3. REMARKS ON THE TAXONOMY OF MEGAPODAGRIONIDAE WITH EMPHASIS ON THE LARVAL GILLS (ODONATA)

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A list of genera presently included in Megapodagrionidae and Pseudolestidae is provided, together with information on species for which the larva has been described. Based on the shape of the gills, the genera for which the larva is known can be arranged into four groups: (1) species with inflated sack-like gills with a terminal filament; (2) species with flat vertical gills; (3) species in which the outer gills in life form a tube folded around the median gill; (4) species with flat horizontal gills. The possible monophyly of these groups is discussed. It is noted that horizontal gills are not found in any other family of Zygoptera. Within the Megapodagrionidae the genera with horizontal gills are, with the exception of *Dimeragrion*, the only ones lacking setae on the shaft of the genital ligula. On the basis of these two characters it is suggested that this group is monophyletic.

INTRODUCTION

In the last decade many studies have been devoted to the phylogeny of damselflies (for a review, see Trueman 2007). Studies that included a large selection of species of most families have been most successful in providing an understanding of the limits of families. Notable studies include those of Rehn (2003), who analysed morphological data for over 150 species, and Bybee et al. (2008), who analysed morphological and molecular data for over a 100 species from 30 families. The monophyly for most damselfly families is well established and Calopterygidae, Chlorocyphidae, Euphaeidae, Isostictidae, Lestidae, Platystictidae, 'Disparoneurinae' (= Old World Protoneuridae) and Polythoridae are established as monophyletic groups in Bybee et al. (2008). In addition to this, Coenagrionidae is monophyletic when Pseudostigmatidae and Protoneuridae s.str. are included (Carle et al. 2008; Pessacq 2008). A more recently published phylogeny based on DNA data of 229 species largely agrees with these results (Dumont et al. 2009). However the Holy Grail of zygopteran phylogeny, a well-resolved tree showing the inter-family relations, remains to be found, although we now at least have some good working hypotheses (Bybee et al. 2008).

One of the most problematic groups in the work of Bybee et al. (2008) and Dumont et al. (2009) is that which includes the families Megapodagrionidae, Pseudolestidae and Amphipterygidae. The only generally recognised member of Pseudolestidae, *Pseudolestes mirabilis* Kirby, 1900, and also the genus *Rhipidolestes*, which is sometimes included in Pseudolestidae, are shown by Bybee et al. (2008) as falling within Megapodagrionidae and are considered here to belong to that family. Amphipterygidae includes the genera *Amphipteryx* Selys, 1853, *Devadatta*, Kirby 1890 (Amphipteryginae), *Pentaphlebia* Förster, 1909 and *Rimanella* Needham, 1934 (Rimanellinae), all of which show a convincing synapomorphy in the form of paired, highly plumose, filamentous gill tufts. Neither molecular study cited above recognizes

Amphipterigidae as a monophyletic group. Bybee et al. (2008) did not find *Devadatta* and *Rimanella* to be monophyletic, but the authors suggest that as no molecular data were available for *Rimanella*, a close relationship might yet be found. Similarly Dumont et al. (2009) failed to establish the monophyly of *Devadatta* and *Pentaphlebia*. We consider that these results may well represent methodological artefacts and in this paper we consider Amphi pterygidae to be monophyletic, falling outside the limits of the Megapodagrionidae. In many publications *Philoganga* Kirby, 1890 is also included in the Amphipterygidae. However, because the larvae lack gill tufts, Novelo-Gutiérrez (1995) removed this genus from the Amphipterygidae, and placed it in Lestoideidae (incorrectly designating it as Diphlebiidae) together with *Diphlebia* Selys, 1869 and *Lestoidea* Tillyard, 1913. The latter two genera are recovered as a monophyletic group in all trees presented by Bybee et al. (2008). These genera are however never grouped with *Philoganga*, which is shown either as a separate linage or forming a monophyletic group together with *Rimanella*. The position of *Philoganga* thus remains problematic, for which reason we treat it as equivalent to a family under the name '*Philoganga*' leaving Lestoideidae with only *Diphlebia* and *Lestoidea*. Furthermore, in some of the trees presented by Bybee et al. (2008), the Polythoridae also lie within Megapodagrionidae. As with Amphipterygidae, this tropical American group has some well-defined autapomorphies, mainly manifested in the larvae. The abdomen bears dorsal hooks, the caudal gills are swollen, with three to six finger-like projections, and they have latero-ventral abdominal gills on S2-7. The only other family in which abdominal gills occur is the Euphaeidae, where they are found ventro-laterally on S2-8. This apparent similarity suggests a close relation between these families but this is not firmly supported by consideration of adult morphology (Rehn 2003) or by molecular analyses (Bybee 2008). There is no reason, other than certain uncorroborated phylograms of Bybee et al. (2008), to consider the Polythoridae as part of the Megapodagrionidae, and in the following analysis, this family is also disregarded.

VJK is currently studying the taxonomy of the species of Megapodagrionidae occurring east of Huxley's Line: The Philippines, eastern Indonesia, Papua New Guinea, The Solomon Islands, Australia and New Caledonia. This group includes over 80 species and 10 genera and is believed to be monophyletic. The best evidence for their monophyly is to be found in the gills of the larvae, which are placed in a horizontal plane, a character state found in no other group of Zygoptera. With the recent description of the larvae of *Podolestes* (Choong & Orr 2010), *Nesolestes* (Schütte 2010) and the reappraisal of the description of the larva of *Protolestes* (Paulian 1958) it became clear that this character state is not confined to species occurring east of Huxley's Line. The question arises: are horizontal gills found in other genera of Megapodagrionidae? And if so, do the species with horizontal gills form a monophyletic group? In order to answer these questions the present review was made of all described larvae of Megapodagrionidae. During this search it was noted that the shape of the gills was correlated with the presence or absence of setae on the genital ligula or penis shaft. Larval morphology is therefore analysed in association with this easily assessed, unrelated adult male character.

MATERIAL AND METHODS

The review of larval gill morphology was based on published literature. A complete list of references is provided in table 1. The presence or absence of setae on the genital ligula was assessed for all genera from Scanning Electron Microscopy (SEM) images for the Old World genera and from literature and specimens, examined under a stereo light microscope for the New World genera. It must be noted that the setae on the genital ligula are often not drawn and therefore a drawing in which the setae are not shown cannot be used as confirmation of the absence of setae. In order to establish the variation in this character the presence and absence of setae was also studied in a wide selection of genera from all families of Zygoptera.

Table 1. Species of Megapodagrionidae for which the larva is described, their affiliation to morphological groups and their presence or absence of setae on the shaft of the genital ligula. B: balloon megapods; F: fan megapods; L: long-legged megapods; T: tube megapods; ?: group affiliation unknown; +: setae present; –: setae absent.

Genus / species with larva described	**Distribution of genus /** reference to larval description	**Group**	**Setae**
***Agriomorpha* May, 1933**	**Mainland Asia**	?	+
No larva described			
***Allolestes* Selys, 1869**	**Seychelles**	?	–
No larva described			
Allopodagrion Förster, 1910	**America**	?	+
No larva described			
***Amanipodagrion* Pinhey, 1962**	**Tanzania**	?	–
No larva described			
***Archaeopodagrion* Kennedy, 1939**	**America**	?	+
No larva described			
***Archiargiolestes* Kennedy, 1925**	**West Australia**	F	–
parvulus (Watson, 1977)	Theischinger 1998		
pusillissimus Kennedy, 1925	Theischinger 1998		
pusillus (Tillyard, 1908)	Theischinger 1998		
***Argiolestes* Selys, 1862**	**New Caledonia, Solomons, Papua New Guinea, Philippines**	F	–
fontinalis Lieftinck, 1956	Lieftinck 1956, 1976		
ochraceus (Montrousier, 1864)	Lieftinck 1976		
pectitus Lieftinck, 1949 [1]	Lieftinck 1956, 1976		
***Austroargiolestes* Kennedy, 1925**	**East Australia**	F	–
alpinus (Tillyard, 1913) [1]	Theischinger 1998		
aureus (Tillyard, 1906) [1]	Theischinger 1998		
chrysoides (Tillyard, 1913) [1]	Theischinger 1998		
icteromelas (Selys, 1862)	Tillyard 1917; Lieftinck 1976; Theischinger 1998; Hawking & Theischinger 1999		
isabellae Theischinger & O'Farrell, 1986	Theischinger, 1998		
***Bornargiolestes* Kimmins, 1936**	**Borneo**	?	+
No larva described			
***Burmargiolestes* Kennedy, 1925**	**Mainland Asia**	?	+
No larva described			
***Caledargiolestes* Kennedy, 1925**	**New Caledonia**	F	–
uniseries (Ris, 1915) [2]	Willey 1955; Lieftinck 1976		
***Caledopteryx* Kennedy, 1925**	**New Caledonia**	F	–
maculata Winstanley & Davies, 1982 [3]	Lieftinck 1976		
***Celebargiolestes* Kennedy, 1925**	**Sulawesi**	F	–
sp. [4]	Culhane 2005		
***Dimeragrion* Calvert, 1913**	**America**	F	+
percubitale Calvert, 1913 [1]	De Marmels 1999		
***Griseargiolestes* Theischinger, 1998**	East Australia	F	–
albescens (Tillyard, 1913)	Theischinger 1998; Hawking & Theischinger 1999		
bucki Theischinger, 1998	Theischinger 1998b; Hawking & Theischinger 1999		
eboracus (Tillyard, 1913)	Theischinger 1998; Hawking & Theischinger 1999		
griseus (Hagen, 1862)	Tillyard 1917; Theischinger 1998; Hawking & Theischinger 1999		
intermedius (Tillyard, 1913)	Theischinger 1998; Hawking & Theischinger 1999		

Genus / species with larva described	**Distribution of genus** / reference to larval description	**Group**	**Setae**
***Heteragrion* Selys, 1862**	**America**	B	+
albifrons Ris 1918	Novelo-Gutiérrez 1987		
alienum Williamson, 1919	Novelo-Gutiérrez 1987		
aurantiacum Selys, 1862	Santos 1968		
bariai De Marmels, 1989	De Marmels 2004		
breweri De Marmels, 1989	De Marmels 2004		
*chlorotaeniatu*m De Marmels, 1989	De Marmels 2004		
chrysops Hagen in Selys, 1862	Limongi 1983		
consors Hagen in Selys, 1862	Costa & Santos 1999		
erythrogastrum Selys, 1886	Ramírez 1992		
mitratum Williamson, 1919	De Marmels 2004		
tricellulare Calvert, 1901	Novelo-Gutiérrez 1987		
***Heteropodagrion* Selys, 1885**	**America**	?	+
No larva described			
***Hypolestes* Gundlach, 1888**	**America**	B	+
trinitatis Gundlach, 1888	Alayo Soto 1985; Westfall & May 1996		
Megapodagrion Selys, 1885	**America**	?	+
No larva described			
***Mesagrion* Selys, 1885**	**America**	?	+
No larva described			
***Mesopodagrion* MacLachlan, 1896**	**Mainland Asia**	?	+
No larva described			
***Miniargiolestes* Theischinger, 1998**	**West Australia**	F	–
minimus (Tillyard, 1908)	Theischinger 1998		
***Nesolestes* Selys, 1891**	**Madagascar**	F	–
sp.	Schütte 2010		
***Neurolestes* Selys, 1882**	**West Africa**	?	–
No larva described			
***Oxystigma* Selys, 1862**	**America**	B	+
petiolatum (Selys, 1862)	Geijskes 1943		
***Paraphlebia* Selys in Hagen, 1861** [5]	**America**	B	+/–
zoe Selys in Hagen, 1861	Novelo-Gutierrez 2008		
***Philogenia* Selys, 1862**	**America**	B	+
carrillica Calvert, 1907	Ramírez-Ulate & Novelo-Gutiérrez 1994		
cassandra Hagen in Selys, 1862	De Marmels, 1982		
mangosisa Bick & Bick, 1988	Bybee & Tennessen 2008		
peacocki Brooks, 1989	Ramírez-Ulate & Novelo-Gutiérrez 1994		
terraba Calvert, 1907	Ramírez-Ulate & Novelo-Gutiérrez 1994		
***Philosina* Ris, 1917**	**Mainland Asia**	?	+
No larva described			
***Podolestes* Selys, 1862**	**Southeast Asia**	F	–
orientalis Selys, 1862	Choong & Orr 2010		
***Podopteryx* Selys, 1871**	**Australia, Indonesia, Papua New Guinea**	F	–
selysi (Förster, 1899)	Watson & Dyce 1978; Theischinger & Hawking 2006		
***Priscagrion* Zhou & Wilson, 2001**	**Mainland Asia**	?	+
No larva described			
***Protolestes* Förster, 1899**	**Madagascar**	F	–
proselytus Lieftinck, 1965 [6]	Paulian 1958		
***Pseudolestes* Kirby, 1900**	**Hainan, China**	?	+
No larva described			
***Rhinagrion* Calvert, 1913**	**Southeast Asia**	T	+
mima (Karsch, 1891)	Lieftinck 1956		

Genus / species with larva described	**Distribution of genus** / reference to larval description	**Group**	**Setae**
philippinum (Selys, 1882)	Needham 1911; Needham & Gyger 1939		
***Rhipidolestes* Ris, 1912**	**Mainland Asia, Japan**	B	+
aculeatus Ris, 1912	Asahina 1994; Kawai 1985; Sugimura et al. 2001		
asatoi Asahina, 1994	Sugimura et al. 2001		
hiraoi Yamamoto, 1955	Asahina 1994; Kawai 1985; Sugimura et al. 2001		
okinawanus Asahina, 1951	Sugimura et al. 2001		
***Sciotropis* Racenis, 1959**	**America**	B	+
cyclanthorum Racenis, 1959	De Marmels 2004		
***Sinocnemis* Wilson & Zhou, 2000**	**Mainland Asia**	?	+
No larva described			
***Tatocnemis* Kirby, 1889**	**Madagascar**	B	+
malgassica Kirby, 1889	Paulian 1958		
***Teinopodagrion* De Marmels, 2001**	**America**	L	+
caquetanum De Marmels, 2001	Pérez-Gutiérrez 2007		
decipiens De Marmels, 2001	von Ellenrieder 2006		
meridionale De Marmels, 2001	von Ellenrieder 2006		
oscillans (Selys, 1862)	De Marmels 2001		
vallenatum De Marmels, 2001	Pérez-Gutiérrez 2007		
venale (Hagen in Selys, 1862)	De Marmels 1982		
***Thaumatoneura* McLachlan, 1897**	**America**	B	+
inopinata McLachlan, 1897	Calvert 1915		
***Trineuragrion* Ris, 1915**	**New Caledonia**	F	–

1 Identification of larvae based on supposition.

2 The larva of *Caledargiolestes uniseries* was described and illustrated from a single larva by Lippitt Willey (1955) as an unidentified larva of a megapodagrionid. Lieftinck (1976) redescribed this larva as "Genus et species incert". In the same paper he gave also a description of the larva he supposed to be *C. uniseries*. Winstanley (1983) discovered that the "unidentified larva of a megapodagrionid" described by Lippitt Willey (1955) and Lieftinck (1976) in fact belonged to *Caledargiolestes uniseries* and that the larva described by Lieftinck as *Caledargiolestes uniseries* belongs to another megapodagrionid-species.

3 *Caledopteryx maculata* had not been discovered when Lieftinck (1976) described the larva of *Caledargiolestes* as *C. sarasini*. Winstanley & Davies (1982) state that Lieftinck used larvae from a locality, where only *C. maculata* has been collected. Lieftincks' description of *C. sarasini* is therefore believed to pertain to *C. maculata*.

4 Culhane (2005) published pictures of a megapodagrionid larva from Buton Island, Sulawesi. The genus *Celebargiolestes* is widespread and relatively common on Sulawesi while only a single record of *Argiolestes* is known (Kalkman 2007). It is therefore tentatively assumed that the larva in Culhane (2005) belongs to *Celebargiolestes*.

5 Of the three species checked two had a few small setae (*Paraphlebia zoe*, *P.* sp. 1) and one seemed to lack setae (*P.* sp. 2).

6 This larva was described as *Protolestes fickei* Foerster, 1899 but according to Lieftinck (1965) it belongs to *P. proselytus*.

This was partly done based on literature and specimens held by AGO, but mostly based on specimens in the Nationaal Natuurhistorisch Museum Naturalis, Leiden (RMNH).

For non-megapodagrionid taxa the following arrangements were followed (see table 3).
The species of the monotypic genera *Leptocnemis cyanops* (Selys, 1869), *Oreocnemis phoenix* Pinhey, 1971, and *Thaumatagrion funereum* Lieftinck, 1932 are often placed in Platycnemididae, but are here placed in Coenagrionidae. The original placement of *Thaumatagrion* was doubted by Gassmann (2005), whereas unpublished DNA studies indicate that *Leptocnemis cyanops* and *Oreocnemis phoenix* belong in Coenagrionidae. The placement in Coenagrionidae of the species formerly included in Pseudostigmatidae follows

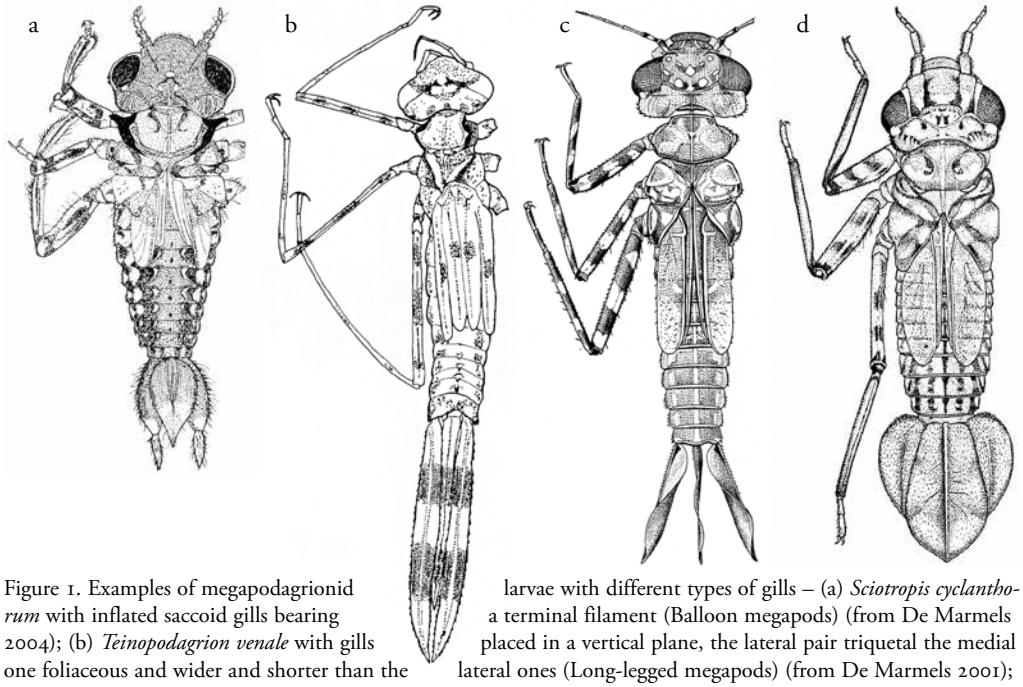

Figure 1. Examples of megapodagrionid larvae with different types of gills – (a) *Sciotropis cyclanthorum* with inflated saccoid gills bearing a terminal filament (Balloon megapods) (from De Marmels 2004); (b) *Teinopodagrion venale* with gills placed in a vertical plane, the lateral pair triquetal the medial one foliaceous and wider and shorter than the lateral ones (Long-legged megapods) (from De Marmels 2001); (c) *Rhinagrion mima* in which the outer gills in life form a tube folded around the median gill; in preserved specimens these gills present as short thick, vertical laminate forms, similar to the general condition found in most Zygoptera (Tube megapods) (from Lieftinck 1956); (d) *Argiolestes pectitus* with flat horizontal gills (Fan megapods) (from Lieftinck 1956).

the results presented by Carle et al. 2008.
The placement in Coenagrionidae of Protoneuridae s.str. follows the results of Pessacq (2008) who showed that all New World species of the Protoneuridae, including the type genus, fall within Coenagrionidae (Pessacq 2008). The unrelated Old World species of Protoneuridae s.l. are here given as 'Disparoneurinae'.
Subfamilies thus far defined within Megapodagrionidae have been shown to be of little taxonomic value. For this reason we refrain from using these names and instead have devised descriptive cognomens for definable groups based on the structure of larval gills.

RESULTS

Larvae fell into four definable groups: 'Balloon megapods' or species in which the larval gills were saccoid or balloon-shaped, 'Long-legged megapods' for species in which the larvae had flat, often elongate vertical gills, 'Tube megapods' for species in which the outer gills formed a tube in life and 'Fan megapods' for species in which the larvae have flat horizontal gills. Table 1 gives, for each megapodagrionid genus, a list of described larvae and information on the shape of the gills. In this table also the presence or absence of rows of setae on the sides of the ligula is noted. The distribution of gill types within the family could be summarized as follows:

(1) Species with inflated saccoid gills bearing a terminal filament (fig. 1a) (Balloon megapods). In some genera the gills were only slightly inflated but then the dorsal, ventral and lateral keels are clearly thickened making the gills three dimensional (triquetral).
- Africa, Madagascar: *Tatocnemis*
- Asia west of Huxley's Line: *Rhipidolestes*

	Fan megapods	Balloon, Long-legged or Tube megapods	Larvae unknown
Setae present	1	10	12
Setae sometimes absent	0	1	0
Setae absent	13	0	3

Table 2. Number of megapodagrionid genera with or without setae on the genital ligula for different larval types.

Family	genera known	Setae present	Setae absent
Amphipterygidae	4	4 (7)	0
Calopterygidae	16	16 (16)	0
Chlorocyphidae	18	0	14 (18)
Coenagrionidae	110+	32	31
Dicteriadidae	2	0	1 (1)
'Disparoneurinae'	9	0	7 (17)
Euphaeidae	12	9 (20)	2 (2)
Hemiphlebiidae	1	1	(1) 0
Isostictidae	12	4 (8) [1]	3 (6) [2]
Lestidae	8	0	7 (15)
Lestoideidae	2	2	(3) 0
Perilestidae	3	0	3 (7)
'Philoganga'	1	0	1 (1)
Platycnemididae	21	0	17 (20)
Platystictidae	6	6 (34)	0
Polythoridae	7	3 (14)	1 (1) [3]
Synlestidae	8	0	7 (12)

Table 3. Presence or absence of setae on the genital ligula in families of Zygoptera other than Megapodagrionidae. For each family the following data are included: the total number of genera known worldwide largely based on Kalkman et al. (2008), the number of genera and species (in parentheses) known to possess setae and the number of genera and species (in parentheses) known to lack setae.

1 Setae seem present in Australian and New Caledonian genera (*Isosticta* Selys, 1885; *Neosticta* Tillyard, 1913; *Oristicta* Tillyard, 1913; *Rhadinosticta* Watson, 1991).

2 Setae seem absent in New Guinean and Solomon Island genera (*Cnemisticta* Donnelly, 1993; *Selysioneura* Förster, 1900; *Tanymecosticta* Lieftinck, 1935).

3 *Euthore fasciata* (Hagen in Selys, 1853) is the exception.

- tropical America: *Heteragrion*, *Oxystigma*, *Paraphlebia*, *Philogenia*, *Sciotropis*, *Thaumatoneura*, *Hypolestes*

(2) Species with gills placed in a vertical plane, the lateral pair long and thickened, each with a median outer ridge along its length, the median one foliaceous and wider and shorter (fig. 1b) (Long-legged megapods).
- tropical America: *Teinopodagrion*

(3) Species in which the outer gills in life form a tube folded around the median gill; in preserved specimens these gills present as short thick, vertical laminate forms, superficially similar to the general condition found in most Zygoptera (fig. 1c) (Tube megapods). This type of gills is unique to the group and is not found in other Zygoptera.
- tropical Asia west of Huxley's Line and also the Philippines: *Rhinagrion*

(4) Species with flat horizontal gills (fig. 1d) (Fan megapods). This structure is unique to the group and is not found in other Zygoptera.
- Africa, Madagascar: *Nesolestes*, *Protolestes*
- Asia west of Huxley's Line: *Podolestes*
- Asia east of Huxley's Line (Philippines, eastern Indonesia, Papua New-Guinea Solomons, Australia and New Caledonia): *Archiargiolestes*, *Argiolestes*, *Austroargiolestes*, *Caledargiolestes*, *Caledopteryx*, *Celebargiolestes*, *Griseargiolestes*, *Miniargiolestes*, *Podopteryx*, *Trineuragrion*
- tropical America: *Dimeragrion*

For four American genera, eight Asian genera and three African megapodagrionid genera no larva

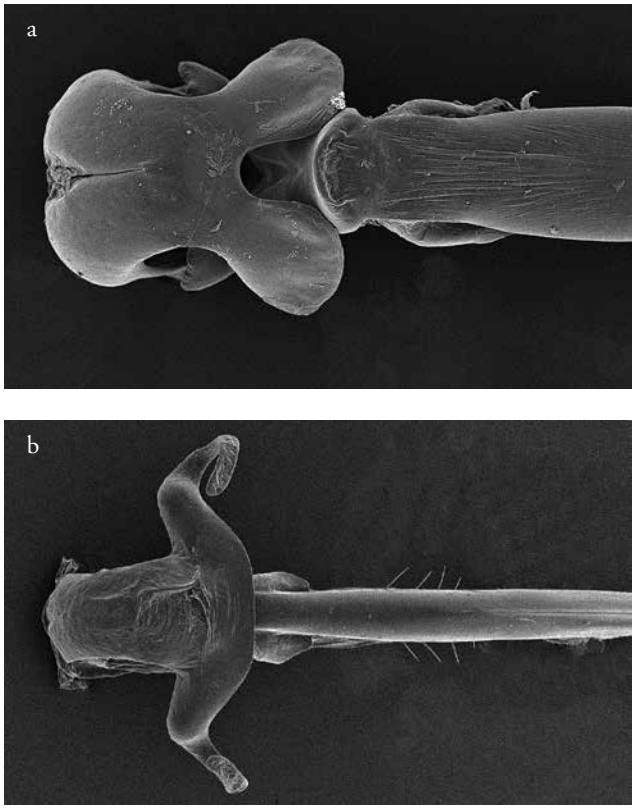

Figure 2. Examples of different structures of the genital ligula in two megapodagrionid species, ventral view – (a) *Neurolestes trinervis* (Selys, 1885) without setae on the ligula; (b) *Oxystigma williamsoni* Geijskes, 1976 with setae on the ligula.

have ever been described. In 13 genera with horizontal gills (Fan megapods) the setae on the genital ligula were absent (fig. 2a). The only exception to this rule is *Dimeragrion* which has horizontal gills and setae on the genital ligula. The setae on the genital ligula were always present in all other genera for which the larvae were known (n = 10), with the exception of *Paraphlebia* (fig. 2b). The information on larval gills and the presence of setae on the genital ligula is summarised in table 2. Table 3 provides an overview of the presence or absence of setae on the genital ligula for non-megapodagrionid families of Zygoptera.

DISCUSSION

Within the Zygoptera, the general morphology of the larval gills appears very conservative within families, and within most families, only one gill-type occurs (Corbet 1999: 77-86). For this reason it is believed that considerable weight can be assigned to this character. The presence or absence of setae on the genital ligula is a seldom-used character. Our analysis of the distribution of this character within families shows it to be fairly consistent within families (table 3) with 13 of the 17 families only exhibiting just one character state. In all families of the Chlorocyphidae, Dicteriadidae, 'Disparoneurinae', Lestidae, Synlestidae, Perilestidae, '*Philoganga*' and Platycnemididae setae were always absent on the genital ligula. In the families Amphipterygidae, Calopterygidae, Lestoideidae and Platystictidae setae were always present. In Coenagrionidae, Euphaeidae, Isostictidae and Polythoridae both character states were found. However with the exception of Coenagrionidae, no variation was found within genera, and genera with setae form the great majority,

suggesting that in these genera presence of setae is the plesiomorphic character state. In all species with setae studied by us the setae point away from the apex of the genital ligula. This gives the impression that they may function to 'dock' the genital ligula in the vagina, and/or perhaps prevent the shaft of the genital ligula from grinding against the wall of the vagina and so protect both from abrasive damage. Males may be capable of erecting the setae slightly. If the setae function in this way, they may provide the genital ligula with the firm grip needed to facilitate freedom of movement by elements of the penis head during insemination and the removal of sperm from other males. If this is true than it seems logical that there would be a link between the development of the setae and the importance of sperm removal in a species. However this topic is outside the scope of this study. Thirteen genera of Megapodagrionidae were found to have horizontal gills and no setae on the genital ligula, whereas setae are present and well developed in 10 genera with other types of gills (table 2). The only exceptions to this general rule are *Dimeragrion* and *Paraphlebia*. Of the three species of *Paraphlebia* checked two had a few relatively small setae while one lacked setae. *Dimeragrion* is the only genus to have horizontal gills and setae on the genital ligula. As both characters are conservative between families and are not developmentally or selectively associated we consider these results potentially useful in resolving the phylogeny of the megapods. Based on these results Megapodagrionidae fall into four groups:

Balloon megapods This group includes genera from America, *Tatocnemis* from Madagascar and *Rhipidolestes* from Asia. Based on the presence of setae on the genital ligula, all American genera for which the larva have not yet been described, might fall in this group. Based on the same character the Asian genera *Mesopodagrion*, *Priscagrion* and *Sinocnemis* as well as *Agriomorpha*, *Bornargiolestes* and *Burmargiolestes* might also belong in this group. However the former three genera might have completely different and unexpected affinities while the latter three seem to form a monophyletic group on their own which may or may not fall in Megapodagrionidae. The genus *Pseudolestes* is aberrant in many respects, which led to the establishment of the family Pseudolestidae. However the results of Bybee et al. (2008) suggest that it falls within Megapodagrionidae and is 'just' a highly advanced species within this family. The same might be true for *Thaumatoneura inopinata*, which was often placed in its own subfamily, but is now considered, based on adult and larval morphology, to be closely related to *Paraphlebia* (Garrison et al. 2010). The genera included here in this group might form a monophyletic clade but could very well be a paraphyletic or polyphyletic group. It must also be noted, in support of the latter suggestions, that this type of gill structure also occurs in Euphaeidae, Lestoideidae, '*Philoganga*', some Isostictidae, some Platystictidae, and in the platycnemidids *Stenocnemis pachystigma* (Selys, 1886) and *Allolestes leucosticta* (Selys, 1863), although the latter lacks the terminal filaments. The Balloon megapods is the least well-defined of our groups, and within any grouping of higher taxa considered the character may represent a symplesiomorphy, or in some cases, homoplasy.

Long-legged megapods This group currently contains only *Teinopodagrion*. According to De Marmels (2001), this genus forms a monophyletic group together with *Allopodagrion* and *Megapodagrion*. Based on adults he gives four 'possible synapomorphies' for this group, of which the second 'legs exceedingly long and spidery' is in our opinion the most convincing. These long and spidery legs are also prominent in the six larvae that have thus far been described. In addition to this the larvae are further remarkable having dorsal hooks on the abdominal segments, a character not found in other genera of Megapodagrionidae, for which the larvae have been described, and very rare in Zygoptera. The larvae of *Allopodagrion* and Megapodagrion are not yet known but are expected to have the same gills as found in *Teinopodagrion*. De Marmels (2002) suggested that the Chinese *Priscagrion* might be related to

the group *Allopodagrion*, *Megapodagrion* and *Teinopodagrion* based on the shape of the apical segment of the genital ligula. *Priscagrion* has like these genera also very long legs, which supports this suggestion.

Tube megapods When describing the larva of *Rhinagrion mima* Lieftinck (1956) remarked that the structure of the caudal gills is 'unlike anything found in other larvae that I know of'. Currently only the genus *Rhinagrion* falls in this group. However, preliminary DNA results suggest that the genus Philosina, whose larva is undescribed, is closely related to *Rhinagrion*, which is supported by peculiarities in the morphology of the genital ligula. Neither *Philosina* nor *Rhinagrion* were analysed in Bybee et al. (2008). Preliminary DNA analyses do not show these genera to be closely related to other megapodagrionid genera and they might form a monophyletic group of their own.

Fan megapods In Bybee et al. (2008) six genera with horizontal gills from Australasia are included and these form a monophyletic group at the end of the pectinate Megapodagrionidae branch. Genera with horizontal gills from Africa and Asia are lacking from their analyses. Based on the information on the larva presented here and the absence of setae on the genital ligula we suggest the Madagascan genus *Nesolestes* and the Asian genus *Podolestes* are more closely related to the Australasian genera than to any of the Balloon megapods or Tube megapods. For the genera *Allolestes*, *Amanipodagrion* and *Neurolestes* no larvae have been described. *Allolestes* and especially *Neurolestes* resemble *Nesolestes* (Dijkstra 2003), lack the setae on the genital ligula and are therefore believed to belong to this group. *Amanipodagrion* does not strongly resemble any other megapodagrionid genus. Based on the absence of setae on the genital ligula and unpublished preliminary results of DNA analyses we tentatively suggest that it also belongs in this group. We also provisionally place the Madagascan *Protolestes* within this grouping; we note that, although it has in a general sense horizontal gills, their detailed morphology may not entirely conform to the typical Fan megapod pattern, and re-examination of fresh larval material is needed to resolve this issue. *Dimeragrion* is the only genus with horizontal gills to occur in South-America. The larva of this genus is described based on one exuvia and it is possible the gills would be inflated in life in which case it would belong to the Balloon megapods. It differs from all other genera with horizontal gills in the respect that it has setae on its genital ligula and that the gills have a terminal filament both better fitting the Balloon megapods than the Fan megapods. If the gills are indeed flat than these characters suggest that either the horizontal gills in *Dimeragrion* have evolved independently or, when considering the presence of setae as a plesiomorphic character, that *Dimeragion* is basal to the other genera with horizontal gills. In the description of the larva of *Dimeragrion* De Marmels (1999) pointed out the resemblance of the prominent, bilobed median lobe of the labium with that of two species of Fan megapods from New Caledonia: *Argiolestes ochraceus* and a unidentified megapodagrionid larva (Lieftinck 1976) which might be seen as an indication that *Dimeragrion* is more closely related to other Fan megapods. All genera included by us in the Fan megapods, with the possible exception of *Dimeragrion* and *Protolestes*, are believed to form a monophyletic clade.

The present article discusses possible relationships within Megapodagrionidae based on consideration of the thorough phylogenetic work by Bybee et al. (2008) and the interpretation of two highly informative morphological characters. Based on these we consider the Long-legged megapods, the Tube megapods and the Fan megapods, with the possible exception of *Dimeragrion* and *Protolestes*, to be monophyletic groups. Further DNA work on a wider set of megapodagrionid genera is needed to test these hypotheses. There is however also a need for extensive fieldwork in order to understand megapodagrionid taxonomy. Finding and describing the larvae of the 'unknown' genera would be a very valuable contribution. The larvae of four genera or groups are of special interest:

- *Philosina*: Demonstration of tube-like gills in the larva of *Philosina* would confirm its relation with *Rhinagrion*.
- *Pseudolestes*: Demonstration of saccoid gills in larva of this genus would strengthen the suggestion that this aberrant species falls within Megapodagrionidae and is related to species included in the Balloon megapods.
- *Amanipodagrion*: This genus is difficult to place as it has several aberrant characters. Finding the larva might clarify its relationship with the Fan megapods.
- *Agriomorpha*, *Bornargiolestes*, *Burmargiolestes*: This group of seemingly closely related genera might fall in the group of the Balloon megapods.

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