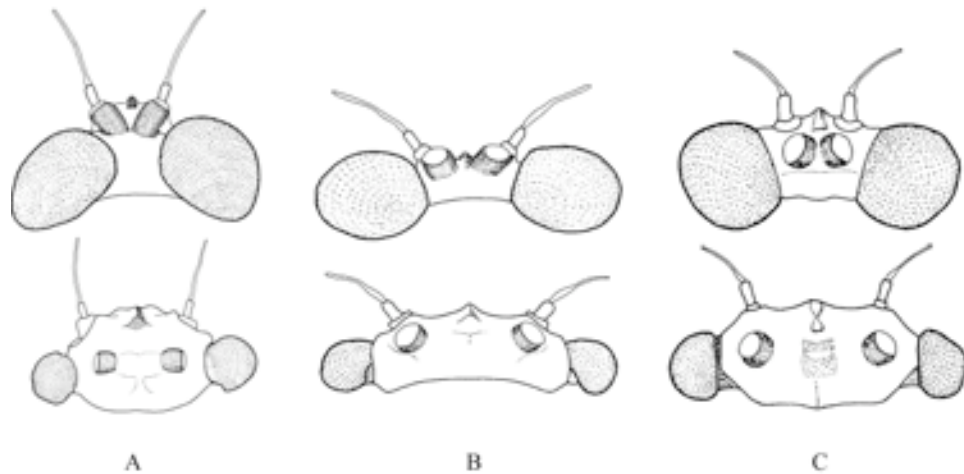


Figure 4. Heads of adult males (above) and females (below) of genera which have male eyes larger than female eyes (adults illustrated, but also evident in the nymphs). (A) *T. discolor* group (material from Mukhutswi stream, Mpumalanga, South Africa). (B) *Ranorythus* (redrawn from Oliarinony and Elouard 1997). (C) *Spinirythus* (redrawn from Oliarinony 1998). *Dicercomyzon* not included.

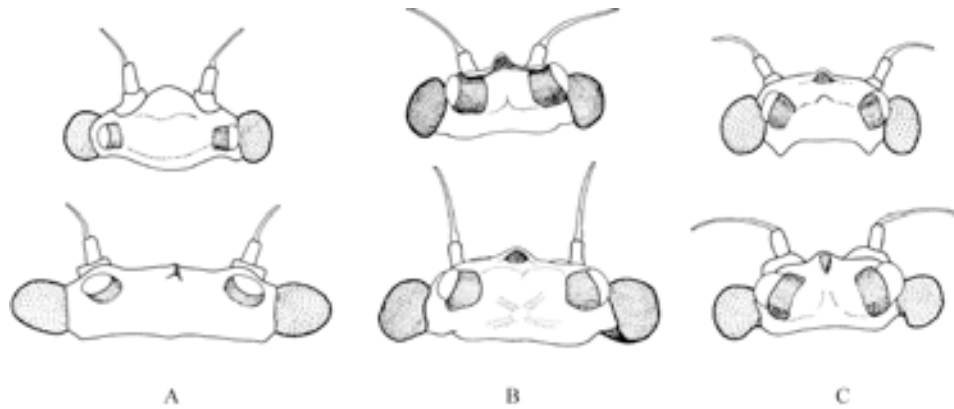


Figure 5. Heads of adult males (above) and females (below) of genera which have male eyes similar in size to female eyes (adults illustrated, but also evident in the nymphs). (A) *Tricorythus* sp. (Madagascar) (redrawn from Oliarinony et al. 1998b). (B) *Tricorythus reticulatus* (material from Mooi River, KwaZulu-Natal). (C) *T. tinctus* group (material from the Sabie River, Kruger National Park, South Africa).

Apart from male eye size differences in some species and the extended mandibles evident in the *T. tinctus* group, the nymphs of all genera except *Dicercomyzon* are very similar. In order to clarify the relationships between these seemingly similar nymphs, one has to look at their adults. Certain of the groups have very unusual and distinctive male genitalia (Figs. 3A–H), which clearly distinguish them as different genera. Wing venation does not seem very helpful as it is very variable between specimens within a species. Table 2 provides a useful summary of the salient morphological features of the adult males of each genus.

Discussion

The information gathered during this study demonstrates the presence of two new Tricorythidae genera in Africa (Table 3). While the adult characteristics of *Dicercomyzon* lie within the variation shown by the other genera of African, Malagasy and the Asian Tricorythidae, the nymphs of *Dicercomyzon* species show many distinctive morphological features (Demoulin 1954a, Kimmins 1957). These include a very flattened body form with broad, flattened tibiae; highly derived mouthparts; uniquely fibrillate gills; and a unique arrangement of ventral abdominal setae, which apparently form a suction disc. Until recently, the Tricorythidae contained two other genera, which have been given their own family status (McCafferty and Wang 2000), these being Machadorythidae and Ephemerythidae. At this point, *Dicercomyzon* clearly stands out from the other members of the

Tricorythidae in its nymphal stage, and further consideration needs to be given to decide whether it also deserves its own family status.

Table 2. Diagnostic features of adult males in the Afrotropical Tricorythidae genera.

	Eyes	Auxiliary processes (Gonostyle)	Penes	Length of auxiliary processes	Spines at base of penes
<i>Dicercomyzon</i>	♂ larger than ♀	present	Fused for most of length	Longer than penis	absent
<i>Madecassorythus</i>	♂ larger than ♀	present	Completely separated	Much shorter than penis	present
<i>Spinirythus</i>	♂ larger than ♀	present	Completely separated	Only slightly shorter than penis	present
<i>Ranorythus</i>	♂ larger than ♀	absent	Fused for half of length	No auxiliary processes	absent
<i>Tricorythus</i>	♂ similar to ♀	absent	Fused except near apex	No auxiliary processes	absent
“ <i>discolor</i> ” group	♂ larger than ♀	absent	Fused for half of length	No auxiliary processes	absent
“ <i>tinctus</i> ” group	♂ similar to ♀	absent	Fused except near apex	No auxiliary processes	absent

Table 3. Revised estimate of number of genera and species of Tricorythidae in Africa and Madagascar.

Genus	No. of species	Distribution
<i>Dicercomyzon</i>	4 spp	Africa
<i>Madecassorythus</i>	4 spp	Madagascar
<i>Spinirythus</i>	3 spp	Madagascar
<i>Ranorythus</i>	2 spp	Madagascar
“ <i>discolor</i> ” group (new genus)	3 spp	Africa
“ <i>tinctus</i> ” group (new genus)	5 spp	Africa
<i>Tricorythus</i> (<i>varicauda</i> group)	17 spp	Madagascar and Africa

With the realization that *T. discolor* belongs in a genus distinct from *Tricorythus*, it is apparent that no nymphs of “true *Tricorythus*” have been associated with adults and described, apart from the description of *T. reticulatus*. This, however, was poorly described by Crass (1947) and was not associated with the type material of that species described by Barnard (1932). Nymphs and reared adult males of *T. reticulatus* need to be found and associated in the western Cape to confirm whether Crass’ nymphs and adults from KwaZulu-Natal are the same species as those found in the western Cape. To get a better understanding of the relationships between the genera, it is essential to collect nymphs of the type species of *Tricorythus* (*T. varicauda*) from Egypt. It is also important for the other African species currently described as adults to have the nymphal stage correlated with them.

One may question how the seemingly obvious character of eye size between males and females can have been overlooked in the earlier descriptions of *T. discolor*. Esben-Petersen's (1913) drawing and notes of the species are very vague. Burmeister (1839) described only the female subimago and in his description of his genus *Oxycypha* he says “compound eyes small, simple ...”, so due to lack of sufficient material he missed the important sex-related eye dimorphism. Examining some of the material used by Barnard 1932 (Hex River, Western Cape), the adult male has distinctly larger eyes than the females, which has also not been mentioned in the literature. Looking at nymphs from the same collection, there are several female nymphs, but only a few males, with the bigger eyes. Until recently, this dimorphism has remained unnoticed, despite the fact that the genus is widespread in South Africa. The observation of male-female sexual dimorphism was first reported by Barber-James (1995) in an unidentified species from the northeast Cape.

It is interesting to note that all descriptions of female specimens by the various authors have apparently been of subimagos. Closer observation of many female specimens in the Albany Museum collection has revealed that none have shed the subimaginal skin on their wings. Males do, however, go through a moult from subimago to imago. Whether the females do not moult at all or just retain the subimaginal skin on their wings is not clear. It is known, for example, that some of the Oligoneuriidae shed the subimaginal cuticle from the body but not from the wings (Edmunds and McCafferty 1988). Detailed studies of the cuticle from the body of each of the Tricorythidae genera will have to be undertaken to confirm what is happening in this family. The weak, reticulate venation observed in some specimens may be due to the fact they are subimagos. Crass (1947) observes that the reticulate appearance of the wings in his male specimens of *T. reticulatus* is less obvious than in the female.

Selected characters from both nymphal and adult stages of known or described species from each genus (Table 4) were assessed to produce a matrix of character states, which are considered either plesiomorphic or derived (Table 5). These are by no means comprehensive, but access to material of some of the genera to closely investigate further characters is needed before producing a more comprehensive set of characters.

Table 4. Fourteen characters of the adult and nymphal stages of Afrotropical Tricorythidae. Polarity is determined against a hypothetical outgroup which is entirely plesiomorphic (0 = ancestral state; 1,2 = derived states). Multistate characters are ordered.

Character	Character States
<i>Adults</i>	
1. ♂ genitalia (penes)	completely separated = 0 partially fused = 1 fused (apex notched) = 2
2. Auxiliary process on ♂ genitalia	Absent = 0 present = 1
3. Spines at base of penes	Absent = 0 present = 1
4. ♂ eyes size relative to ♀	same size = 0 bigger = 1
5. Median cercus	present = 0 absent = 1
<i>Nymphs</i>	
6. Arrangement of setae on fore-femur	scattered = 0 in a pattern = 1
7. Ratio of fore-femur length/width	>1.5 (relatively longer) = 0 <1.5 (relatively wider) = 1
8. Claw denticle distribution	many along length of claw = 0 specialized = 1
9. Gill structure	lamellate with fibrillar tufts beneath = 0 fibrillate only = 1
10. Maxillary palps	well developed = 0 reduced = 1 absent = 2
11. Mandible - incisors	incisors small and even = 0 outer and inner incisors well developed but approx even in size = 1 outer incisor greatly produced = 2
12. Mandible - setae	without fringe of setae = 0 lateral margin fringed with setae = 1
13. Labium	glossae and paraglossae not reduced or fused = 0 glossae reduced = 1 glossae and paraglossae fused = 2
14. Shape of hypopharyngeal superlingua	not produced laterally = 0 produced laterally = 1

Table 5. Matrix of selected character states for seven taxa in the Afrotropical Tricorythidae. For definition of characters refer to Table 4. "-" indicates character state uncertain at present.

Taxon	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Diceromyzon</i>	2	1	0	1	1	0	1	0	1	0	0	0	1	1	2
<i>Madecassorythus</i>	0	1	1	0	0	1	0	1	0	1	1	1	2	0	1
<i>Spinirythus</i>	0	1	1	1	0	-	0	-	0	1	1	1	2	0	1
<i>Ranorythus</i>	1	0	0	1	0	1	0	1	0	1	1	1	2	0	2
<i>Tricorythus</i>	2	0	0	0	0	1	0	1	0	1	1	1	2	0	0
"discolor" group	1	0	0	1	0	1	0	1	0	1	1	1	2	0	1
"tinctus" group	2	0	0	0	0	1	0	1	0	1	2	1	2	0	0

The selected characters were analyzed using the program HENNIG86 (Farris 1988) using the exhaustive tree-finding process known as implicit enumeration (i.e.). All multistate characters were ordered by default by HENNIG86. A hypothetical plesiomorphic outgroup was chosen. Of the nine equally parsimonious trees produced, one of these is represented in Fig. 6. In all of the trees, *Diceromyzon* remained clearly separated from the other groups. Three other clades grouped in pairs as in Fig. 6, though the relationships of these pairs varied. Thus, this analysis indicates a close relationship between *Ranorythus* and the new genus represented by *T. discolor*, between *Madecassorythus* and *Spinirythus*, and between *Tricorythus* (characters from *T. reticulatus* and the Madagascan *Tricorythus* species) and the new genus represented by *T. tinctus*. Molecular work and comparative studies of the eggs of each group, and accumulation of more morphological feature will help to refine this preliminary analysis.

Conclusions

Much works needs to be done on the African Tricorythidae to resolve subtle differences between the nymphs of as yet undescribed species in the two new genera. It is also necessary for many species currently described as adults only to have the nymphal stage correlated with them. Scanning electron microscopy is underway in collaboration with Professor Elda Gaino of Perugia University to compare the eggs of as many species within each genus as possible. Molecular analysis is being carried out in association with Dr. Michael Monaghan at the Natural History Museum, London. Such additional information will help to test the phylogenetic relationships between the different genera that are proposed here.

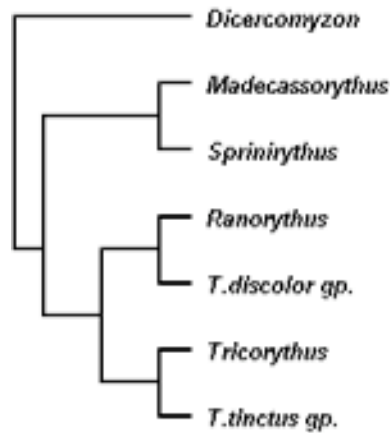


Figure 6. Possible phylogenetic relationships between the genera of the Afrotropical Tricorythidae based on a cladistic analysis of the character matrix in Table 5. Length = 22; ci = 77; ri = 68.

Acknowledgments

The NRF has generously supported the cost of my attending this conference. Dr. Fred Gess is thanked for his help with translating difficult old German scripts. Nick James helped with the French. Dr. Jean-Marc Elouard has very generously shared information on West African and Malagasy Tricorythidae, which he has studied. Sylvia de Moor is thanked for her help with the illustrations of eyes. Dr. Ferdy de Moor and Professor Martin Villet made useful comments on the manuscript. The Directorate of Museums and Heritage Resources, Eastern Cape, are thanked for providing research facilities.

Literature Cited

- Barber-James, H. M. 1995. A preliminary survey of the Ephemeroptera of the north east Cape rivers, South Africa. Pages 97–109 in L. D.Corkum, and J. H. Ciborowsky, editors. Current Directions in Research on Ephemeroptera. Canadian Scholars Press, Toronto.
- Barnard, K. H. 1932. South African may-flies (Ephemeroptera). Transactions of the Royal Society of South Africa **20**:201–259.
- Burmeister, H. 1839. Handbuch der Entomologie II. Besondere Entomologie 2. Gymnognatha. 2. Neuroptera. Berlin. 757–1004.
- Corbet, P. S. 1960. Larvae of certain East African Ephemeroptera. Revue de zoologie et de botanique africaines **61**(1–2):119–129.

- Crass, R. S. 1947. The mayflies (Ephemeroptera) of Natal and the Eastern Cape. *Annals of the Natal Museum* **11**:37–110.
- Crosskey, R.W., and G. B. White. 1977. The Afrotropical Region. A recommended term in zoogeography. *Journal of Natural History* **11**:541–544.
- Demoulin, G. 1954a. Description préliminaire d'un type larvaire nouveau d'Éphéméroptères Tricorythidae du Congo belge. *Institut royal des Sciences naturelles de Belgique* **30**(6):1–4.
- Demoulin, G. 1954b. Recherches critiques sur les Éphéméroptères Tricorythidae d'Afrique et d'Asie. *Bulletin et Annales de la société d'entomologie de Belgique* **90**(9–10):264–277.
- Demoulin, G. 1957. Le type larvaire probable des *Tricorythus* Eaton (Ephemeroptera Tricorythidae). *Institute Royal des Sciences naturelles de Belgique* **33**(19):1–4.
- Demoulin, G., and G. F. Edmunds. 1954. Note à propos des nom et quteurs de deux genres d'Éphéméroptères. *Bulletin et Annales de la Société d'entomologie de Belgique* **90**(1–2):46–48.
- Eaton, A. E. 1868. An outline of the re-arrangement of the genera of Ephemeridæ. *Entomologist's Monthly Magazine* **5**:82–91.
- Eaton, A. E. 1883–1888. A revisional monograph of Recent Ephemeridae or mayflies. *Transactions of the Linnean Society of London, Zoology Second Series* Vol. 3:1–352. pl. 1–65.
- Edmunds Jr., G. F., and W. P. McCafferty. 1988. The Mayfly Subimago. *Annual Review of Entomology* **33**:509–529.
- Elouard J.-M., and R. Oliariny. 1997 - Biodiversité aquatique de Madagascar. 6-*Madecassorythus* un nouveau genre de Tricorythidae définissant la nouvelle sous-famille des Madecassorythinae (Ephemeroptera, Pannota). *Bulletin de la Société entomologique de France*. **102**(3):225–232.
- Esben-Petersen, P. 1913. Ephemeridae from South Africa. *Annals of the South African Museum* **10**:177–187.
- Esben-Petersen, P. 1920. New Species of Neuropterous Insects from South Africa. *Annals of the South African Museum* **17**:499–505.
- Jacob, U. 1974. Zur Kenntnis zweier *Oxycypha* – Arten Hermann Burmeisters (Ephemeroptera, Caenidae). *Reichenbachia* **15**:93–97.
- Kimmins, D. E. 1956. New Species of Ephemeroptera from Uganda. *The Bulletin of the British Museum (Natural History)* **4**(2):71–87.
- Kimmins, D. E. 1957. New species of *Dicercomyzon* Demoulin (Ephemeroptera, fam. Tricorythidae). *Bulletin of the British Museum (Natural History) Entomology* **6**(5):129–136.
- Lestage, J. A. 1924. Les Ephémères de l'Afrique du Sud. Catalogue critique and systématique des espèces connues et description de trois genres nouveaux et de sept espèces nouvelles. *Revue zoologique africaine* **12**(3):316–351.
- Lestage, J. A. 1942. Contribution à l'étude des Éphéméroptères. XVIII. Notes critiques sur les anciens Caenidiens d'Afrique et sur l'indépendance de

- l'évolution tricorythido-caenidienne. Bulletin du Musée royal d'Histoire naturelle de Belgique **48**:1–20.
- McCafferty, W. P., and T. Q. Wang. 2000. Phylogenetic systematics of the major lineages of pannote mayflies (Ephemeroptera: Pannota). Transactions of the American Entomological Society **126**:9–101.
- Navás, L. 1936. Insectes du Congo belg. Série IX. Revue de zoologie et de botanique africaines **28**(3):333–368.
- Needham, J. G. 1920. African Stone-flies and May-flies collected by the American Museum Congo Expedition. Bulletin of the American Museum of Natural History **43**:35–40.
- Oliariny, R. 1998. Systématique et biogéographie des Tricorythidae malgaches, (Ephéméroptères: Pannotes). Mémoire de D.E.A. Option "Ecologie et Environnement". Université d'Antananarivo, Madagascar. vol. 1 text 60 pp, vol. 2 figs 61 pp.
- Oliariny R., and J.-M. Elouard. 1997 - Biodiversité aquatique de Madagascar. 7. *Ranorythus* un nouveau genre de Tricorythidae définissant La nouvelle sous-famille des Ranorythinae (Ephemeroptera Pannota). Bulletin de la Société entomologique de France **102**(5):439–447.
- Oliariny R., J.-M. Elouard, and N. H. Raberiaka. 1998a. Biodiversité aquatique de Madagascar. 8. *Spinirythus* un nouveau genre de Tricorythidae (Ephemeroptera Pannota). *Bulletin de la Société entomologique de France* **103**(3):237–244.
- Oliariny R., J.-M. Elouard, and N. H. Raberiaka. 1998b – Biodiversité aquatique de Madagascar. 19. Neuf nouvelles espèces de *Tricorythus* Eaton (Ephemeroptera Pannota, Tricorythidae). *Revue française d'entomologie* **20**(3):73–90.
- Oliariny, R., M. Sartori, and J.-M. Elouard. 2000. Première description des larves et des oeufs du genre malgache *Madecassorythus* (Ephemeroptera, Tricorythidae). *Mitteilung der Schweizerischen Entomologischen Gesellschaft / Bulletin de la Société Entomologique Suisse* **73**:69–378.
- Pictet, F. J. 1843–1845. Histoire naturelle générale et particulière des insectes névroptères, Famille des éphémérides 1–319.
- Sroka, P., and T. Soldán. 2006. Revision of the family Tricorythidae (Ephemeroptera) in the Oriental region. Mayfly-Stonefly Conference Proceedings, University of Montana, Biological Station.
- Ulmer, G. 1913. Ephemérides aus Java, gesammelt von Edw. Jacobson. Notes from the Leyden Museum **35**:102–120.
- Ulmer, G. 1915/16. Epheméropteren von Aquatorial-Afrika. *Archiv für Naturgeschichte* 81(A) **7**:1–19.
- Ulmer, G. 1921. Über einige Epheméropteren - Typen älterer Autoren. *Archiv für Naturgeschichte* 87(A) **6**:229–267.
- Ulmer, G. 1930. Entomological Expedition to Abyssinia, 1926–27; Trichoptera and Ephemeroptera. *Annals and Magazine of Natural History* **10**(6):479–511.

Ulmer G. 1939. Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. Archiv für Hydrobiologie, Supplement **16**:443–692.

Appendix A

Checklist of Afrotropical Tricorythidae as they currently stand.

- current valid species names
- subordinate names

Family **TRICORYTHIDAE** Lestage, 1942

1. Genus ***Diceromyzon*** Demoulin, 1954 [Africa]
 - *Diceromyzon costale* Kimmins, 1957 [Tanzania, Malawi, South Africa]
 - *Diceromyzon femorale* Demoulin, 1954 [Congo, Ghana]
 - *Diceromyzon sjösterdti* (Ulmer, 1910) [Tanzania, Ghana]
 - *Caenis sjösterdti* Ulmer, 1909 (orig.)
 - *Tricorythus sjösterdti* Lestage, 1918 (comb.)
 - *Diceromyzon sjösterdti* Demoulin 1954 (comb.)
 - *Diceromyzon marginatum* Kimmins, 1957 (syn.)
 - *Diceromyzon verrierae* Demoulin, 1964 [Guinea]
2. Genus ***Madecassorythus*** Elouard and Oliarioniny, 1997 [Madagascar]
 - *Madecassorythus hertui* Elouard and Oliarioniny, 1997 [Madagascar]
 - *Madecassorythus linae* Elouard and Oliarioniny, 1997 [Madagascar]
 - *Madecassorythus ramanankasinae* Elouard and Oliarioniny, 1997 [Madagascar]
 - *Madecassorythus raphaeli* Oliarioniny and Sartori, 2000 [Madagascar]
3. Genus ***Ranorythus*** Oliarioniny and Elouard, 1997 [Madagascar]
 - *Ranorythus violettai* Oliarioniny and Elouard, 1997 [Madagascar]
 - *Ranorythus langrani* Elouard and Oliarioniny, 1997 [Madagascar]
4. Genus ***Spinirythus*** Oliarioniny and Elouard, 1998 [Madagascar]
 - *Spinirythus colasi* Elouard and Oliarioniny, 1998 [Madagascar]
 - *Spinirythus martini* Oliarioniny and Elouard, 1998 [Madagascar]
 - *Spinirythus rosae* Oliarioniny and Raberiaka, 1998 [Madagascar]
5. Genus ***Tricorythus*** Eaton, 1868 [Africa and Madagascar]
 - *Tricorythus abyssinica* Ulmer, 1930 [Ethiopia]
 - *Neurocaenis abyssinica* Demoulin, 1954 (comb.)
 - *Tricorythus abyssinica* Oliarioniny, Elouard and Raberiaka, 1998 (comb.)
 - *Tricorythus ambinintsoae* Oliarioniny and Elouard, 1998 [Madagascar]

- *Tricorythus discolor* (Burmeister, 1839) [South Africa]
 - *Oxycypha discolor* Burmeister, 1839 (orig.)
 - *Cloeon discolor* Walker, 1853 (comb.)
 - *Caenis discolor* Eaton, 1871 (comb.)
 - *Tricorythus discolor* Eaton, 1884 (comb.)
 - *Neurocaenis discolor* Demoulin, 1954 (comb.)
 - *Tricorythus discolor* McCafferty and de Moor, 1995 (comb.)
- *Tricorythus fyaе* Oliarinony and Raberiaka, 1998 [Madagascar]
- *Tricorythus fuscata* (Navás, 1936) [Congo]
 - *Neurocaenis fuscata* Navás, 1936 (orig.)
 - *Tricorythus fuscata* Oliarinony, Elouard and Raberiaka, 1998 (comb.)
- *Tricorythus goodmani* Elouard and Oliarinony, 1998 [Madagascar]
- *Tricorythus jeanne* Oliarinony and Elouard, 1998 [Madagascar]
- *Tricorythus lanceolatus* Kimmins, 1960 [Uganda]
- *Tricorythus latus* Ulmer, 1916 [Congo, Sudan]
 - *Tricorythurus latus* Lestage, 1942 (comb.)
 - *Tricorythus latus* Demoulin, 1954 (comb.)
- *Tricorythus longus* Ulmer, 1916 [Congo, Sudan, Uganda]
 - *Caenis regia* Navás, 1932 (orig.)
 - *Caenis collarti* Navás, 1933 (comb.)
- *Tricorythus pierrei* Elouard and Oliarinony, 1998 [Madagascar]
- *Tricorythus poincinsi* Navás, 1926 [Kenya]
 - *Neurocaenis poincinsi* Demoulin, 1954 (comb.)
 - *Tricorythus poincinsi* Oliarinony, Elouard and Raberiaka, 1998 (comb.)
- *Tricorythus reticulatus* Barnard, 1932 [South Africa]
 - *Neurocaenis reticulata* Demoulin, 1954 (comb.)
 - *Tricorythus reticulatus* McCafferty and de Moor, 1995 (comb.)
- *Tricorythus rolandi* Oliarinony and Raberiaka, 1998 [Madagascar]
- *Tricorythus sylvestris* Oliarinony and Elouard, 1998 [Madagascar]
- *Tricorythus tinctus* Kimmins, 1956 [Uganda]
- *Tricorythus variabilis* Oliarinony and Raberiaka, 1998 [Madagascar]
- *Tricorythus varicauda* (Kollar and Pictet, 1843) [Egypt]
 - *Caenis varicauda* Kollar and Pictet, 1843 (orig.)
 - *Tricorythus varicauda* Eaton, 1868 (comb.)
- *Tricorythus vulgaris* Raberiaka and Oliarinony, 1998 [Madagascar]