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4. GENERIC REVISION OF ARGIOLESTIDAE (ODONATA), WITH FOUR NEW GENERA

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The subfamilyArgiolestinae is raised to family level to include all zygopteran genera in which the gills of the larvae are flat and held in a horizontal plane. A diagnosis of the family is given and characters for both adults and larvae are presented. The family is divided into two subfamilies based on characters in the genital ligula, with the subfamily Argiolestinae found in Australasia east of Huxley's Line and the subfamily Podolestinae found in Africa and Asia west of Huxley's Line. Four genera are newly described: *Eoargiolestes* (New Caledonia, type species *Sympecma ochracea* Montrouzier, 1864), *Luzonargiolestes* (Philippines, type species *Argiolestes realensis* Gapud & Recuenco, 1993), *Solomonargiolestes* (Bougainville, Papua New Guinea and Malaita, Solomon Islands, type species *Argiolestes bougainville* Kalkman, 2008) and *Pyrrhargiolestes* (Papua New Guinea, type species *Argiolestes sidonia* Martin, 1909). In addition *Metagrion* (type species *Argiolestes postnodalis* Selys, 1878) and *Wahnesia* (type species *Argiolestes kirbyi* Förster, 1900), two genera not in use for over 70 years, are reinstated. Based on molecular data the African genera *Neurolestes* and *Nesolestes* have been shown to be good genera and are here treated as such, *Nesolestes nigeriensis* is transferred to *Neurolestes*. All 20 genera included in Argiolestidae are discussed, with type species, key characters of adults, distribution and habitat being given. In addition a diagnosis is presented for each genus and information is given on their identification together with a map of the distribution of the genus and scanning electron microscope images of the genital ligula of most genera. A key to the genera of the Australasian region is presented and keys to the species of *Caledargiolestes, Caledopteryx* and *Podopteryx* are given. New distributional records of *Caledargiolestes, Caledopteryx, Luzonargiolestes, Solomonargiolestes* and *Podopteryx* are provided.

INTRODUCTION

Megapodagrionidae sensu lato, with more than 260 species, is the second largest family of Zygoptera. Nearly all species included are tropical or subtropical and most reproduce in running waters and seepages in tropical forest. The taxonomy of the group has long been considered problematic and in the last few years it has slowly become clear that Megapodagrionidae sensu lato comprises several monophyletic groups, some of which are only distantly related (Bybee et al. 2008, Dumont et al. 2009, Rehn 2003).

Several proposals have been made to divide the family into subfamilies, most of these based on wing venation. The most recent proposals for subfamilies within Megapodagrionidae *sensu lato* are those of Davies & Tobin (1984) and Bechly (2003); the former was also used by Silsby (2001). These do not however reflect monophyletic groups. Several recent studies of the phylogeny

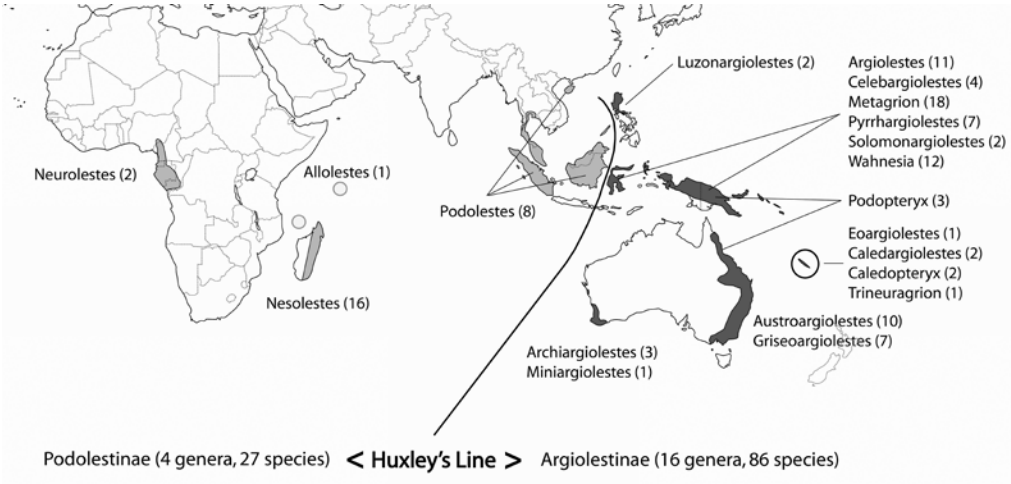

Figure 1. Distribution of the genera included in Argiolestidae, with those belonging to Argiolestinae in dark grey and those belonging to Podolestinae in pale grey. The number of species is shown after the genus names.

of dragonflies based on morphology and/or DNA were only partially successful in dividing Megapodagrionidae *sensu lato* into welldefined monophyletic groups, and a final division of genera included in Megapodagrionidae *sensu lato* into monophyletic groups is still needed (Bybee et al. 2008, Dumont et al. 2009, Rehn 2003). Based on the larval gills Kalkman, Choong et al. (2010) divided Megapodagrionidae *sensu lato* into four groups, three of which were suggested to be monophyletic. One of those groups was nicknamed Fanmegapods because the gills are flat and held in a horizontal plane, a character state not found in any other group of Odonata. Subsequent DNA sequence analysis has shown that the Fan megapods as proposed by Kalkman, Choong et al. (2010) are indeed largely monophyletic and the present paper therefore elevates the subfamily Argiolestinae to family level to contain all species of the Fan megapods with the exclusion of three genera. The three genera originally included in Fan megapods but which molecular work has shown to fall outside the Argiolestidae are *Dimeragrion* Calvert, 1913, *Amanipodagrion* Pinhey, 1962 and *Protolestes* Förster, 1899. The South American genus *Dimeragrion* was included in this group with some doubts by Kalkman, Choong et al. (2010) because the larva has flat gills which are held in a horizontal plane. Tennessen (2010) argued that the larvae of *Dimeragrion* are different from other genera with fan-shaped gills because they have a terminal filament not present in Fan megapods. This is however not completely correct as some genera (*Archiargiolestes*, *Griseargiolestes* and *Miniargiolestes*) within Australian genera of Argiolestidae have a filament (Theischinger 1998b). However, in these genera the filaments are articulated at the base, whereas in *Dimeragrion* the terminal filament is unarticulated. Based on the larval characters both Tennessen (2010) and Pérez-Gutiérrez & Montes-Fontalvo (2011) suggested *Dimeragrion* to be more closely related to one of the genera in which the gills are saccoid. This also fits better with the presence of setae on the shaft of the genital ligula in *Dimeragrion* given that these are absent in all other species included in Argiolestidae but present in most other genera of Megapodagrionidae *sensu lato*. *Amanipodagrion* was provisionally placed in the group with larvae having fan shaped gills based on the absence of spines on the shaft of the genital ligula, although its larva was unknown. The adult differs from the adults of Argiolestidae

Table 1. List of species included in Argiolestidae. The species belonging to the new genera were formerly all included in *Argiolestes*. Type species of genera are indicated by a dot.

Family ARGIOLESTIDAE Fraser, 1957

Subfamily ARGIOLESTINAE Fraser, 1957

***Archiargiolestes* Kennedy, 1925**

parvulus (Watson, 1977) – Australia: West Australia

• *pusillissimus* Kennedy, 1925 – Australia: West Australia

pusillus (Tillyard, 1908) – Australia: West Australia

***Argiolestes* Selys, 1862**

alfurus Lieftinck, 1956 – Indonesia: Moluccas

amphistylus Lieftinck, 1949 – Indonesia: mainland Papua

• *australis* (Guérin Meneville, 1830) – Indonesia: mainland Papua,Waigeo

celebensis Kalkman, 2007 – Indonesia: Sulawesi

foja Kalkman et al., 2010 – Indonesia: mainland Papua

macrostylis Ris, 1913 – Indonesia: mainland Papua

muller Kalkman et al., 2010 – PNG: mainland

obiensis Lieftinck, 1956 – Indonesia: Moluccas

pallidistylus Selys, 1878 – Indonesia: mainland Papua

roon Kalkman et al., 2010 – Indonesia: Roon Island, Mioswaar Island

tuberculiferus Michalski & Oppel, 2010 – PNG: mainland

***Austroargiolestes* Kennedy, 1925**

alpinus (Tillyard, 1913) – Australia: New South Wales

amabilis (Förster, 1899) – Australia: New South Wales, Queensland

aureus (Tillyard, 1906) – Australia: Queensland

brookhousei Theischinger & O'Farrell, 1986 – Australia: New South Wales

calcaris (Fraser, 1958) – Australia: New South Wales, Victoria

christine Theischinger & O'Farrell, 1986 – Australia: New South Wales

chrysoides (Tillyard, 1913) – Australia: Queensland

elke Theischinger & O'Farrell, 1986 – Australia: Queensland

• *icteromelas* (Selys, 1862) – Australia: New South Wales, Victoria, Queensland

ssp. – *icteromelas* (Selys, 1862)

syn: – *icteromelas nobilis* (Tillyard, 1913)

ssp. – *nigrolabiatus* Theischinger & O'Farrell, 1986. Lectotype (of *calcaris tenuis*)

syn: – *calcaris tenuis* (Fraser, 1959)

A. icteromelas nigrolabiatus is nom. nov. for *A. calcaris tenuis*; Theischinger & O'Farrell (1986) erroneously designated the lectotype of *A. calcaris tenuis* as holotype of *A. icteromelas nigrolabiatus* (Houston & Watson, 1988).

isabellae Theischinger & O'Farrell, 1986 – Australia: New South Wales

***Caledargiolestes* Kennedy, 1925**

janiceae Lieftinck, 1975 – New Caledonia

• *uniseries* (Ris, 1915) – New Caledonia

***Caledopteryx* Kennedy, 1925**

maculata Winstanley & Davies, 1982 – New Caledonia

• *sarasini* (Ris, 1915) – New Caledonia

***Celebargiolestes* Kennedy, 1925**

• *cinctus* (Selys, 1886) – Indonesia: Sulawesi

syn: *karnyi* (Fraser, 1926)

***Eoargiolestes* Kalkman & Theischinger, 2012**

• *ochraceus* (Montrouzier, 1864) – New Caledonia

syn: *rouxi* (Ris, 1915)

***Griseargiolestes* Theischinger, 1998**

albescens (Tillyard, 1913) – Australia: New South Wales, Queensland

bucki Theischinger, 1998 – Australia: New South Wales

eboracus (Tillyard, 1913) – Australia: New South Wales, Victoria, Queensland

fontanus (Tillyard, 1913) – Australia: New South Wales, Queensland

• *griseus* (Selys, 1862) – Australia: New South Wales

Table 1. Continued

ssp. – *griseus* (Selys, 1862)
ssp. – *subgriseus* (Fraser, 1959)
ssp. – *tenuis* (Tillyard, 1913)
intermedius (Tillyard, 1913) – Australia: New South Wales, Victoria
metallicus (Sjöstedt, 1917) – Australia: Queensland

***Luzonargiolestes* Kalkman & Theischinger, 2012**
baltazarae (Gapud & Recuenco, 2001) – Philippines: Luzon
• *realensis* (Gapud & Recuenco, 1993) – Philippines: Luzon

***Metagrion* Calvert, 1913**
aurantiacum (Ris, 1898) – PNG: New Britain, New Ireland
coartans (Lieftinck, 1956) – Indonesia: Waigeo
connectens (Lieftinck, 1956) – Indonesia: mainland Papua
convergens (Lieftinck, 1949) – Indonesia: mainland Papua
fontinale (Lieftinck, 1956) – Indonesia: mainland Papua
fornicatum (Theischinger & Richards, 2007) – PNG: mainland
indentatum (Theischinger & Richards, 2006) – PNG: mainland
lamprostoma (Lieftinck, 1949) – Indonesia: mainland Papua
montivagans (Förster, 1900) – PNG: mainland
ochrostoma (Lieftinck, 1949) – Indonesia: Waigeo
ornatum (Selys, 1878) – Indonesia: mainland Papua
syn: *obscurum* (Selys, 1878)
pectitum (Lieftinck, 1949) – Indonesia: mainland Papua
• *postnodale* (Selys, 1878) – Indonesia: mainland Papua, Japan
sponsum (Lieftinck, 1956) – Indonesia: mainland Papua
subornatum (Lieftinck, 1935) – Indonesia: mainland Papua, Japan
trigonale (Theischinger & Richards, 2008) – PNG: mainland
triste (Lieftinck, 1935) – Indonesia: mainland Papua
verrucatum (Michalski & Oppel, 2010) – PNG: mainland

***Miniargiolestes* Theischinger, 1998**
• *minimus* (Tillyard, 1908) – Australia: West Australia

***Podopteryx* Selys, 1871**
casuarina Lieftinck, 1949 – Indonesia: mainland Papua
• *roseonotata* Selys, 1871 – Indonesia: mainland Papua, Salawati,Waigeo, Aru; PNG: mainland
selysi (Förster, 1899) – Australia: Queensland; PNG: mainland; Indonesia: mainland Papua

***Pyrrhargiolestes* Kalkman & Theischinger, 2012**
angulatus (Theischinger & Richards, 2007) – PNG: mainland
aulicus (Lieftinck, 1949) – Indonesia: mainland Papua; PNG: mainland
kula (Englund & Polhemus, 2007) – PNG: mainland
lamington Kalkman et al., 2013 – PNG: mainland
• *sidonia* (Martin, 1909) – PNG: mainland
tenuispinus (Lieftinck, 1938) – PNG: mainland
yela Kalkman et al., 2013 – PNG: Rossel Island

***Solomonargiolestes* Kalkman & Theischinger, 2012**
• *bougainville* (Kalkman, 2008) – PNG: Bougainville
malaita (Kalkman, 2008) – Solomon Islands: Malaita

***Trineuragrion* Ris, 1915**
• *percostale* Ris, 1915 – New Caledonia

***Wahnesia* Förster, 1900**
annulipes (Lieftinck, 1956) – PNG: Goodenough Island
armeniaca (Lieftinck, 1956) – PNG: Goodenough Island
ephippiata (Lieftinck, 1956) – PNG: mainland
esuriens (Lieftinck, 1956) – PNG: mainland
gizo (Kalkman, 2008) – Solomon Islands: Gizo, Vella Lavella, Rendovo

Table 1. Continued

- *kirbyi* (Förster, 1900) – PNG: mainland
  luteipes (Lieftinck, 1956) – PNG: mainland
  microstigma (Lieftinck, 1956) – PNG: mainland
  prothoracalis (Lieftinck, 1956) – PNG: mainland
  saltator (Lieftinck, 1956) – PNG: mainland
  saltuaria (Lieftinck, 1956) – PNG: mainland
  simplex (Lieftinck, 1949) – Indonesia: mainland Papua

Subfamily PODOLESTINAE Kalkman & Theischinger, 2012

***Allolestes* Selys, 1869**

- *maclachlanii* Selys, 1869 – Seychelles
  syn: *nigra* Martin, 1896

***Nesolestes* Selys, 1891**

albicauda Fraser, 1952 – Madagascar
albicolor Fraser, 1955 – Madagascar

- *alboterminatus* Selys, 1891 – Madagascar

angydna Schmidt, 1951 – Madagascar
drocera Fraser, 1951 – Madagascar
elizabethae Lieftinck, 1965 – Madagascar
forficuloides Fraser, 1955 – Madagascar
mariae Aguesse, 1968 – Madagascar
martini Schmidt, 1951 – Madagascar
pauliani Fraser, 1951 – Comoros: Mohéli
pulverulans Lieftinck, 1965 – Madagascar
radama Lieftinck, 1965 – Madagascar
ranavalona Schmidt, 1951 – Madagascar
robustus Aguesse, 1968 – Madagascar
rubristigma Martin, 1902 – Madagascar
tuberculicollis Fraser, 1949 – Madagascar

***Neurolestes* Selys, 1882**

nigeriensis (Gambles, 1970) – Nigeria

- *trinervis* Selys, 1885 – Cameroon, Equatorial Guinea, Gabon, Republic of Congo

***Podolestes* Selys, 1862**

atomarius Lieftinck, 1950 – Indonesia: Kalimantan
buwaldai Lieftinck, 1940 – Malaysia: Peninsular Malaysia; Indonesia: Sumatra
chrysopus Selys, 1889 – Brunei; Malaysia: Sarawak; Indonesia: Kalimantan
coomansi Lieftinck, 1940 – Indonesia: Sumatra; Thailand (?)
furcifer Lieftinck, 1950 – Indonesia: Kalimantan
harrissoni Lieftinck, 1953 – Malaysia: Sarawak

- *orientalis* Selys, 1862 – Brunei; Indonesia: Kalimantan, Sumatra; Malaysia; Singapore
  pandanus Wilson & Reels, 2001 – China: Hainan

in lacking supplementary sectors in the tip of the wing and having a dark band in the wing. The larvae of *Protolestes* were shown to have fan-shaped gills, but the adults also lack supplementary sectors in the tip of the wing. Both *Amanipodagrion* and *Protolestes* seem to form separate lines in the evolution of damselflies and do not seem to have close relatives.

In the present paper the former subfamily Argiolestinae is elevated to family level to contain all species of the Fan megapods as discussed above and a definition of this family is given. Table 1 lists all genera and species we propose to include in Argiolestidae. We consider the present family to comprise 20 genera including new genera described here. For eight of these the larvae have not been described and inclusion within this family is based only on adult morphology and, with the exception of *Solomonargiolestes*, for which DNA-material was not available, supporting molecular data.

The members of Argiolestidae are found in Madagascar and Seychelles (two genera, 17 species), mainland Africa (one genus, two species), mainland SE Asia, Borneo and Sumatra (one genus, eight species) and in the Australasian region from the Philippines, through Sulawesi to the Moluccas, New Guinea, the Solomon Islands, Australia and New Caledonia (16 genera, 83 species) (fig. 1). In the last region the highest diversity is found in Australia, New Caledonia and New Guinea. New Guinea has proven to be exceedingly rich, and in recent years numerous new species have been described from this region

(Englund & Polhemus 2007, Kalkman 2008, Kalkman, Richards et al. 2010, Michalski & Oppel 2010, Theischinger & Richards 2006, 2007, 2008). The genera of Africa, Madagascar, mainland SE Asia, Borneo and Sumatra have always been considered monophyletic in the literature, with only some discussion on whether *Nesolestes* is a synonym of *Neurolestes*. The genera of the Australasian region are more problematic. Those in Australia and most in New Caledonia are relatively well defined partly due to the work of Lieftinck (1975, 1976) and Theischinger (1998a). The 53 species currently placed in the genus *Argiolestes* occurring in the Philippines, Sulawesi, the Moluccas, New Guinea, the Solomons and New Caledonia remain poorly resolved. Earlier attempts to split the genus *Argiolestes* into separate genera resulted in the creation of the genera *Metagrion* Calvert, 1913 and *Wahnesia* Förster, 1900. The description of these genera was poor, partly due to the lack of material, and the characters on which the genera were based were found to be quite variable even within species (Lieftinck 1935a). For this reason these generic names were seldom used after having been established. In Kalkman, Richards et al. (2010) a definition was established for *Argiolestes sensu stricto* in which 10 species were included. In order to accommodate all species of *Argiolestes* excluded from *Argiolestes sensu stricto* we describe four new genera and redefine the genera *Metagrion* and *Wahnesia*. New definitions and a key to all genera included in Argiolestidae are given. For all genera information on key generic characters, identification, habitat and distribution is provided. Our results are based on morphology only but the division proposed here is supported by a molecular study which will be published separately.

METHODS

We examined adults of all genera, 90% of the described species and almost all of the original descriptions. Species for which no material was studied are *Podolestes pandanus* and 11 species of *Nesolestes* (*albicaudus*, *albicolor*, *angydna*, *drocera*, *elisabethae*, *forficuloides*, *mariae*, *pauliani*, *robustus*, *rubristigma*, *tuberculicollis*). Most studied specimens are present in Naturalis Biodiversity Center, Leiden (RMNH) in which collection nearly all species studied for this revision are available. Additional material, mainly types, has been studied in the BMNH, HNHM and IRSN. Listed material is present in the RMNH unless otherwise noted.

The information on larvae was derived from the literature. Larvae of eight of the 20 genera have not been described (including *Celebargiolestes* for which only an illustration is available) and the larvae of only a small selection of the total number of species have been described (see Kalkman, Choong et al. 2010, for an overview) for four additional genera. Our present study therefore relies largely on adult characters. Morphological terminology largely follows Garrison et al. (2010).

ABBREVIATIONS

BMNH: Natural History Museum, London, UK; HNHM: Hungarian Natural History Museum, Budapest, Hungary; IRSN: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KSP: Koleksi Serangga Papua, Jayapura, Indonesia; PNG: Papua New Guinea; RMNH: Naturalis Biodiversity Centre, Leiden, Netherlands.

SYSTEMATIC PART

Argiolestidae Fraser, 1957 (fig. 1-6)

Unique characters within Zygoptera
Adult. We have found no unequivocally unique character available for adult Argiolestidae. However the row of small dark denticles present on the apex of the cerci (see diagnosis) might have independently evolved in Argiolestidae and could

be regarded as unique although a structure very much reminiscent of this is found in the New World genera *Heteragrion* and *Oxystigma*.
Larva. Gills are flat and held in a horizontal plane (shared with *Protolestes* and *Dimeragrion*, see Introduction) (fig. 2).

Diagnosis of adults
Small to large damselflies, all resting with wings open and many lacking bright colours. Venation allows discrimination from most other families with the exception of those formerly placed in Megapodagrionidae (fig. 3): (1) 2, seldom 3 Ax; (2) supplementary sectors between IR1 and RP2 and between RP2 and IR2 present; (3) Pt longer than broad (except in *Caledargiolestes*); and (4) IR2 originating near the subnodus, starting clearly closer to nodus than to arculus. Adults of Argiolestidae can be distinguished from other genera formerly placed in Megapodagrionidae by the absence of setae on the shaft of the genital ligula. The only other genera formerly placed in Megapodagrionidae lacking these setae are *Amanipodagrion* and *Protolestes*; these however lack the supplementary sectors in the wings (character 2 as mentioned above).

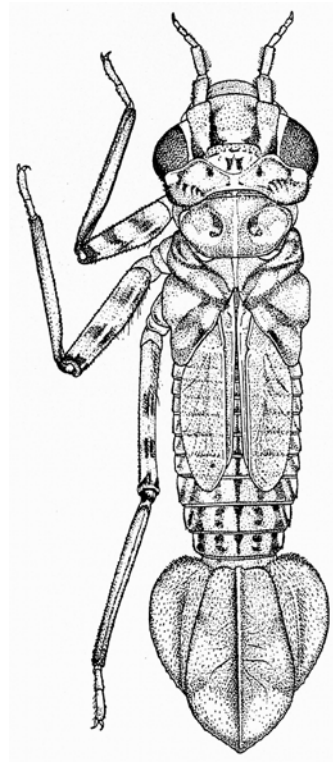

Figure 2. Larva of *Metagrion pectitum* showing the build of Argiolestidae larvae and the distinctive flat horizontal gills. Illustration from Lieftinck (1956).

The main colour of most species is pale brown to black but many species have some blue or red on the face, thorax and/or legs. The abdomen generally lacks bright colours with the exception of the very strikingly coloured *Eoargiolestes ochraceus*. The following characters found in several genera of Argiolestidae are rare or absent in other damselflies:

(1) A row of small dark denticles is present on the upper flange of the apex of the cerci (fig. 4). The length of this row varies among genera and its visibility depends partly on the colour of the cerci. Generally the row is easiest to see in less mature specimens as the cerci tend to be paler, whereas the denticles are already black. In some genera the individual denticles merge forming a low undulated ridge which is difficult to detect (for example in *Caledargiolestes* and *Caledopteryx*). The row of denticles is present in 16 of the 20 genera but seems to have become lost in *Archiargiolestes*, *Austroargiolestes*, *Trineuragrion* and *Pyrrhargiolestes* (except in *P. angulatus*). A single species of the genus *Argiolestes* also lacks the row (*A. tuberculiferus*). Males of only four of the 16 species of *Nesolestes* were studied and only one, *Nesolestes pulverulans*, lacked a row of denticles, suggesting that this row is a prevalent character state within this genus. This row of denticles is absent in most Zygoptera but a similar row is found in some genera of Calopterygidae and some Neotropical genera such as *Heteragrion*, *Oxystigma* and *Heteropodagrion*.

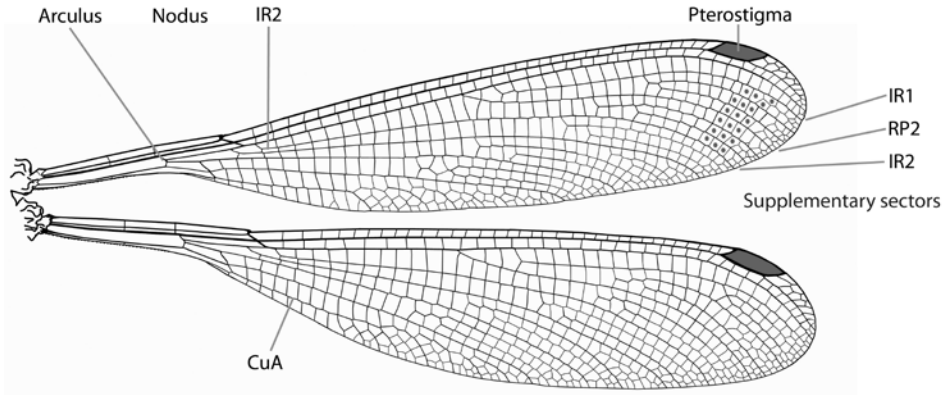

Figure 3. Forewing and hind wing of *Celebargiolestes* sp. showing the general venation found in family Argiolestidae. Drawing by A.G. Orr.

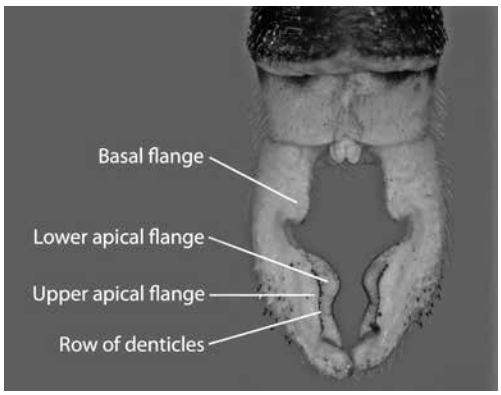

Figure 4. Anal appendages of male *Argiolestes amphistylus* showing the general build of the appendages in Argiolestidae. The white colour of the appendages and the presence of a basal flange are atypical for Argiolestidae and are unique for the genus *Argiolestes*.

(2) The dorsum of S8-9 is weakly sclerotised (in *Metagrion*, *Wahnesia* and to a lesser extent in *Eoargiolestes* and *Caledopteryx*). This character corresponds with the presence of a dorsal spine or bundle of spines on S10 (*Wahnesia*) (fig. 5e) or with the hind rim of S10 being serrated (*Metagrion*) (fig. 5b).

(3) The thorax has a fractured pattern with the pale elements on both sides of the humeral suture not aligned (fig. 9c, 9e, 19b, 19d; present in some species of *Austroargiolestes*, *Caledargiolestes*, *Caledopteryx*, *Griseargiolestes*, *Metagrion*, *Miniargiolestes*, *Nesolestes*, *Podopteryx* and *Solomonargiolestes*). In most other damselfly families the pale pattern either does not cross the humeral suture or is aligned. The taxonomic use of this character is limited as it is often absent simply because the pale pattern is missing either below and/or above the humeral suture.

(4) Pterostigma of adult females bright white to cream yellow in *Celebargiolestes*, *Eoargiolestes*, *Miniargiolestes* and some species of *Austroargiolestes* and *Griseargiolestes*. In *Podopteryx* the pterostigma of females becomes cream white to yellowish above and brown below.

Subfamilies

We partition the family into two subfamilies, Argiolestinae and Podolestinae. This is based on molecular analyses but is supported by the presence of longitudinal microstriae on the shaft of the ligula in Podolestinae (fig. 26c-f) which are absent in Argiolestinae (eg fig. 7c-d). Species of Podolestinae for which the ligula was studied have the base of the apical segment expanded and scoop-shaped; this is not the case or is present to a lesser extent in Argiolestinae. Two character states prevalent in Podolestinae but rare or absent in Argiolestidae are (1) reduction in of the teeth of the ovipositor with the

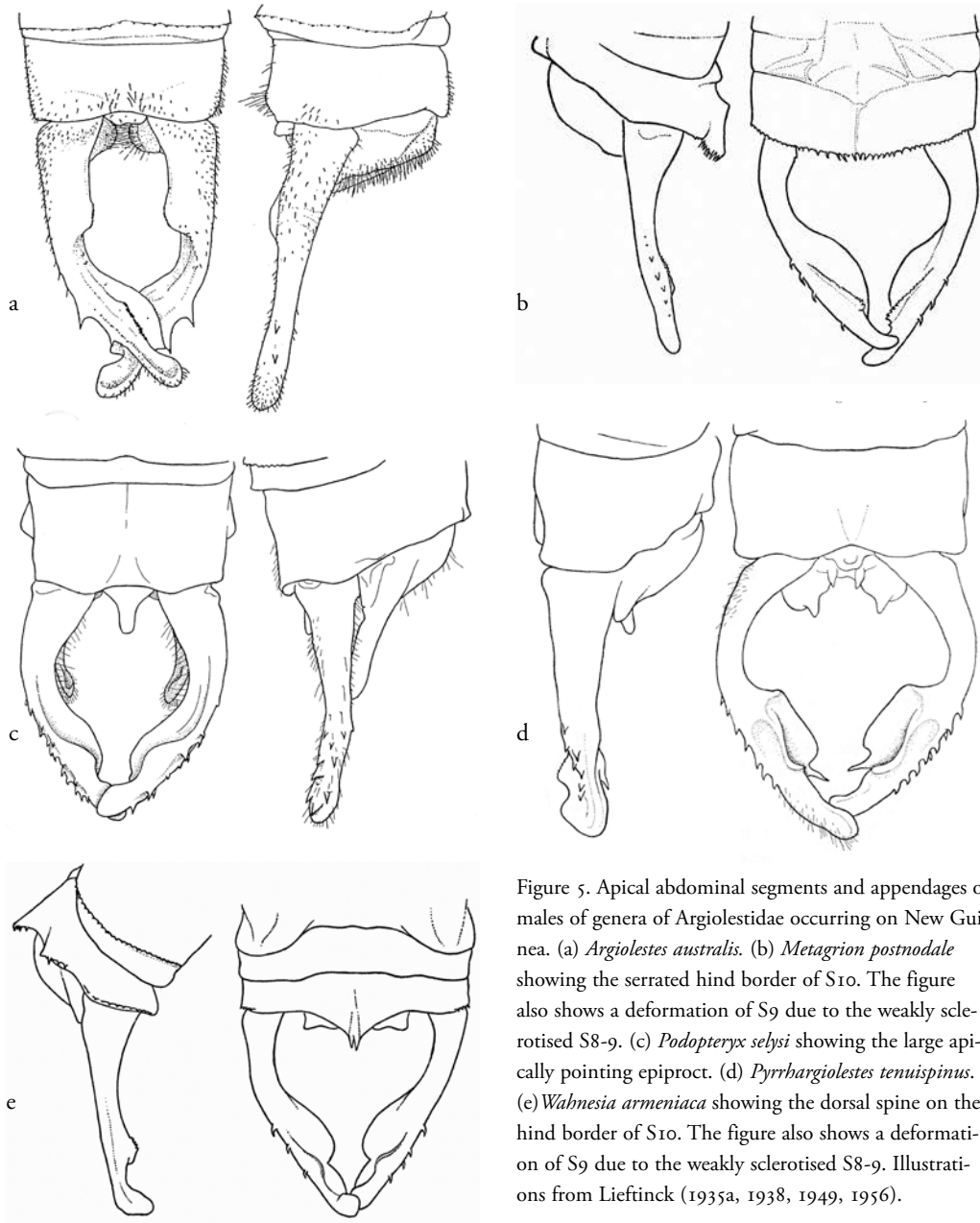

Figure 5. Apical abdominal segments and appendages of males of genera of Argiolestidae occurring on New Guinea. (a) *Argiolestes australis.* (b) *Metagrion postnodale* showing the serrated hind border of S10. The figure also shows a deformation of S9 due to the weakly sclerotised S8-9. (c) *Podopteryx selysi* showing the large apically pointing epiproct. (d) *Pyrrhargiolestes tenuispinus*. (e) *Wahnesia armeniaca* showing the dorsal spine on the hind border of S10. The figure also shows a deformation of S9 due to the weakly sclerotised S8-9. Illustrations from Lieftinck (1935a, 1938, 1949, 1956).

teeth being minute in *Podolestes* and *Allolestes* and absent in *Nesolestes* (fig. 6) (however also present in *Austroargiolestes*); and (2) ovipositor very long and surpassing cerci by at least the length of S10 (present in *Nesolestes*, *Allolestes* and *Podolestes harrisoni*).

Podolestinae includes the four genera found in Africa and Asia west of Huxley's Line while Argiolestinae includes the 16 genera found east of Huxley's Line (fig. 1).

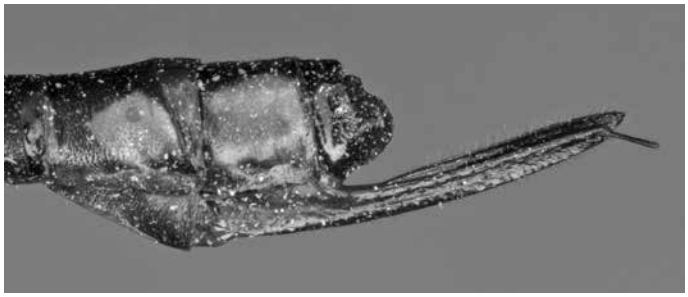

Figure 6. Ovipositor of *Nesolestes ranavalona*.

Argiolestinae Fraser, 1957

Key characters
Adult male. (1) Shaft of ligula smooth, longitudinal microstriae absent.
Adult female. (2) Ovipositor short, not reaching beyond cerci by more than the length of S10.

Archiargiolestes Kennedy, 1925 (fig. 7a, b, 8a, 9a)

Unique characters within Argiolestidae
Adult. (1) Dark colour of head, thorax and abdomen with distinct metallic sheen (shared with *Griseargiolestes*, *Miniargiolestes* and *Trineuragrion*). *Male.* (2) Interior of base of cerci flattened and beset with long pale hairs. (3) Upper and lower apical flange of cercus merged and together forming a medially directed lobe (relatively small in *A. pusillus*). (4) Terminal fold of genital ligula beset with small spines (fig. 7a, b) (*A. parvulus*; not seen but probably also present in *A. pusillus* and *A. pusillissimus*).

Diagnosis and identification
Adult. The only genus of Argiolestidae with which *Archiargiolestes* overlaps in distribution is *Miniargiolestes*, from which it can be easily separated based on the above-mentioned unique characters. Except from *Miniargiolestes* and the New Caledonian *Trineuragrion percostale*, it can be distinguished from all genera by the completely dark dorsum of the thorax in combination with the sides of the thorax having a well-defined dark (brown to black) and yellow pattern.

A revision of the group including a key to the species, figures of the pattern on the thorax and scanning electron microscope (SEM) images of the cerci is found inWatson (1977). Theischinger (1998a) gives a definition of the genus based on adult and larval characters and compares it with other Australian genera of Argiolestidae. Keys to the species can be found inWatson et al. (1991) and Theischinger & Endersby (2009). Theischinger & Hawking (2006) include pictures of all species.
Larva. A key to distinguish larvae of the genus *Archiargiolestes* from those of other Australian Argiolestidae can be found in Theischinger (1998a), Theischinger & Hawking (2006) and in Theischinger & Endersby (2009). Characters to distinguish the individual species of *Archiargiolestes* are not known.

Distribution and habitat
The three species of this genus are limited to the south-western corner of Australia (fig. 8a). Distribution maps of the species can be found in Theischinger & Endersby (2009) and a more detailed map with discussion on their distribution is available in Watson (1977). *Archiargiolestes pusillus* is the most widespread, ranging further inland than *A. parvulus* and *A. pusillissimus*. The distribution of the latter two species falls nearly completely within the distribution of *A. pusillus*. These two have an allopatric distribution, with *A. parvulus* being found at the coastal plain of the west coast, east of the Darling Scarp, while *A. pusillissimus* replaces it on the south coast, south of Busselton. An isolated population of *A. parvulus* is found about 350 km north of its main range at Hutt River, west of Northampton (Watson 1977).

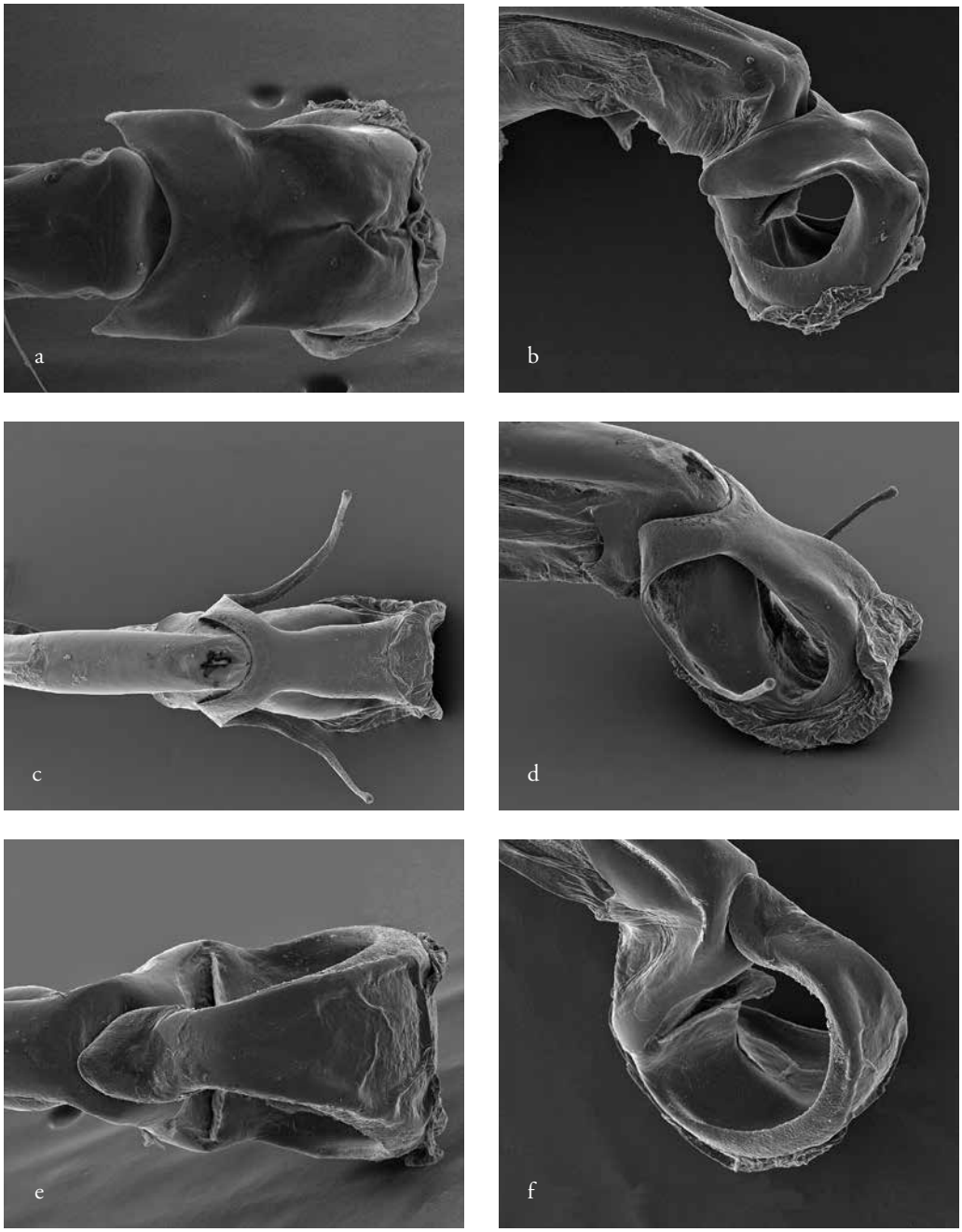

Figure 7. Genital ligula: (a) *Archiargiolestes parvulus*, Australia,West Australia, Gingin, 2010, ventral view; (b) idem, ventrolateral view; (c) *Argiolestes amphistylus*, Indonesia, Papua, Star Mountains, Borme, 2006, ventral view; (d) idem, ventrolateral view; (e) *Austroargiolestes isabellae*, Australia, New South Wales, Barren Ground, 1989, ventral view; (f) idem, ventrolateral view.
Photos: Dirk Gassmann.

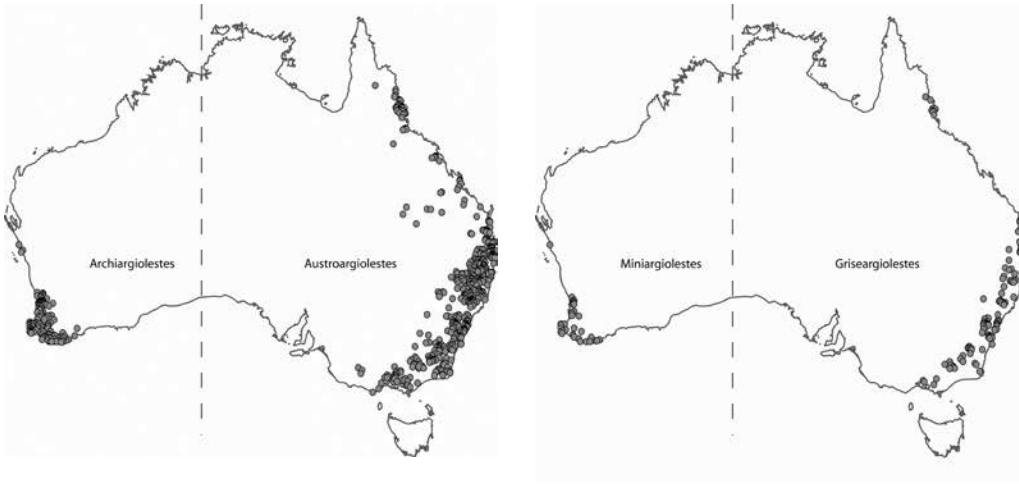

Figure 8. (a) Distribution of *Austroargiolestes* (eastern Australia) and *Archiargiolestes* (western Australia). (b) Distribution of *Griseargiolestes* (eastern Australia) and *Miniargiolestes* (western Australia). Based on records in the Australian Odonata Database.

Watson (1977) described the habitat as shallow, boggy and often seasonal waters, boggy edges of streams and rivers, seepages, marshes and open, shallow, vegetated areas.

Argiolestes **Selys, 1862 (fig. 7c, d, 9b, 10, 11a)**

Unique characters within Argiolestidae

Male. (1) The two apical lobes of the genital ligula are at least four times as long as broad. (2) Part of S10 and cerci are pale (whitish or blue in life) contrasting with darker S9. This is only visible in fully mature specimens and is more easily seen in living individuals. (3) Base of cercus possesses a basal flange in all species except *A. celebensis* and *A. tuberculiferus* (see illustrations of latter two in Kalkman 2007, Michalski & Oppel 2010).
The sole specimen of *A. celebensis* seems to be subadult, which might be the reason that character (2) is not visible in this specimen.

Diagnosis and identification

Adult. The males of the genus have several unique characters, which should facilitate identification. The pale white or blue S10 should make it possible to recognise members of the genus in the field. Kalkman, Richards et al. (2010) contains a key to the species with field pictures of *A. muller* and *A. roon*.
Larva. Unknown.

Distribution and habitat

The group occurs on New Guinea and adjacent islands, the northern islands of the Moluccas and on Sulawesi (fig. 10). Most species seem to have small ranges and none is known from more than five records. The number of specimens encountered in the field is generally low (Kalkman 2007, Kalkman, Richards et al. 2010, Michalski & Oppel 2010). This is in contrast to some other Papuan genera that are often common when found. The limited information on habitats shows that species of *Argiolestes* are found at small, often shallow, brooks in forest (fig. 11a) (Kalkman, Richards et al. 2010, Michalski & Oppel 2010).

Figure 9. (a) *Archiargiolestes parvulus*, male, Australia, Western Australia, Gingin Brook. Photo by Jan Taylor; (b) *Argiolestes muller*, male, PNG,Western Province. Photo by Steve Richards; (c) *Austroargiolestes alpinus*, male, Australia, New SouthWales, Cathedral Rock NP. Photo by Vincent Kalkman; (d) *Caledargiolestes uniseries*, male, New Caledonia, Province Nord. Photo by Steve Richards; (e) *Caledopteryx sarasini*, male, New Caledonia, Province Nord. Photo by Steve Richards; (f) *Caledopteryx sarasini*, male, New Caledonia, Province Nord. Photo by Steve Richards.

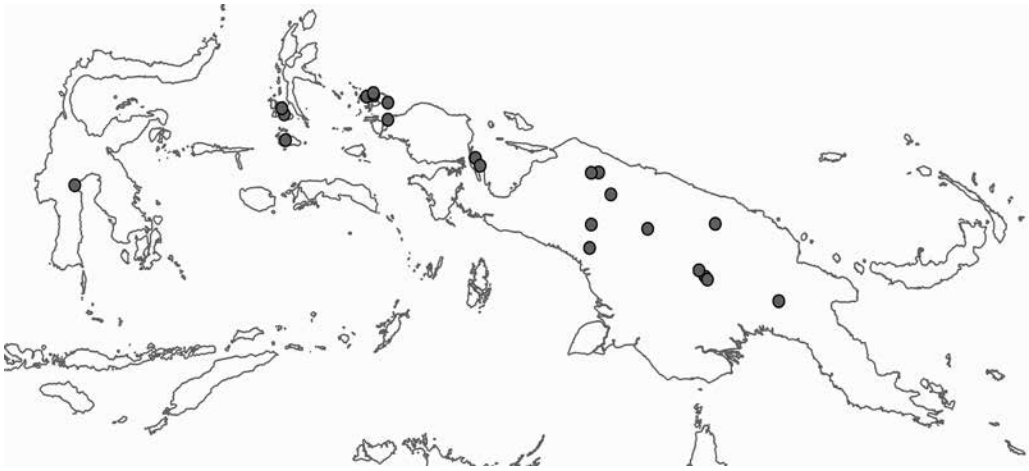

Figure 10. Distribution of *Argiolestes*. Based on record in the Melanesian Odonata Database.

Austroargiolestes Kennedy, 1925 (fig. 7e, f, 8a, 9c)

Risiolestes Fraser (1926)

Unique characters within Argiolestidae
Male. (1) Tip of genital ligula rounded or rounded and widened and never widely bilobed or reduced to a whip-like structure. (2) Sharp ventrally pointing tooth at about two-thirds the length of cerci.

Diagnosis and identification
Adult. Theischinger (1998a) gives a definition of the genus based on adult and larval characters and compares it with other Australian genera of Argiolestidae. A key to the species can be found in Theischinger & O'Farrell (1986), Watson et al. (1991) and Theischinger & Endersby (2009). Theischinger & Hawking (2006) include pictures of all species.
Larva. A key to distinguish larvae of the genus *Austroargiolestes* from those of other Australian Argiolestidae can be found in Theischinger (1998a), Theischinger & Hawking (2006) and in Theischinger & Endersby (2009). Characters to distinguish the individual species of *Austroargiolestes* are not available.

Distribution and habitat
The 10 species of *Austroargiolestes* are endemic to Eastern Australia, occurring from the Grampians and the surroundings of Melbourne in the south to the Atherton Tableland in the north with their distribution centred on the Great Dividing Range (fig. 8a). *Argiolestes icteromelas* is by far the most widespread species, overlapping with all other species. The ranges of the other species are much smaller. Maps of the species can be found in Theischinger & Endersby (2009). The species inhabit streams and rivers, including streams that dry to pools in summer, rainforest streams and boggy seepages. Often co-occurs with *Griseargiolestes*. Little has been published on the behaviour of the species. Murray (1992) noted that *A. isabellae* oviposited unaccompanied by males. Eggs reared at room temperature hatched after 21 days, whereafter it took another 37 weeks for the adults to emerge (Murray 1992). These observations suggest that their development in natural conditions takes one year. Males are normally encountered in higher numbers than females. This makes a note published by Tillyard (1917) the more remarkable: 'An even more extraordinary result than this was obtained by working three or four small streams in dense palm jungle in Queensland. *Argiolestes amabilis* was to be seen on every rock. In a week

I had taken 195 females, but only a single male! Though I sought for the males high and low, they were not to be found. ' He suggested that the males were probably to be found in the top of the trees.

Caledargiolestes Kennedy, 1925 (fig. 9d, 12a, b)

Unique characters within Argiolestidae
Adult. (1) Pt: costal side subequal to basal side. *Male.* (2) Inflated base ("heel") of apical lobes of genital ligula beset with numerous minute spines in *C. uniseries* (shared with *Caledopteryx*; genital ligula of *C. janiceae* not described).

Diagnosis and identification
Adult. Endemic to New Caledonia, and males can easily be separated from other New Caledonian Argiolestidae by the absence of blue on the tip of the abdomen, in lacking enlarged distal membranes of S7-9 and in having two, not three, Ax in the wings. A detailed comparison between the males of both species is found in Lieftinck (1976). The males can be identified with the key below.
Larva. Both Willey (1955) and Lieftinck (1976) give a description of *C. uniseries* as Megapodagrionidae spec. The larva described as *C. uniseries* by Lieftinck (1976) is in fact *Trineuragion percostale* (Marinov 2012). A larval key to the genera of Argiolestidae occurring on New Caledonia can be found in Marinov (2012).

Key to the males of Caledargiolestes

1. Body without conspicuous long raised hairs. Lower apical flange of cerci ending in a bluntly triangular tooth. Larger: hind wing 23-26 mm ..... *C. uniseries*
– Body, especially face, thorax and first two abdominal segments, covered with long raised whitish hairs. Lower apical flange of cerci rounded and not ending in a blunt triangular tooth. Smaller: hind wing 18 mm ..... *C. janiceae*

Distribution and habitat
New records of *C. uniseries*: 2 ♂, 1 ♀: New Caledonia, Yahoue, 17 February 1986, leg. Renevier.

Caledargiolestes uniseries is common and widespread in New Caledonia, whereas *C. janiceae* seems to be very rare, being known only from the holotype collected on Mount Pouedihi (15 km w of Quenarou Forest Station) and a female specimen from "southern New Caledonia between Nouméa and Yaté" (Davies 2002). *C. uniseries* has been found from November to April (Davies 2002), whereas the two records of *Caledargiolestes janiceae* are from 5 November 1972 (holotype) and 18 February 1983. Davies (2002) describes the habitat of *C. uniseries* as "rocky forest streams and their waterfalls on lowground and in mountain areas; exuviae left in abundance on rock ledges and muddy edges at riversides".

Caledopteryx Kennedy, 1925 (fig. 9e, f, 12c, d)

Unique characters within Argiolestidae
Adult. (1) Blue postocular spots present. (2) Postocular lobes slightly enlarged and crenulated. *Male.* (3) Distal membranes of S7-9 enlarged and bright blue. (4) "Heel" of apical lobes of ligula beset with numerous minute spines (shared with *Caledargiolestes*).

Diagnosis and identification
Adult. The blue postocular spots of males and females and the enlarged and bright blue distal membranes of S7-9 of males make this genus easy to recognise. Further distinguished from other genera of Argiolestidae, except *Celebargiolestes*, *Luzonargiolestes* and *Podopteryx*, by its large size (Hw > 32 mm) and by having more than 18 Px (range: 19-28). The two species, both endemic to New Caledonia, are morphologically extremely similar but can be recognised based on size and pattern. The differences between the two were described and illustrated by Winstanley & Davies (1982).

Figure 11. Examples of habitats of genera of Argiolestidae. (a) *Argiolestes muller*, *A. tuberculiferus* and two unidentified species of *Metagrion* (Whip group), PNG, Muller Range, Gugusu Camp. Photo by Vincent Kalkman. (b) *Eoargiolestes ochraceus*, New Caledonia, Thio Province. Photo by Milen Marinov. (c) *Griseargiolestes eboracus*, Polblue Swamp, Australia, New South Wales, Barrington Tops NP. Photo by Vincent Kalkman. (d) *Luzonargiolestes* cf. *baltazarae*, Philippines, Luzon, Cagayan Province, Claveria. Photo by ReaganVillanueva. (e) *Miniargiolestes minimus*, Australia, West Australia, Wooroloo Brook. Photo by Jan Taylor. (f) *Podolestes orientalis*, Malaysia, Selangor, Bangi Forest Reserve. Photo by Chee Yen Choong.

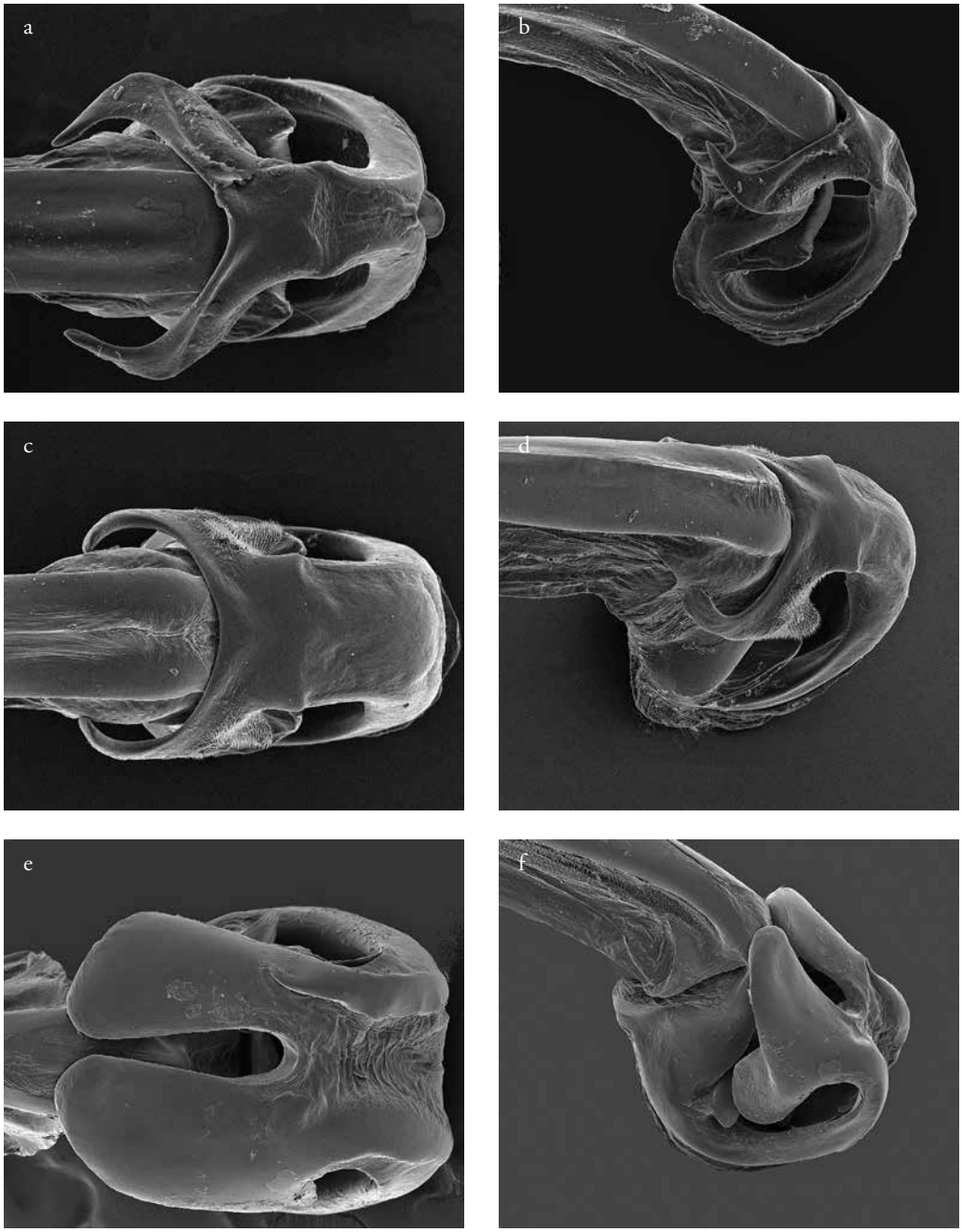

Figure 12. Genital ligula: (a) *Caledargiolestes uniseries*, New Caledonia, Col des Roussettes, 1969, ventral view; (b) idem, ventrolateral view; (c) *Caledopteryx sarasini*, New Caledonia, ventral view; (d) idem, ventrolateral view; (e) *Celebargiolestes cinctus*, Indonesia, Sulawesi, Sulawesi Tengah, 1989, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

Figure 13. Distribution of *Celebargiolestes*. Based on records in the Melanesian Odonata Database.

Larva. Based on distribution the description of the larva of *C. sarasini* by Lieftinck (1976) probably pertains to the, at that time, undescribed *C. maculata*. The larva of *C. sarasini* is undescribed. A larval key to the genera of Argiolestidae occurring on New Caledonia can be found in Marinov (2012).

Key to the males of Caledopteryx

1. Dorsum of S9 blue, connecting blue membrane of S8 with that of S9. S2-8 each with a pair of pale lateral spots at posterior border of the segment each covering about one-tenth length of segment ..... *C. maculata*
– Dorsum of S9 black, blue membrane of S8 not connected by blue of S9. S2-8 uniformly dark without pair of pale lateral spots .... *C. sarasini*

Distribution and habitat

New records of *C. sarasini*, all from New Caledonia: 1 ♂: Valee d'Amoa, 17 February 1963, leg. N.L.H. Krauss. 2 ♂, 1 ♀: Col de Tendo (near waterfall), 22 November 1985, leg. D.A.L. Davies. New records of *C. maculata*, all from New Caledonia: 2 ♂: Mouirance Pass, 10 February 1962, leg. N.L.H. Krauss. – 2 ♂, 2 ♀: La Captive, 18 February 1983, leg. D.A.L. Davies. – 1 ♂, 2 ♀: Mont Koghi Cascades, 5 February 1983, leg. J. Geijskes. – 1 ♂, 2 ♀: Thi, 9 December 1981, leg. D.A.L. Davies. – 3 ♂: Yate road, no date, leg. D.A.L. Davies.

Both species of *Caledopteryx* are endemic to New-Caledonia where they are common at suitable streams (Davies 2002). *Caledopteryx maculata* has mainly been found in the southern tip of New Caledonia and is largely replaced by *C. sarasini* further north although their ranges overlap. Both *C. maculata* and *C. sarasini* have been recorded from November to February. Winstanley & Davies (1982) note that *Caledopteryx* species "generally occur in the steeper sections of forested catchments". Males were found to settle horizontally on prominent perches at potential oviposition sites. Females were observed to "oviposit directly onto steep rock-faces" and "into a small rivulet flowing over a clay bed, and into a steep hillside seepage area where leaf litter had accumulated". An exuvia was found "on a rockface approximately 1 m away from the water about halfway up a 3 m waterfall". They also mention that larvae "were flushed with the point of a stiff leaf from horizontal cracks in the rocks on the faces of waterfalls".

Celebargiolestes **Kennedy, 1925 (fig. 12e, f, 13)**

Unique characters within Argiolestidae

Male. (1) Large lateral lobe present at base of each of apical lobes, which is disc-like and covers the lateral "opening" of genital ligula.

Diagnosis and identification

Adult. The genus can be distinguished from all other members of the family by the combination of the following characters: (1) Fw with 25 or more

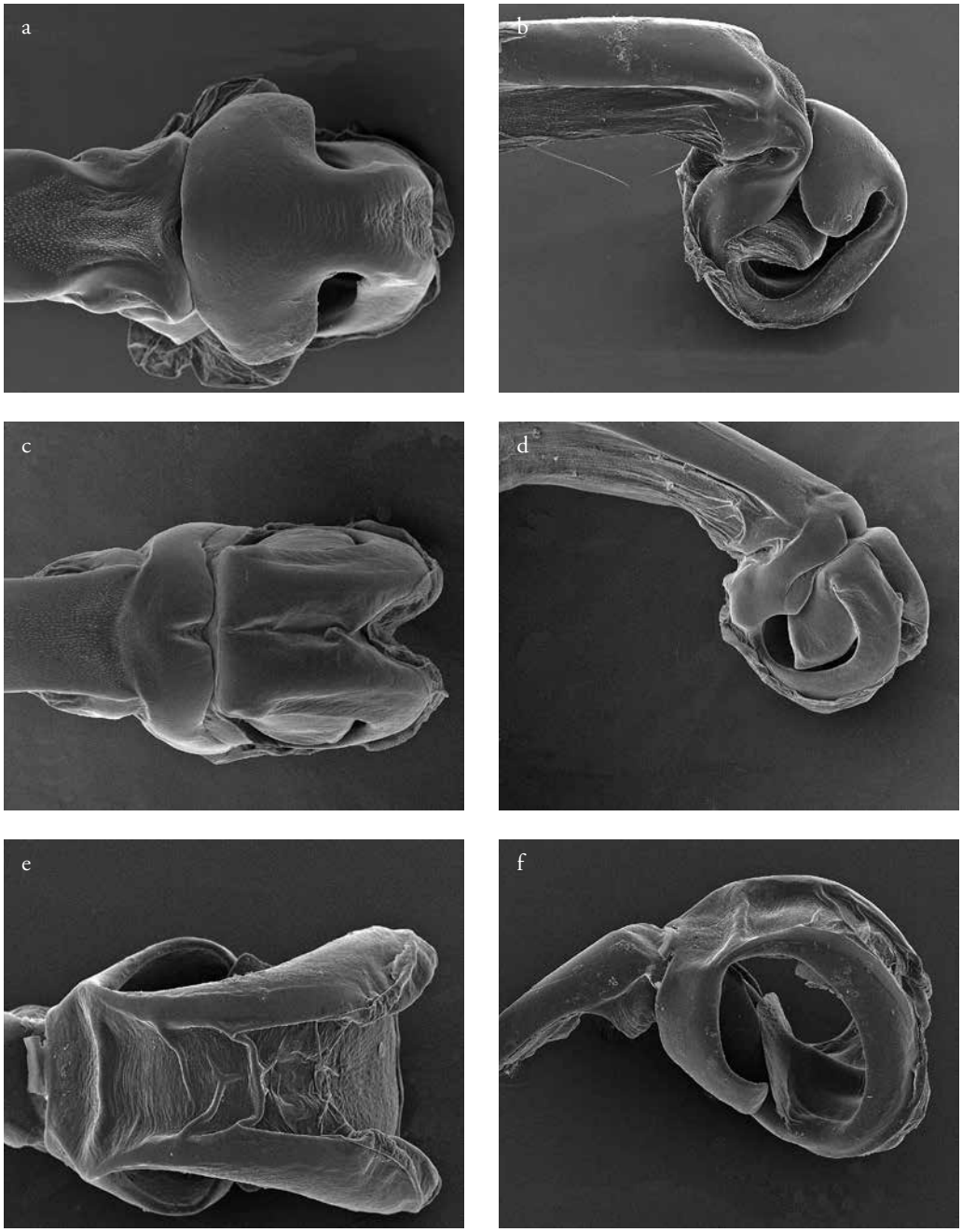

Figure 14. Genital ligula: (a) *Eoargiolestes ochraceus*, New Caledonia, ventral view; (b) idem, ventrolateral view; (c) *Griseargiolestes griseus*, Australia, New South Wales, Wentworth Falls, 2012, ventral view; (d) idem, ventrolateral view; (e) *Luzonargiolestes* cf. *baltazarae*, Philippines, Luzon, Cagayan Province, Claveria, 1997, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

Px; (2) epiproct shorter than one sixth of the length of the cerci; (3) postocular lobes not strongly bulging; and (4) face never with blue. The only other species of Argiolestidae occurring on Sulawesi is *Argiolestes celebensis*. This species is, however, easily distinguished from *Celebargiolestes* by having less than 24 Px and having very long and slender apices of the genital ligula. *Celebargiolestes cincta* is the only species described but descriptions of several new species together with a key by the first author are in preparation.
Larva. No detailed description of the larvae is available. Culhane (2005) published pictures of a megapodagrionid larva from Buton Island which is likely to pertain to *Celebargiolestes* (Kalkman, Choong et al. 2010).

Distribution and habitat
Celebargiolestes is found throughout Sulawesi and the adjacent islands of Sangihe, Peleng and Buton (larva only; Culhane 2005) (fig. 13). Based on the information on the labels of material present in the RMNH the habitat of *Celebargiolestes* is best described as brooks and small rivers in forest. The altitudinal range of the genus extends from 90 to 1500 m. It seems that the species are most common on the lower parts of mountains.

Eoargiolestes **gen. nov. (fig. 11b, 14a, b, 15a)**

Type species
Sympecma ochracea Montrouzier, 1864 by present designation.

Etymology
The name is composed of "Eo-" and the genus name "Argiolestes". Eos is ancient Greek for dawn, referring to the bright orange colour on the thorax and abdomen.

Generic characterisation
Adult male. Head black except for pale stripe running from eye to eye across clypeus and small pale dots between lateral ocelli and sockets of antennae; all pale markings becoming obscured in older specimens. Head slender without prominent postocular lobes. Thorax with ground colour black and with bright orange pattern on sides and on dorsum. Markings on thorax not crossing sutures. Thorax never with pruinosity. Interior of legs not expanded, no strong contrast in colouration between interior and exterior of legs. First pair of legs with one black ring on femora, second and third pair with two black rings. Femora becoming largely blackish with age. S2-6 bright orange, S7-8 black and S9-10 blue. Hw with two rows of cells between CuA and hind border. Discoidal cell of forewing with costal side subequal in length to distal side; Pt in mature males black but strikingly white in immature males. Wings of mature individuals have, especially at base, a distinct orange tinge. Genital valves pointed, longer than broad and gradually tapering towards apex. S9 only weakly sclerotised; S10 without distinct armature. Paraprocts shorter than one half of cerci. In dorsal view distance between cerci subequal to width of cercus at base. Cerci curved inwards from base; dorsally with a knob near apex and 4-6 spines on the outer border. Genital ligula not reduced and with expanded tip; inner fold large and often visible from ventral aspect.
Adult female. Thorax with far less extensive pale pattern than male and lacking bright orange colours; abdomen orange-brown to black lacking bright orange and blue. Pt in adults pale (cream white). Ovipositor short, not surpassing tips of cerci, with dense row of minute spines.

Unique characters within Argiolestidae
Male. (1) S2-6 bright orange. (2) Genital valves about twice as long as broad, gradually tapering towards pointed apex. (3) Wings of mature individuals with distinct orange tinge.
Compared to other genera of Argiolestidae the head is relatively slender, with the space behind the lateral ocelli small and both frons and genae steep and not projecting. *Eoargiolestes* shares with *Metagrion* and *Wahnesia* the weakly sclerotised dorsum of S9; this is, however, less expressed in *Eoargiolestes*

Figure 15. (a) *Eoargiolestes ochraceus*, male, New Caledonia, Province Nord, Roche de la Wayem. Photo by Steve Richards. (b) *Griseargiolestes albescens*, male, Australia, Queensland, Springbrook NP. Photo by Vincent Kalkman. (c) *Luzonargiolestes* cf. *baltazarae*, male, Philippines, Luzon, Cagayan Province, Claveria. Photo by Reagan Villanueva. (d) *Metagrion subornatum*, male, Indonesia, Papua Province, Japen Island. Photo by Vincent Kalkman. (e) *Metagrion aurantiacum*, male, Papua New Guinea, New Britain. Photo by Steve Richards. (f) *Metagrion trigonale*, teneral male, Papua New Guinea. Photo by Steve Richards.

and in contrast to these other genera the segment does not appear wrinkled in dead specimens.

Diagnosis and identification
Adult. Monotypic genus, characters as for genus.
Larva. Lieftinck (1976) gives a description of *E. ochraceus*. A larval key to the genera of Argiolestidae occurring on New Caledonia can be found in Marinov (2012).

Distribution and habitat
New records of *E. ochraceus* all from New Caledonia: 1 ♂, 1 ♀: Bourail to Houailou road, March 1959, leg. N.L.H. Krauss. 2 ♀: Sarramca, 12 Feb 1963, leg. N.L.H. Krauss. 1 ♀: 10 km S of Koh, 300 m, 31 January 1963, leg. N.L.H. Krauss. 1 ♂: Mount Koghi, 500 m, January 1963, leg. N.L.H. Krauss.
The monotypic genus *Eoargiolestes* is endemic to New Caledonia where it is common and widespread. Davies (2002) gives the habitat as "shaded streams at edges of forest" (fig. 11b). Lieftinck (1976) provided the following remarks on the eight larvae he studied: "The body cuticle and gills of all specimens are covered throughout with a thin layer of silt and particles of fine sand adhering to the pubescence, so as to conceal most of the colour design. It is evident, therefore, that *A. ochraceus* lives in slow flowing water with a silty bottom". Recorded from October to March.

Griseargiolestes Theischinger, 1998 (fig. 8b, 11c, 14c, d, 15b)

Unique characters within Argiolestidae
Adult. (1) Dark colour of head, thorax and abdomen with distinct metallic sheen (shared with *Archiargiolestes*, *Miniargiolestes* and *Trineuragrion*).
Male. (2) Genital ligula without inner fold (shared with *Podopteryx*).

Diagnosis and identification
Adult. Theischinger (1998a) gives a definition of the genus based on adult and larval characters and compares it with other Australian genera of Argiolestidae. Theischinger (1998a, 1998b), and Theischinger & Hawking (2006) include pictures of all species. A key to the species can be found in Theischinger & Endersby (2009). The tip of the genital ligula is strongly curved and at least in the genital ligula of *G. griseus* depicted here, the tip is bent inwards (fig. 14c, d), although this is apparently not the case in all species/specimens (see drawing of genital ligula of *G. griseus*, *G. albescens* and *G. eboracus* in Theischinger (1998a)).
Larva. A key to distinguish the larvae of the genus *Griseargiolestes* from those of other Australian Argiolestidae, and a key to some of the species can be found in Theischinger & Endersby (2009).

Distribution and habitat
The seven species of *Griseargiolestes* are restricted to eastern Australia, occurring from the surroundings of Melbourne in the south to the Atherton Tableland in the north with their distribution centred on the Great Dividing Range (fig. 8b). Maps for all species can be found in Theischinger & Endersby (2009). Most species are found at boggy seepages, small runnels, springs and streams (fig. 11c).
They often co-occur with species of *Austroargiolestes*, but compared to these they are mostly found in the slower flowing and more densely vegetated sections. Adults sit low between the vegetation and rarely sit on the ground or on stones. *Griseargiolestes albescens* has been suggested to occur at dune lakes (Theischinger & Endersby 2009).

Luzonargiolestes gen. nov. (fig. 11d, 14e, f, 15c, 16)

Type species
Argiolestes realensis Gapud & Recuenco, 1993 by present designation.
Etymology The name is composed of a reference to Luzon, referring to the Philippine island where the genus occurs and the genus name "Argiolestes".

Generic characterisation
Large, bulky species which are largely brownish and lack bright colours.

Adult male. Front of face, including labrum, mandibles, genae, clypeus and sockets of antennae dark brown to black. Postocular lobes bulging. Prothorax and synthorax brown to black without distinct pale pattern and never with pruinosity. Dorsum of synthorax dark brown to black, sides pale brown. Legs pale brown, lacking distinct dark markings and without contrast between interior and exterior; interior of legs not expanded. S3-6 in all species brown to black with anterior pale mark and smaller posterior pale mark. Wings with two or more rows of cells between CuA and hind border. Discoidal cell of forewing with costal side about three times as long as distal side. Dorsum of S8-9 normal, not weakly sclerotised. Hind rim of S10 without distinct armature, slightly raised in the centre forming low inconspicuous longitudinal crest; hind border slightly concave with epiproct visible in dorsal view. Paraprocts slightly shorter than half the length of cerci. In dorsal view distance between cerci subequal to width of one cercus. Base of cerci without basal flange. Outer border of cerci carrying several medium size spines. Cerci with lower and upper dorsal flange, the latter with row of inconspicuous brown to black denticles. Apical segment of genital ligula well developed with broad apical lobes which are about two to three times as long as wide, whole outer border of genital ligula, up to apex, weakly sclerotised and appearing wrinkled.
Adult female. Pt of adult females black. Ovipositor reaching or surpassing tip of cerci, beset with long yellow hairs and with dense and regularly spaced row of teeth.
Larva. Unknown.

Unique characters within Argiolestidae
Adult. (1) Postocular lobes bulging (shared with *Caledopteryx*, but there lobes are slightly crenulated).
Male. (2) Genital ligula has a distinct morphology which is reminiscent of *Griseargiolestes*: two apical lobes of genital ligula are broad and about two to three times as long as wide, the whole outer border of genital ligula, up to where apical lobes begin, is slightly hollow and appears wrinkled.

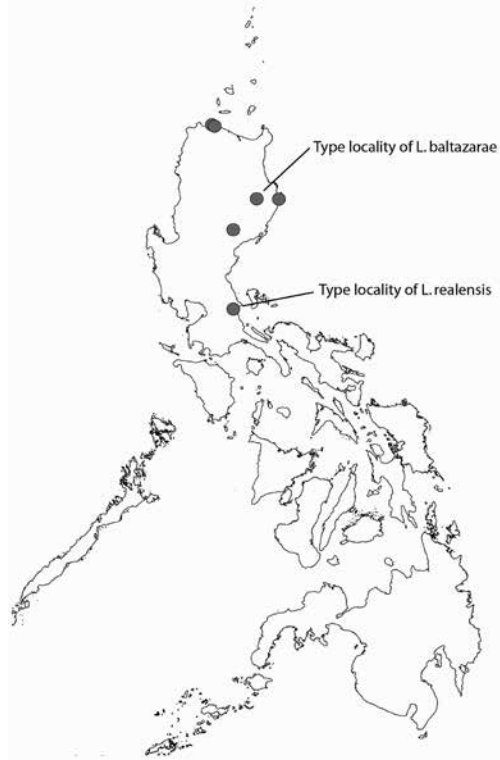

Figure 16. Distribution of *Luzonargiolestes*.

Diagnosis and identification
Adult. The only genus of Argiolestidae occurring in the Philippines. The genus can be easily distinguished from most other members of the family by S8-10 being normally sclerotised (neither weakly sclerotised nor with pale white or blue), the face, thorax and legs lacking blue or red and the thorax lacking a well defined pattern. The genus most resembles *Celebargiolestes* in its large size and the absence of bright colours but can easily be distinguished by its bulging postocular lobes and the shape of the genital ligula.
Information on the identification of the two species can be found in Gapud & Recuenco-Adorada (2001). The material recorded here for the first time was compared with a male from the type locality of *L. realensis* present in the RMNH (Luzon, National Botanical Garden, 14 April 1987, V.P. Gapud). This showed that all new

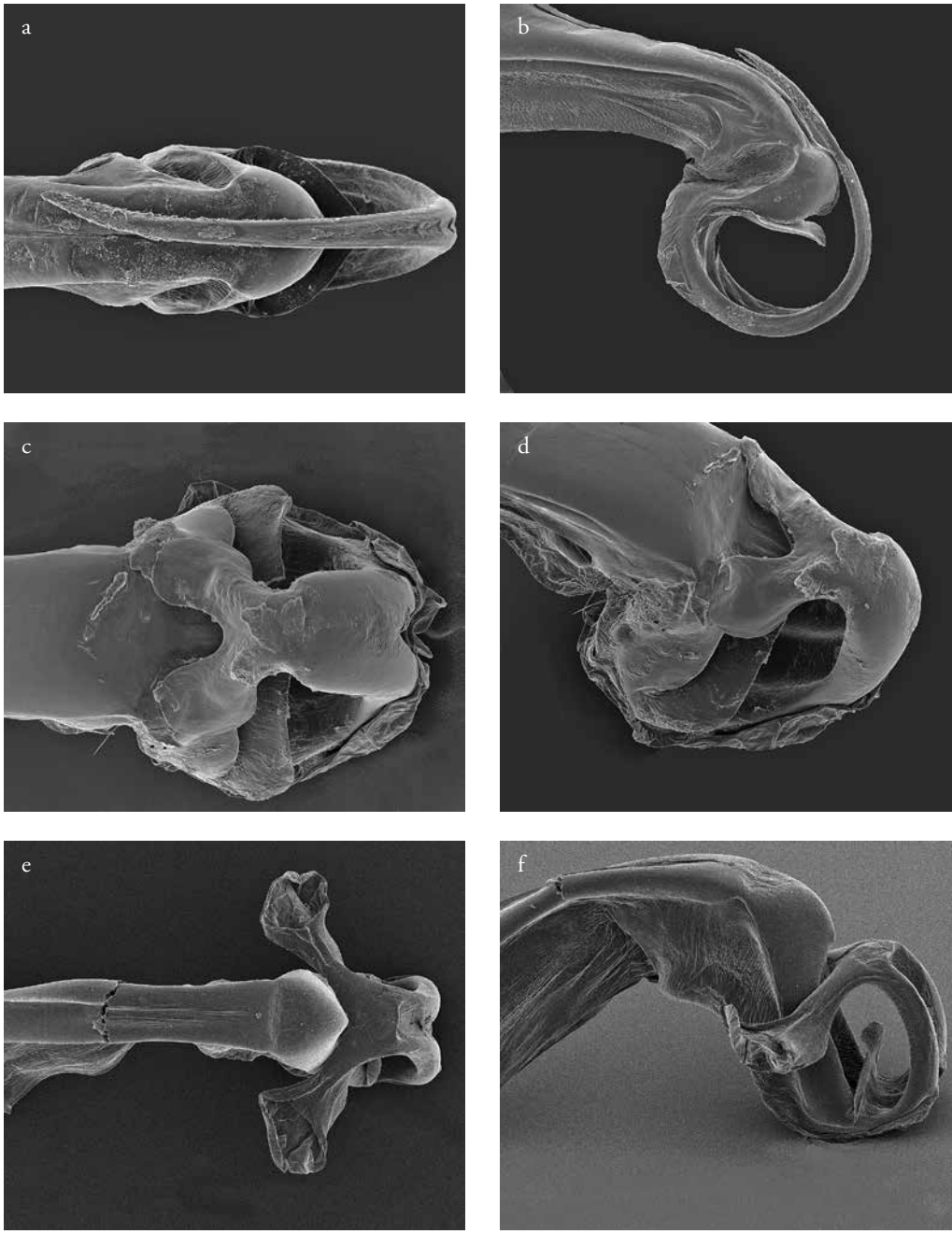

Figure 17. Genital ligula: (a) *Metagrion triste*, Indonesia, Jayapura, Cyclop Mountains, ventral view; (b) idem, lateral view; (c) *Metagrion connectens*, Indonesia, Sorong, 1948, ventral view; (d) idem, lateral view; (e) *Miniargiolestes minimus*, Australia, West-Australia, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

material is different from *L. realensis* and best fits *L. baltazarae* as the Hw has more than two rows of cells between CuA and hind border and the paraprocts are less slender with a less clear constriction halfway. There is however some variation in the shape of the paraprocts between new material from different localities. We do not have material from the type locality of *L. baltazarae* at hand and therefore have chosen to publish these records as *L.* cf. *baltazarae*.
Larva. Unknown.

Distribution and habitat
New records of *Luzonargiolestes* cf. *baltazarae*, all from Philippines, Luzon: 1 ♂: Quirino Province, Maddela, Sierra Madre, 15-30 August 1996, 400-600 m, leg. C.M. Nazareno (specimen mentioned as *Argiolestes* sp. n. in Hämäläinen and Müller 1997). – 2 ♂, 1 ♀: Isabela Province, Northern Sierra Madre Natural Park, Dipinantahikan (campsite 1), 300 m, 16°53. 398'E 122°20. 471'N, 12-20 September 2008, leg. R.J. Villanueva (record without details mentioned in Villanueva et al. 2009). – 15 ♂, 2 ♀: Cagayan Province, Claveria, Barangay Labla-Big, 200-500 m, 20-30 May 1997, leg. C. M. Nazareno. – 34 ♂, 2 ♀: Cagayan Province, Claveria, Barangay Union, 100-500 m, 20-30 May 1997, leg. C.M. Nazareno.
The genus *Luzonargiolestes* is known from six localities on Luzon with *Luzonargiolestes realensis* only known from its type locality at the National Botanical Garden and *L.* (cf.) *baltazarae* known from five widely scattered more northern localities (fig. 16). The mountain regions of Luzon have been insufficiently studied and it seems likely that the genus is present throughout the mountains of Luzon at localities where larger blocks of forest remain at low elevation. Gapud & Recuenco-Adorada (2001) suggest that the species might be absent from the southern part of Luzon (the Bicol region) as it was not encountered there despite several field collections.
Information on habitat is scant. Gapud & Recuenco-Adorada (2001) give the habitat of *Argiolestes baltazarae* as a small stream covered with undergrowth vegetation, although specimens were also found further away near a river and at a place where the small stream widened into a mountain stream with rock boulders. *Luzonargiolestes* cf. *baltazarae* was found in deeply shaded and moist forest (R.J. Villanueva, pers. comm.) (fig. 11d). The habitat of the larvae is unknown but observations of *Luzonargiolestes* cf. *baltazarae* at Isabela Province suggest that they live in seepages and small streams (R.J. Villanueva, pers. comm.).

Metagrion **Calvert, 1913 (fig. 5b, 11a, 15d-f, 17a-d, 18)**

General
Calvert (1913) created *Metagrion* with *M. postnodalis* as the only species but without studying material of the species. He did not give a separate description of the genus but included it in a venation-based key to the species of the Legion Podagrion (= Megapodagrionidae *sensu lato*).
Ris (1915) doubted the validity of the genus and Lieftinck (1935a) studied the specimens and showed that the main character on which the genus was separated from *Argiolestes* (IR2 being distal to the subnodus) varied within the specimens. The genus has subsequently been considered a synonym of *Argiolestes*. Here the genus is reinstated for a group of 18 species all endemic to New Guinea and sharing a serrated hind rim of S10 (character state lost in *M. fornicatum* and *M. verrucatum*).

Generic characterization
Adult male. Labrum in most species either completely pale blue or completely dark metallic. Ground colour of head dark brown to black with three types of pattern: (1) a pale (whitish) line running from eyes to clypeus, and together with pale anteclypeus, forming a pale bar (can become obscured in older specimens; (2) lower part of face, including parts of clypeus and an area along eyes, pale blue; (3) front of face black, lacking clear pale pattern. Ground colour of prothorax and synthorax brown in immature adults, becoming black in fully mature ones. Pale pattern on dorsum of synthorax absent or small and often confined to

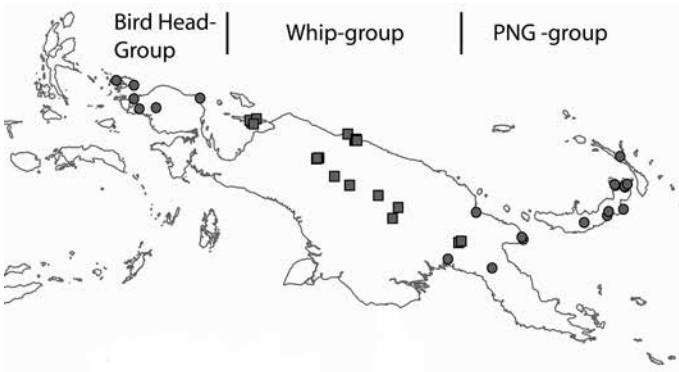

Figure 18. Distribution of *Metagrion*. Based on records in the Melanesian Odonata Database.

anterior corner. Sides of synthorax varying from an extensive blue pattern to completely dark. Legs in most species dark brown but with red on inside or completely red in species of the PNG group. Wings always with at least two and mostly with three rows of cells between the CuA and hind border. Discoidal cell of forewing with costal side 1. 5 to 2. 2 times as long as distal side. Dorsal surface of S8-9 only very lightly sclerotised, often appearing wrinkled in dead specimens. Hind rim of S10 completely or partially serrated (fig. 5b) (absent in *M. fornicatum* and *M. verrucatum*). Paraprocts shorter than half the length of cerci. In dorsal view distance between cerci is clearly greater than the width of one cercus. Cerci without basal flange but with lower and upper apical flange, the latter with row of sometimes inconspicuous brown to black denticles. Apical segment of genital ligula always slender and in the Whip group reduced to a whip-like structure.

Adult female. Pt of adult females dark brown to black. Ovipositor reaching or slightly surpassing tip of cerci, in some species with dense and regular spaced row of teeth, whereas in others species the teeth are widely and irregularly spaced.

Unique characters within Argiolestidae

Male. (1) S8-S9 weakly sclerotised, often wrinkled in dead specimens (as in *Wahnesia* and to a lesser extent in *Eoargiolestes*). (2) Hind rim of S10 serrated (fig. 5b) (except in *M. fornicatum* and *M. verrucatum*).

Diagnosis and identification

Adult. The above-mentioned unique characters make it easy to recognise the genus. *Metagrion fornicatum* and *M. verrucatum* do not have the serrated S10 but can be recognised by the weakly sclerotised S8 and S9 in combination with a reduced and whip-like apex of the genital ligula. The genus is species-rich with currently 18 described and numerous undescribed species. Together with the relatively small morphological differences this makes identification to species level difficult. No review of the group is available and (re)descriptions of the species must be consulted for identification (Kalkman 2008, Lieftinck 1935a, 1938, 1949, 1956, Michalski & Oppel 2010, Theischinger & Richards 2006, 2007, 2008). Table 2 facilitates identification of the species by dividing them into three groups mainly based on the shape of the ligula. Each of these groups is centred on a different part of New Guinea. Further study is needed to determine if these groups are monophyletic.

Larva. The larvae of *M. fontinale* and *M. pectitum* were described by Lieftinck (1956, 1976).

Distribution and habitat

Metagrion is the most widespread genus of Argiolestidae in New Guinea and occurs throughout the island with exception of the southern lowlands (fig. 18). The PNG group is endemic to Papua New Guinea with *M. aurantiacum* being found on New Britain and New Ireland and the three others occurring in mainland Papua

Table 2. Characters separating the three groups of *Metagrion*.

	PNG group	Whip group	Bird Head group
Included	*aurantiacum, montivagans, indentatum, trigonale*	*fornicatum, lamprostoma, pectitum, sponsum, subornatum, triste, verrucatum*	*coartans, connectens, convergens, fontinale, ochrostoma, ornatum, postnodale*
Colour of legs in life	At least interior of legs orange to red	Never with orange or red	All described species without red, one undescribed species known with red legs
Colour of pale parts of thorax in life	Orange to red	Blue or dull yellow	Blue or dull yellow
Inner side of legs	Clearly expanded	Not clearly expanded	Not clearly expanded
Genital ligula	Apex slender with two ort terminal lobes	Head of ligula reduced to a long whip, without terminal lobes (Figure 17a, b)	Apex slender with two short terminal lobes (Figure 17c-d), genital ligula of *M. coartans* not studied
Labrum	Completely metallic	Varies per species, can be non-metallic, partly metallic or completely metallic	Varies per species, can be non-metallic, partly metallic or completely metallic
Distribution	New Britain and mainland Papua New Guinea	Mainland New Guinea excluding Bird Head Peninsula, Huon Peninsula and the easternmost tip of the mainland	Bird Head Peninsula

New Guinea. The Whip group occurs on mainland New Guinea to the west of the PNG group but is replaced on the Bird Head by the Bird Head group. The latter includes two species endemic toWaigeo, *M. coartans* and *M. ochrostoma*. The species of *Metagrion* are among the more common inhabitants of forest brooks in New Guinea (fig. 11a). They are, less often than species of *Argiolestes* and *Wahnesia*, found at seepages and seem to prefer small, largely shaded brooks although they are sometimes also found at larger rivers. Males sit in the vegetation above or near the water and show little activity. No information is available on territoriality, courtship, mating or oviposition.

Miniargiolestes **Theischinger, 1998 (fig. 8b, 11e, 17e, f, 19a)**

Unique characters within Argiolestidae
Adult. (1) Dark colour of head, thorax and abdomen with distinct metallic sheen (shared with *Archiargiolestes*, *Griseargiolestes* and *Trineuragrion*). *Male.* (2) Genital ligula with distinct shape: lateral lobes of genital ligula shaped like trumpets, slender at base but widening towards apex. (3) Intersegmental annulus of S8 and S9 white, strongly contrasting with the dark segments.

Diagnosis and identification
Adult. The only genus of Argiolestidae with which

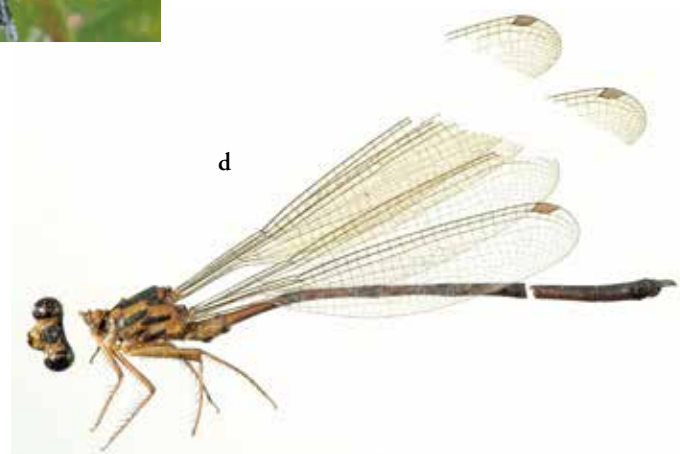

Figure 19. (a) *Miniargiolestes minimus*, male, Australia, Western Australia, Dandalup near Pinjarra. Photo by Jan Taylor. (b) *Podopteryx selysi*, male, Papua New Guinea. Photo by Steve Richards. (c) *Podopteryx selysi*, male, Papua New Guinea. Photo by Steve Richards. (d) *Solomonargiolestes malaita*, male, Solomon Islands, Malaita Island. Photo by Vincent Kalkman. (e) *Wahnesia* spec., male, Papua New Guinea. Photo by Steve Richards.

Miniargiolestes overlaps is *Archiargiolestes*, from which both sexes can be easily separated in the field by having their intersegmental annuli of S8 and S9 white and strongly contrasting with the dark segments. In addition females of *Miniargiolestes* and most males except for very old specimens have a white Pt (in *Archiargiolestes* only white when immature). Illustrations and pictures of the only species, *Miniargiolestes minimus,* can be found in Watson et al. (1991), Theischinger (1998a), Theischinger & Hawking (2006) and Theischinger & Endersby (2009).
Larva. A key to distinguish larvae of the genus *Miniargiolestes* from those of other Australian Argiolestidae can be found in Theischinger (1998a), Theischinger & Hawking (2006) and Theischinger & Endersby (2009).

Distribution and habitat
The only species of the genus, *Miniargiolestes minimus*, is confined to south-western Australia where it overlaps with the three species of *Archiargiolestes* (fig. 8b). *Miniargiolestes minimus* is restricted to streams and rivers (fig. 11e), in contrast to the three species of *Archiargiolestes*, which are also found at boggy seepages and marshes (Watson 1977). The larvae have been found under stones or on submerged sticks (Watson 1977).

Podopteryx **Selys, 1871**
(fig. 5c, 19b, c, 20a, 21)

Unique characters within Argiolestidae
Male. (1) Genital ligula strongly reduced and consisting of a long and slender whip which is round in basal cross section (fig. 20a). The genital ligula of *Podopteryx* resembles that of the Whip group of *Metagrion* but there the base of the whip is broad, gradually tapering towards the tip and the inner fold on the ligula head is always present. (2) Inner fold on ligula head absent (shared with *Griseargiolestes*) (fig. 20a). (3) Epiproct large and very conspicuous, pointed apically and when seen dorsally, more than twice as long as broad and about one sixth the length of cerci (not so in *P. casuarina*) (fig. 5c).
Female. (4) Pt brown below but white above.

Diagnosis and identification
Adult. The genus overlaps in range both with genera from New Guinea and with genera occurring in eastern Australia. It can easily be distinguished from all these by its superior size, the large number of Px in Fw (>28), by having four or more rows of cells between the CuA and the hind border of the Hw and by the conspicuous and apically directed epiproct which is about twice as long as broad (except in *P. casuarina*).
The males can be identified with the key below. The characters to distinguish *P. selysi* and *P. roseonotata* based on the pattern and colouration of the thorax given in Lieftinck (1935a) have been found to be incorrect (Lieftinck 1949, 1951), as the colour probably varies with age, whereas the pattern shows individual or possibly regional variation.
Larva. The larva of *P. selysi* was described and illustrated by Watson & Dyce (1978) and Theischinger & Hawking (2006).

Key to the males of Podopteryx

1 Paraprocts about half as long as cerci ... *P. selysi*
– Paraprocts less than one fourth as long as cerci 2

2 Epiproct conspicuous and about twice as long as broad. Metanepisternum dark with pale marking starting near lower posterior margin then bending towards mesopleural suture. Cerci in lateral view slightly upturned ..... *P. roseonotata*
– Epiproct small, less than twice as long as broad. Metanepisternum dark with pale line running from just above metastigma from posterior margin of metanepisternum towards anterior margin. Cerci in lateral view straight ..... *P. casuarina*

Distribution and habitat
New records of *P. roseonotata*: 1 ♂: Indonesia, Papua, Kabupaten Mimika, Akimuga, Fakafuku, 50 m asl, 2 August 2001, leg. E.M. Rosarianto (KSP).
New records of *P. selysi*: 1 ♂: Indonesia, Papua, Kabupaten, Mamberamo Tengah, Marina Valen,

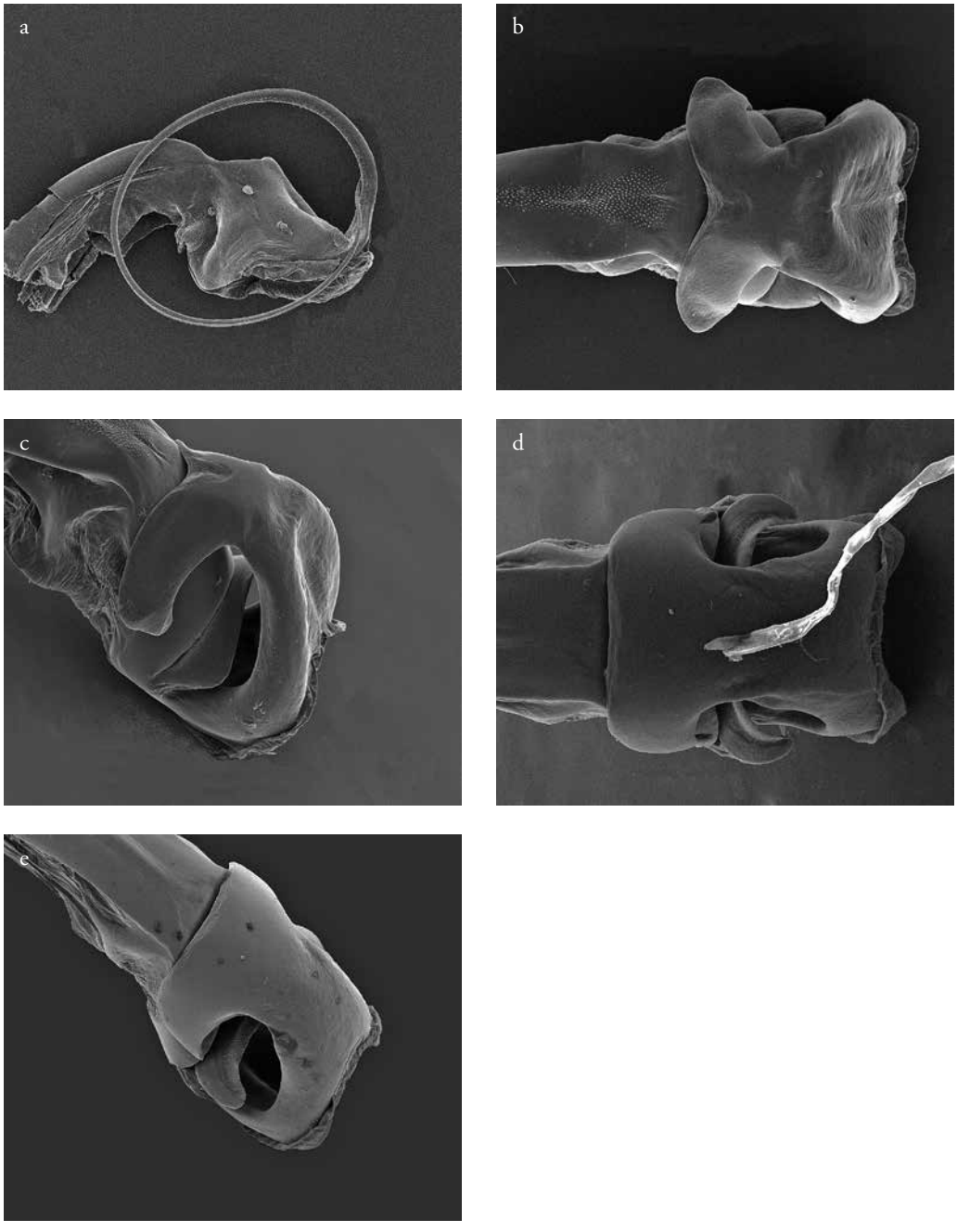

Figure 20. Genital ligula: (a) *Podopteryx selysi*, Indonesia, Jayapura, 1938, lateral view; (b) *Pyrrhargiolestes kula*, Papua New Guinea, Milne Bay Province, Modewa Bay, 1956, ventral view; (c) idem, ventrolateral view; (d) *Trineuragrion percostale*, New Caledonia, Yahoue, 1983, ventral view; (e) idem, ventrolateral view.
Photos: Dirk Gassmann.

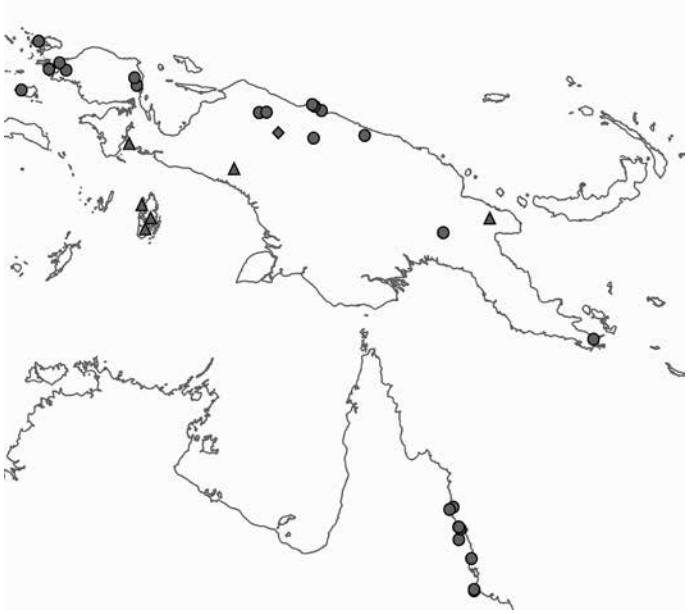

Figure 21. Distribution of *Podopteryx*. *Podopteryx selysi* (dots), *P. roseonotata* (triangles) and *P. casuarina* (diamond). Based on records in the Melanesian Odonata Database and the Australian Odonata Database.

Gunung Acaua, 540 m asl, 17-20 July 2004, leg. H. van Mastrigt (KSP). – 2 ♀ (one adult, 1 immature): Indonesia, Papua Barat, Klamono Oilfields, 18-24 August 1948, leg. M.A. Lieftinck. – 1 ♂: Indonesia, Papua Barat, Misool, Id (W), 0-75 m, 8 September to 20 October 1948, leg. M.A. Lieftinck. – 1 ♀: Indonesia, Papua Barat, Sorong, 26 August 1948, leg. M.A. Lieftinck. – 1 ♀: Indonesia, Papua Barat, Sorong, sea-level forest, 28 August 1948, leg. M.A. Lieftinck. – 1 ♀: Indonesia, Papua Barat, Sorong, forest, 2 September 1948, leg. M.A. Lieftinck. – 2 ♂: Indonesia, Papua, Manokwari, plain of Momi River, 5-10 m, 15-31 August 1948, leg. A.J. Kosterman. – 1 ♂: Indonesia, Papua Barat, Arfak Mts, Angigita, 1800-2000 m, 15-25 October 1948, leg. A.J. Kosterman. – 1 ♂: Papua New Guinea, Kokoda trail, 600 m, 7 December 1971, leg. R. Straatman.

The distribution of the three species of *Podopteryx* is shown in fig. 21. *Podopteryx casuarina* is only known from the male holotype from Bernhard Camp, Papua Province, Indonesia (400 m). *Podopteryx roseonotata* is known from several islands in the Aru Archipelago, from one location on the Huon Peninsula and one hitherto unpublished record from southern lowland of Papua, Indonesia. *Podopteryx selysi* is the most widespread with records from Australia (Cape York Peninsula, Queensland), mainland New Guinea and the islands of Salawati and Waigeo. One male specimen is labelled "Darwin" in the Northern Territory in Australia. No other records are known from this area and as long as none become known this record is probably in error. Several authors, eg Lieftinck (1935a, 1949, 1951) and Watson (1974), mentioned *P. roseonotata* as occurring in North Queensland, but these records have never been confirmed (Watson & Dyce 1978). All records are from forest, often away from water. Most records are from lowland but *P. selysi* has been recorded from 1650 m in the Foja Mountains and from 1800 m in the Arfak Mountains.

All species appear to be rare and are usually encountered one at a time. Stüber, a collector living in present-day Jayapura (Papua, Indonesia), wrote that all seven specimens of *P. selysi* he collected were found away from water hanging on bushes along paths in forest (cited in Lieftinck 1935a). He also remarked that it was rare, having found only seven specimens in three years of collecting.

Similar observations on *P. selysi* were made near Cairns and on the Atherton Tableland by R. Dobson who noted that "adults of these damselflies occur in forest away from water" (cited in Watson & Dyce 1978). Oppel (2005), who found only three specimens of *P. selysi* at Crater Mountain-Wildlife Management Area (Papua New Guinea) during 112 sampling days, remarked that it was found "generally well away from any water source in sunny clearings of the rainforest". The text on the envelope of the only specimen of *P. casuarina* states that it was collected in dense tropical forest far away from water. All these observations do not necessarily mean that the species are rare but that they are difficult to find as they are found in forest away from more usual dragonfly habitats. Watson & Dyce (1978) mention that *P. selysi* appears to be not uncommon in the rainforest of North Queensland. The first description of the larva and its biology was published byWatson & Dyce (1978) who recorded two larvae being found in cavities about 60-80 cm above ground in trees bordering a small clearing. Each of these contained 2-3 l water, submerged plant litter and organic sludge. Based on this it seems clear that *P. selysi* is a phytotelmata breeder which explains why the species is found in forest away from visible water. The only other record of larvae of *Podopteryx* is from Kitching (1990) who found one larva "probably of the tree hole genus *Podopteryx*" in a water-filled treehole in Madang (Papua New Guinea). Information on the habitat of the other two species is lacking but it seems likely that they also breed in phytotelmata. As far as is known, *Podopteryx* is the only genus of Argiolestidae breeding in phytotelmata, and in all other genera either larvae have been found in running water or adults are mostly found near running water. It is also the only genus outside Libellulidae, Aeshnidae and Coenagrionidae (including the former Pseudostigmatidae and New World Protoneuridae) to breed in phytotelmata (Corbet 1999). In contrast with other species of Argiolestidae, adults of *Podopteryx* hang with the abdomen held vertically. *Podopteryx selysi* seems to be on the wing throughout the year in New Guinea. In North Queensland the species is found only in the wet season from the start of October to the start of April (Watson & Dyce 1978; Australian Odonata Database).

Pyrrhargiolestes **gen. nov. (fig. 20b, c, 22)**

Type species
Argiolestes sidonia Martin, 1909 by present designation.

Etymology
The name is composed of the word "pyrrhos" which is the Greek word for flame-like, referring to the bright red-orange colours of many of the species, and the genus name "Argiolestes".

Generic characterisation
Medium large species with striking orange to red colours on face, legs and thorax.
Adult male. Labrum dark metallic with green or blue gloss, anteclypeus pale (whitish). Mandibles, genae, frons and dorsum of head black with a pale line running from eye-margin to postclypeus and partly continuing on sides of postclypeus, centre of postclypeus dark metallic. Prothorax dark with varying amount of pale pattern on pronotum. Synthorax with mesepisternum, mesepimeron, metepisternum matt black with narrow to broad pale orange band running just above intersegmental suture from near hind border of synthorax to just past metastigma. A short longitudinal orange streak is present on dorsum of synthorax in some species. Lower half of metepimeron dull orange, upper half dirty brown. Legs, including coxae and trochanters, yellow orange in museum specimens but probably bright orange to red in all species when alive. Inner side of femora clearly expanded. Spines orange-brown. Abdomen either dark throughout, or S3-6 pale with a posterior black ring. Wings with one to three rows of cells between CuA and hind border. Discoidal cell of forewing with costal side 1.2 to 1.3 times as long as distal side. S8-9 not weakly sclerotised and S10 lacking spines on dorsum or row of spines on hind

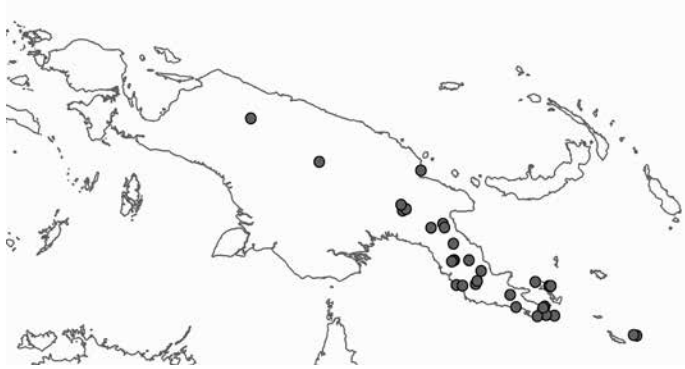

Figure 22. Distribution of *Pyrrhargiolestes*. Based on records in the Melanesian Odonata Database.

margin. Paraprocts shorter than half the length of cerci. In dorsal view distance between cerci subequal to or greater than width of one cercus. No basal flange at base of cerci. Outer border of cerci carrying several medium large spines. Cerci with lower and upper dorsal flange, the latter with or without a row of inconspicuous brown to black denticles. The genital ligula was studied for all species with the exception of *P. angulatus*. All of these have the same general structure, with a well-developed apical segment bearing two apical lobes which are about twice as long as broad. The outer side of the apical segment of ligula is weakly sclerotised up to the point where the apical lobes begin.
Adult female. Pt of adult females black. Ovipositor just reaching or surpassing tip of cerci and with dense row of small and well-developed teeth.

Unique characters within Argiolestidae
Male. (1) Tibiae and femora slightly expanded and orange to red throughout, lacking distinct black marking (shared with some species of *Wahnesia* and *Metagrion*).

Diagnosis and identification
Adult. The species of *Pyrrhargiolestes* are easily recognised as such by having the tibiae and femora orange to red throughout and by lacking modifications on S10. In addition to this the following characters distinguish them from most other species of Argiolestidae occurring on New Guinea: (1) labrum completely dark metallic blue or green; and (2) S8-9 normal (not weakly sclerotised).
A key to the species with description of the species is found in Kalkman et al. (2012).
Larva. Unknown.

Distribution and habitat
Whereas six species are endemic to Papua New Guinea, *P. aulicus* has been recorded in the Indonesian part of the island (fig. 22). A map showing the distribution of all species can be found in Kalkman et al. (2012). The genus is found from sea-level to 1800 m, and in general the species seem to occupy a wide altitudinal range. The species are restricted to seeps and brooks in forest and they seem to have a preference for steeper brooks, waterfalls and seep rheocrenes.

Solomonargiolestes **gen. nov.**
(fig. 19d, 23)

Type species
Argiolestes bougainville Kalkman, 2008 by present designation.

Etymology
The name is composed of a reference to the Solomons, referring to the island group where the genus occurs, and the genus name "Argiolestes".

Generic characterisation
Adult male. Front of face largely bright blue or orange. Postocular lobes not prominent.
Thorax with extensive bold blue or orange pattern.

Figure 23. Distribution of *Wahnesia* (dots) and *Solomonargiolestes* (squares). Based on records in the Melanesian Odonata Database.

Pale markings on thorax cross sutures. Thorax never with pruinosity. Interior of legs not expanded, pale brown or orange and without strong contrast in colouration between interior and exterior. Femora with or without one, clear dark ring. S3-6 brown with apical sixth of each segment dark brown. Wings with two rows of cells between CuA and hind border. Discoidal cell of forewing with costal side about twice as long as distal side. S8-9 not weakly sclerotised and S10 without modification but with the middle of the hind rim slightly depressed and concave. Paraprocts about one fourth to one third the length of cerci. In dorsal view distance between cerci is subequal to width of one cercus. The genital ligula was not studied as only holotypes are available.
Adult female. Unknown.

Unique characters within Argiolestidae
Male. (1) Thorax has a bold orange or blue pattern with markings crossing the sutures. The character of these markings is very distinct although difficult to describe concisely. It is not unlikely that unique characters can be found in the genital ligula but the genital ligula of neither species could be studied.

Diagnosis and identification
Adult. Solomonargiolestes bougainville and *S. malaita* can readily be recognised by the combination of pale brown or orange legs and the face and thorax being largely blue and orange respectively.
Larva. Unknown.

Distribution and habitat
New record of *Solomonargiolestes* spec.: 1 ♀, Solomon Islands, Santa Isabel Island, Hageulu, 400-650 m, 13 September 1964, leg. R. Straatman.

Both species belonging to this genus are known from a single male each. The single specimen of *S. bougainville* was caught on 2 January 1970 on Bougainville without further indication of locality or habitat (fig. 23). The single male *S. malaita* was caught on 27 September 1957 at Tagatalau, E of Auki on the island Malaita at an altitude of 200 m. Bougainville was never thoroughly sampled for dragonflies, and it is difficult to say if *S. bougainville* is genuinely rare or was simply overlooked. *Solomonargiolestes malaita* was not encountered during sampling for aquatic invertebrates at 10 different sites on Malaita between 28 July and 1 August 2005, which indicates that the species is not common (Polhemus et al. 2008). The single female from Hageulu lacks the tip of the abdomen. It can be recognised as *Solomonargiolestes* based on the bold pattern on the thorax resembling that of the two known species. The pattern on the thorax is discoloured but is

probably blue in life. The specimen has 2 Ax and 16-17 Px which is clearly less than the 20-21 and 25-27 Px of the males of *S. malaita* and *S. bougainville*, suggesting that it pertains to an undescribed species.

Trineuragrion **Ris, 1915**
(fig. 20d, e, 24a, b)

Unique characters within Argiolestidae
Adult. (1) Wings with three Ax, sometimes one or two wings with two Ax (shared with *Neurolestes trinervis*). (2) Dark colour of head, thorax and abdomen has a distinct metallic sheen (shared with *Archiargiolestes*, *Griseargiolestes* and *Miniargiolestes*).

Diagnosis and identification
Adult. Trineuragrion shares its range with three other genera of Argiolestidae. Males lack bright blue colours on abdomen and thorax, except for some pruinosity on S9-10, which easily separates them from males of *Eoargiolestes* and *Caledopteryx*. From the two species of *Caledargiolestes* it is separated by the metallic green ground colour of its body and the abdomen being dark throughout. A small number of available photographs suggest that partially mature males and females have the eyes pale blue throughout. These become black in the upper twothirds and pale greenish in the lower third when mature. The pale blue colour of the eyes is not found in any Argiolestidae, except for and to a lesser extent in the south-western Australian *Miniargiolestes*, and allows easy identification of specimens in life. *Trineuragrion percostale* is the only argiolestine species of which mature adults often sit with their wings closed or partly open. *Larva.* A description of the larva of *Trineuragion percostale* can be found in Lieftinck (1976: as *Caledargiolestes uniseries*) and in Marinov (2012). The latter paper also includes a larval key to the genera of Argiolestidae occurring on New Caledonia.

Distribution and habitat
New records of *T. percostale*, all New Caledonia: 1 ♂: Yahoue, 15 February 1983, leg. D.A.L. Davies; 1 ♂: Yahoue, 18 February 1986, leg. D.A.L. Davies. – 1 ♂: Col de la Pirogue, 13 February 1962, leg. N.L.H. Krauss.

The genus *Trineuragrion* is endemic to New Caledonia. It is widespread but seems to be scarcer than other New Caledonian argiolestids such as *Eoargiolestes ochraceus* and *Caledopteryx maculata*. A record of a male collected on Banks Island, Vanuatu, in November 1929 by Miss L.E. Cheesman published by Kimmins (1936) is the only record outside New Caledonia. This record seems unlikely and is regarded as incorrect as long as no other supportive evidence is available.

Davies (2002) mentions collecting the species from small falls of less than a metre stating that these "will customarily be watched over by a male *Trineuragrion*, perched on the nearest large stone above the pool below, in which the female will be busy ovipositing". According to Marinov (2012) it mainly inhabits moderate sized rivers up to 5-6 m wide although it was also found at a 20m wide, shallow and rocky river. River banks where the species occurs are typically densely vegetated and fallen tree trunks and branches in the middle course of the river were found to be of great importance for mating and ovipositing (Marinov 2012).

This is the only species of Argiolestidae in which mature specimens regularly have their wings closed when resting (fig. 24a, b). It was estimated that this was the case in 25% of the observed specimens (S. Richards, pers. comm.). Recorded from November to April (Davies 2002).

Wahnesia **Förster, 1900**
(fig. 5e, 19e, 23, 25a-d, 27c)

General
Förster (1900) described the genus *Wahnesia* based on material of two, at the time undescribed, species (*Wahnesia kirbyi* and *Metagrion montivagans*). *Wahnesia kirbyi* was designated as the type of the

Figure 24. (a) *Trineuragrion percostale*, male, New Caledonia, Province Nord, Roche de la Wayem. Photo by Steve Richards. (b) *Trineuragrion percostale*, female, New Caledonia, Province Nord, Dawenia. Photo by Steve Richards. (c) *Allolestes maclachlani*, male, Seychelles, Silhouette Island. Photo by Mike Samways. (d) *Nesolestes ravanalona*, female, Madagascar, Ranomafana NP, Talatakeli. Photo by Julien Renoult. (e) *Neurolestes trinervis*, male, Gabon, Moyabi. Photo by Nicolas Mézière. (f) *Podolestes buwaldai*, male, Malaysia, Pahang. Photo by CheeYen Choong.

genus by Kennedy (1925). Neither Förster (1900) nor Kennedy (1925) presented a full description of these species but Förster (1900) did note characters separating the two species included in his new genus, and this therefore qualifies as a formal description of the species (for details see Garrison et al. 2003). The first proper description of both species was provided by Lieftinck (1935a) who subsequently has sometimes been incorrectly regarded as author of this species (eg Davies & Tobin 1984). Lieftinck (1935a) discussed the genus and its characters and deemed it invalid as it was based on two undescribed (but see above) species whose characters did not warrant the erection of a new genus. The genus has subsequently always been considered a synonym of *Argiolestes*. Here the genus is reinstated to receive all species with weakly sclerotised S8-9 and with the dorsum of S10 having a single spine or a bundle of spines originating from one point. The only species missing the dorsal spine(s) on S10 is *W. saltator*. Based on the weakly sclerotised S8-9 this species belongs to either *Metagrion* or *Wahnesia*. It is here placed in *Wahnesia* as the general shape of the cerci and the pattern on the thorax do not fit *Metagrion* and clearly resemble *Wahnesia*.

Generic characterisation

Small to medium sized species, largely brown to black with, in at least some species, blue pattern on thorax and blue tip of abdomen. More so than in other genera the colour of thorax and legs fade in preserved specimens to such an extent that blue marking on the thorax became pale brownish or greyish and the orange or red markings on legs became yellow-brown. Based on pictures of live specimens of *W. annulipes* (Polhemus et al. 2004) and *W. gizo* (Polhemus et al. 2008) we deem it likely that in all species the pale pattern on face and thorax is pale blue in life, whereas pale parts of legs are orange to red. Additional problems in this genus are caused by the distinct change in pattern and colouration due to age, with the pattern on the thorax and face becoming obscured with age. Many species are known from only a handful of specimens which, combined with the aforementioned variation, renders members of this genus poorly known.

Adult male. Labrum with outer third to outer two-thirds dark metallic and remainder pale whitish to blue, labrum in *W. simplex* completely metallic. Face and dorsum of head pale brownish in immature specimens, later becoming dark brown to black, with pale (whitish) line running from eyes to clypeus, and together with pale anteclypeus forming pale bar. In older specimens pale line running from eyes to clypeus becomes dark. Postocular lobes not bulging. Ground colour of prothorax and synthorax pale brown in immature adults, becoming black in fully mature individuals. Pattern on synthorax poorly defined, blue in living specimens but becoming pale brownish in preserved specimens. Extent of pattern varies with age and becomes completely obscured (black) with age in at least some species. Colour of legs varies between species and can be dark throughout, dark on the outside and pale (reddish) on the inside, reddish with dark bands on the femora or uniform reddish. Reddish colour becoming yellow-brown in preserved material. S3-6 brown to black with anterior and posterior black annulus. Wings with mostly two, but in some species three, rows of cells between CuA and hind border. Discoidal cell of forewing with costal side about 1.8 to 2.0 times as long as distal side. Dorsal surface of S8-9 only very lightly sclerotised, often appearing wrinkled in preserved specimens. S10 short, about 5 to 6 times as broad as long. Posterior margin of S10 with single large raised spine (fig. 5e) (absent in *W. saltator*); this spine can consist of a tightly packed bundle of smaller spines (*W. kirbyi*). Posterior margin of S10 never serrated. Paraprocts shorter than half the length of cerci. In dorsal view distance between cerci clearly greater than width of one cercus. Cerci without basal flange but with lower and upper dorsal flange, the latter with row of sometimes inconspicuous brown to black denticles. Apical segment of genital ligula well developed with small apical lobes which are about one to two times as long as wide.

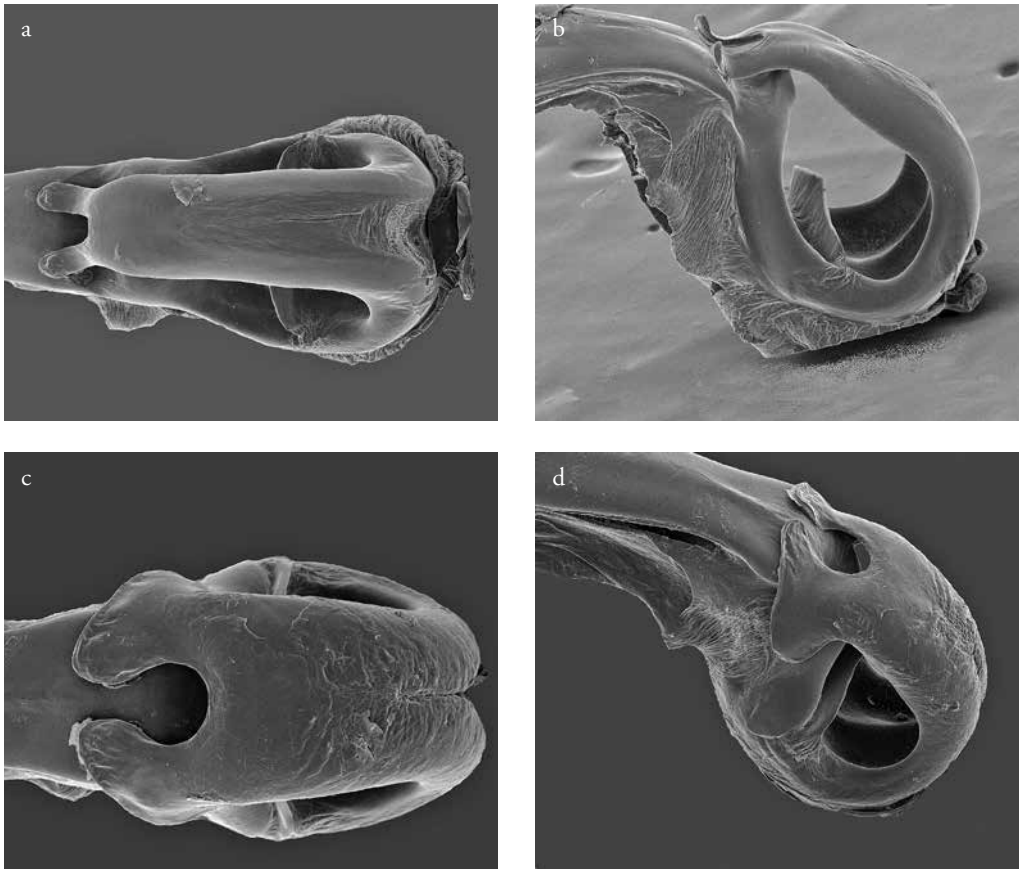

Figure 25. Genital ligula: (a) *Wahnesia armeniaca*, Papua New Guinea, Fergusson Island, ventral view; (b) idem, lateral view; (c) *Wahnesia* spec., Papua New Guinea, Sudest Island, 1956, ventral view; (d) idem, ventrolateral view. Photos: Dirk Gassmann.

Adult female. Pt of adult females black. Ovipositor reaching or surpassing tip of cerci, in some species with dense and regularly spaced row of teeth, whereas in others the teeth are widely and irregularly spaced.

Unique characters within Argiolestidae

Male. (1) S8-S9 weakly sclerotised, often wrinkled in dead specimens (as also in *Metagrion* and to a lesser extent in *Eoargiolestes*). (2) Dorsum of S10 bears near the hind rim a single, often slightly raised, spine (fig. 5e) or, in *W. kirbyi*, a bundle of smaller spines more or less originating from one point (absent in *W. saltator*).

Diagnosis and identification

Adult. With the exception of *W. saltator* all species can easily be recognised as *Wahnesia* based on the above-mentioned unique characters. In *W. saltator* the mid-dorsal spine on S10 is lacking but this species is easily recognised by lacking a row of spines on the posterior margin of S10 and having S8-9 strongly expanded and about twice as broad as S10. Identification to species level is difficult due to the high number of species, the relatively weak morphological differences between species and the large variation of patterns and colouration due to age. A key and illustrations of all species can be found in Michalski (2012).

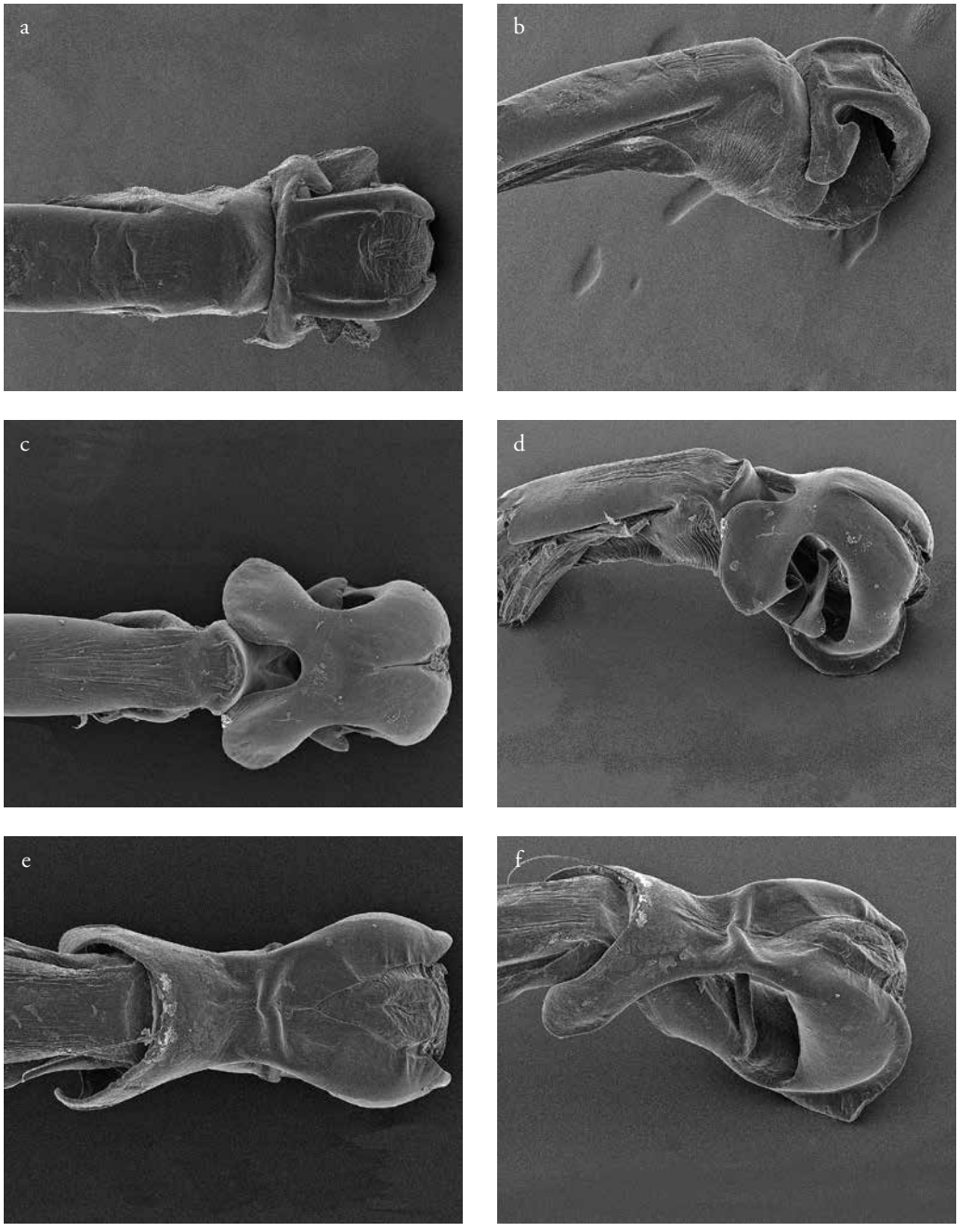

Figure 26. Genital ligula: (a) *Allolestes maclachlani*, Seychelles, Silhouette, La Pase, 2001, ventral view; (b) idem, ventrolateral view; (c) *Neurolestes trinervis*, Cameroon, Meme District, Ngombo Hills, 1999, ventral view; (d) idem, ventrolateral view; (e) *Podolestes orientalis*, Indonesia, Borneo, Ampah, 1948, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

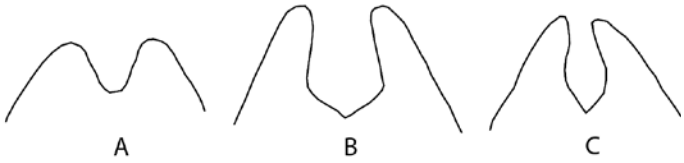

Figure 27. Shape of median cleft of labium: (a) *Allolestes maclachlani*; (b) *Nesolestes ranavalona*; (c) *Wahnesia gizo*.

Distribution and habitat
The genus *Wahnesia* is, with the exception of *W. simplex*, endemic to Papua New Guinea and the Solomon Islands (fig. 23). The highest diversity is found in the eastern part of the Central Mountain Range of Papua New Guinea and the Finisterre Range. To date, 12 species have been described, but a paper with six additional species is in preparation. Only a few specimens of many species are known, suggesting that they have relatively small ranges and are not abundant. This makes it likely that numerous species await discovery and that the genus may well have more than 30 species. *Wahnesia* seems absent from the Bismarck Archipelago but it has reached the d'Entrecasteux Islands, Louisiade Archipelago (undescribed species) and one species, *W. gizo*, occurs on three of the Solomon Islands (Gizo, Vella Lavella, Rendovo). The presence of this genus on these island groups suggests that it arrived there windborne. *Wahnesia kirbyi* is the only species with a reasonably large range and is seemingly not uncommon within its range. It has been reported as the most common species of Argiolestidae in Crater MountainWildlife Management Area (Oppel 2005).

Details on habitat are lacking for most species. *Wahnesia kirbyi* was observed in "all types of shady streams and creeks, with some individuals even occurring along major rivers and others at small temporary seepages" (Oppel 2005). Oppel (2005) furthermore notes that shading is crucial for *W. kirbyi* as the species did not occur along "those streams in Herowana where much of the canopy had been removed". Tenerals were observed near a medium-sized boulder creek which was supposed to be their larval habitat. Other species for which some habitat details are known are *W. saltuaria*, which was found at running waters of different sizes, ranging from large rivers to shady temporary streams, and *W. microstigma*, which was found at small, fully shaded creeks under closed canopy, *c.* 1-2 m wide with very irregular water flow and a gravel bed (Oppel 2005).

Podolestinae subfam. nov.

Key characters
Adult male. (1) Shaft of genital ligula with longitudinal microstriae. (2) Base of loop (lateral margin of segment 3 of genital ligula distinctly laterally expanded (in *Neurolestes*, *Podolestes* and probably in *Nesolestes*).
Adult female. (3) Ovipositor long, reaching beyond cerci by more than the length of S10 (in *Allolestes*, *Nesolestes* and *Podolestes harrisoni*).

Allolestes Selys, 1869 (fig. 24c, 26a, b, 27a)

Unique characters within Argiolestidae
Adult. (1)Apical corner of discoidal cell surpassing nodus. (2) Only one cell between quadrangle and subnodus. (3) Median cleft of labium shallow, less deep than wide (fig. 27a).
Female. (4) Ovipositor long and surpassing cerci by at least the length of S10 (shared with *Nesolestes* and *Podolestes harrisoni*).

Diagnosis and identification
Adult. Can easily be separated from all other species of the family by the above-mentioned unique characters. In addition the pattern on the abdomen is unique, with S3-7 dark with an anterior pale annulus or mark and the dorsum of S9-10 and

anterior two-thirds to three-fourths of S8 blue. It is the only species of the family occurring on the Seychelles where it can easily be recognised in the field, being the only damselfly to rest with open wings.
Larva. Unknown.

Distribution and habitat
The monotypic genus is endemic to the Seychelles, with its sole species *A. maclachlani* being found on the islands of Mahé, Praslin and Silhouette. The species is restricted to rocky forest streams, and fewer than 10 localities are known. Blackman & Pinhey (1967) state that it is often found below a complete canopy of trees and that it is found at elevations around 300 m, being absent from the coastal lowlands. The species is listed as Endangered on the IUCN red list as forest streams on Mahé and especially Praslin frequently desiccate due to over-extraction of water (Martens 2009).

Nesolestes **Selys, 1891 (fig. 6, 24d, 27b)**

Taxonomy
The West African *Neurolestes* and the Madagascan *Nesolestes* are closely related and their relationship has repeatedly been discussed (Dijkstra 2003, Fraser 1955, Gambles 1970, Schmidt 1966). *Neurolestes* has been considered a monotypic genus separated from *Nesolestes* by the presence of a third Ax and by having two to five cubito-anal cross veins instead of one. In the publication in which he described *Nesolestes nigeriensis* from Nigeria, Gambles (1970) discusses the differences between the two genera and concludes that with the description of *N. nigeriensis* "the differences between the two genera are reduced to the unusual venational characters of *Neurolestes* (the additional Ax and the extra Cuq), and in general appearance and other detailed characters the new species further bridges the gap". Although he obviously believed his *nigeriensis* to be more closely related to *Neurolestes* than to *Nesolestes*, he placed it in the latter, retaining the venation-based definition of both genera. Molecular analysis has shown that the two western African species are clearly more closely related to each other than to the Madagascan species (Kalkman, unpublished). For this reason *Nesolestes nigeriensis* is transferred to *Neurolestes*. The venational characters of *N. trinervis* are therefore considered to have evolved after the western African group became separated from the Madagascan group. The only character known to separate these two genera is the ovipositor, which is remarkably long and reaches beyond the cerci by at least the length of S10 in all six species of *Nesolestes* for which information on the female is available, but is short in the two known species of *Neurolestes*. Relatively little material of these genera was studied and SEM images of the genital ligula of *Nesolestes* could not be made. Further study might therefore very well result in finding additional characters separating the two genera.

Unique characters within Argiolestidae
Female. (1) Ovipositor smooth and long, reaching beyond cerci by at least the length of S10, and in most species by more than the length of S9-10 (fig. 6).

Diagnosis and identification
Adult. This is the only genus of Argiolestidae found on Madagascar and the Comoros, and it can within its range be identified by the venational characters of Argiolestidae. Together with *Tatocnemis* and *Protolestes* it is the only damselfly genus in the region with species sitting with open wings and with the abdomen nearly horizontal. *Tatocnemis* and *Protolestes* however lack the supplementary sectors between IR1 and RP2 and between RP2 and IR2. In addition males of *Tatocnemis* have a red abdomen (never so in *Nesolestes*), whereas the species of *Protolestes* have a clearly more slender head. Fraser (1955) gives a review of the genus and a key and illustrations to the males of all species known at the time (10 of the presently known 16). Nonetheless identification to species level is problematic as many descriptions are brief and based on a limited amount of material so that the variation within the species is poorly known.

Larva. The only description of the larvae available is that of an unidentified larva published by Schütte (2010).

Distribution and habitat
The genus *Nesolestes* contains 16 species, 15 of which are confined to the eastern half of Madagascar while one (*N. pauliani*) is found on Mohéli (Mwali), Comoros. Most species of *Nesolestes* are very poorly known, as females are unknown for half of the species and nine are known only from the type locality. Most species probably have restricted ranges. The absence of the genus in the western part of Madagascar is likely due to the arid conditions there. The scant information available suggests that the genus occupies a broad altitudinal range with some species found at sea level, for instance *N. mariae* which occurs on the coastal island of Santa Maria, and some found in the mountains, such as *N. robustus* at 1300m and both *N. albicolor* and *N. forficuloides* at 1800 m. The latter two species have both been found in the Andohahela National Park, showing that the ranges of species can overlap. Information on the habitat of the species is virtually absent and information on behaviour is not available. Schütte (2009) remarked that species of *Nesolestes* were observed at small running waters in rainforest and littoral forest habitat.

Neurolestes **Selys, 1882**
(fig. 24e, 26c-d, 28)

Taxonomy
See *Nesolestes*.

Unique characters within Argiolestidae
No unique characters available.

Diagnosis and identification
Adult. Neurolestes strongly resembles *Nesolestes* but lacks the long and sword-like ovipositor. The genus does not overlap in range with any other genus of Argiolestidae and can within its range be identified by the venational characters of Argiolestidae. Together with *Lestes* it is the only damselfly genus in the region with species sitting with open wings but *Neurolestes* sits, in contrast to *Lestes*, with the abdomen near horizontal while *Lestes* perches with body pendent or at a 45° angle to its perch. The two species of the genus can easily be told apart by *N. trinervis* having a third antenodal vein (two in *N. nigeriensis*) and a black with orange anterior synthorax (black, yellow and bluish in *N. nigeriensis*). A detailed comparison of the two species can be found in Gambles (1970). *Larva.* Unknown.

Distribution and habitat
The genus currently holds two described, and probably a third undescribed, species. *Neurolestes trinervis* has been recorded from Cameroon, Equatorial Guinea, Gabon and the Republic of Congo (fig. 28). *Neurolestes nigeriensis* is known only from the type locality, the Obudu Plateau in Nigeria, where it has an estimated extent of occurrence of less than 100 km^2. This species is assessed as Critically Endangered on the IUCN Red List as its forest habitat is expected to deteriorate in the future. Specimens from adjacent Cameroon might be conspecific with *N. nigeriensis* or might belong to an undescribed species (Piney 1974). *Neurolestes trinervis* is found along cool streams in submontane (above 700 m) rainforest and *N. nigeriensis* is found in rainforest where it probably occurs in streams (Clausnitzer & Dijkstra 2010).

Podolestes **Selys, 1862**
(fig. 11f, 24f, 26e, f, 29)

Unique characters within Podolestinae
No unique characters known.

Diagnosis and identification
Adult. Podolestes is the only representative of Argiolestidae occurring in Sundaland and mainland South-East Asia. *Podolestes* resembles *Nesolestes* and *Neurolestes* in general morphology but has, in contrast to these two genera, but in accordance with most other genera of Argio-

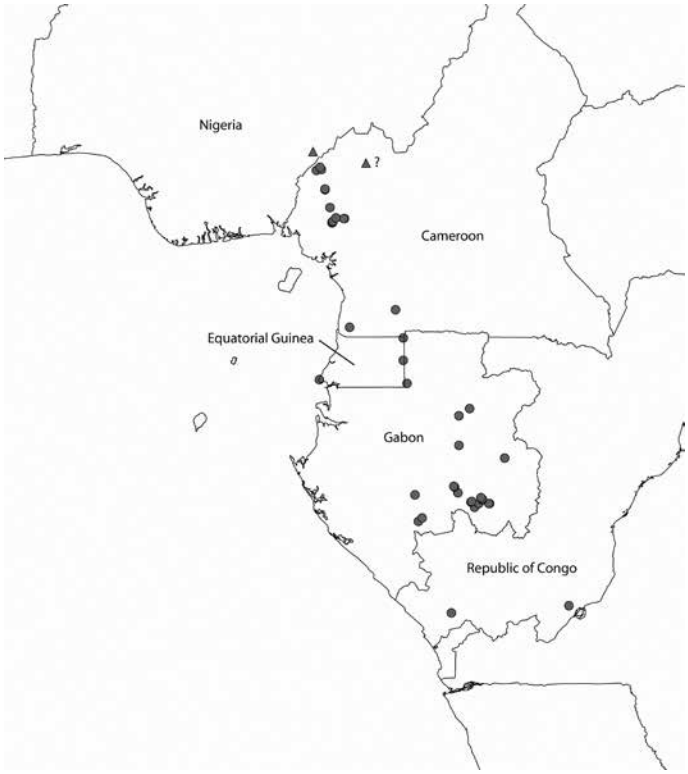

Figure 28. Distribution of *Neurolestes*. *Neurolestes trinervis* (dots) and *N. nigeriensis* (triangle). The triangle with question mark refers to the locality of a possibly third species close to *N. nigeriensis*. Largely based on records in the Odonata Database Africa.

lestidae, a serrated ovipositor. Although there are no clear characters setting it apart from *Nesolestes* and *Neurolestes* it is easily distinguished from these two by the general pattern and colouration of thorax and abdomen. The genus does not overlap with other genera of Argiolestidae and can, within its range, be recognised by the venational characters of the family. Within its range it is, together with the far more colourful *Rhinagrion*, the only damselfly genus including species sitting with open wings and with the abdomen near horizontal. A review of the genus is not available and identification should be based on the descriptions and redescriptions provided by Lieftinck (1935b, 1940, 1950, 1953) and Wilson & Reels (2001).

Larva. The only larva described thus far is that of *P. orientalis* (Choong & Orr 2010). The remark on the microhabitat of the larvae of *P. atomarius* by Lieftinck (1954) suggests that he collected larvae but for some reason never described them.

Distribution and habitat

Seven of the eight species of *Podolestes* are found in Borneo, Sumatra and Peninsular Malaysia (fig. 29). Of these *P. orientalis* has the widest distribution, being relatively common throughout the region. The islands of the Sunda Shelf have, at least at the genus level, largely the same fauna and it is therefore surprising that the genus has not been recorded from Java. The discovery in 1999 of *Podolestes pandanus*, endemic to the Chinese province of Hainan (Wilson & Reels 2001), was rather surprising as the genus was at the time not known to occur in Thailand, Cambodia, Laos or Vietnam. From 2008 on a *Podolestes* species close to the Sumatran *P. coomansi* has been recorded from two provinces in Central and South Thailand (R. Ruangrong, O. Kosterin, pers. comm.), making it likely that the genus also occurs in Cambodia and Vietnam, which would close the gap with *P. pandanus*. The species of *Podolestes* are confined to swamp forest in lowland where they are found mostly

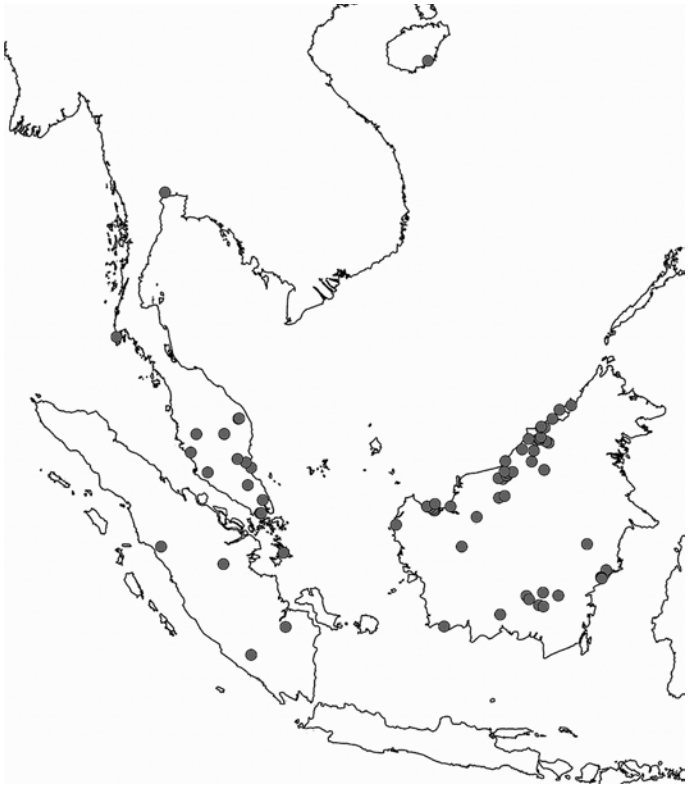

Figure 29. Distribution of *Podolestes*. Based on records in the Melanesian Odonata Database, including unpublished records by Rory Dow.

near shallow pools and slow, sluggish streams (Lieftinck 1954) (fig. 11f). Lieftinck (1954) mentions that *P. atomarius* from Borneo breeds in rain puddles and shallow marshes and that the larvae are found among root-masses and decaying vegetable matter. The larvae of *P. orientalis* were found in a shallow, leafy, forest pool were they lived among submerged or semi-submerged leaves and sticks at the shallow edge of the pools, down to 10 cm depth (Choong & Orr 2010). Females of *Podolestes orientalis* oviposit in leaf stalks above puddles of water. During oviposition the female is guarded by the male (Tang et al. 2010).

KEY TO GENERA FOR MALES OF AUSTRALASIAN ARGIOLESTIDAE

1 S1-6 bright orange, S7-8 black and S9-10 and posterior fifth of S8 blue (fig. 15a) ..... *Eoargiolestes*

– Pattern and colouration on abdomen different, never with a combination of blue and orange 2

2 Dorsum of head with blue postocular spots (fig. 9e, f). Annulus between S8 and S9 and between S9 and S10 conspicuously blue (fig. 9e) ..... *Caledopteryx*

– Dorsum of head without blue postocular spots. Annulus between S8 and S9 and between S9 and S10 not enlarged and never blue 3

3 Dorsal surface of S8-9 only very lightly sclerotised (fig. 5b, e), often appearing wrinkled in dead specimens. Most species with either a single large raised spine on S10 or with posterior margin of S10 serrated 4

– Dorsal surface of S8-9 normal, as strongly sclerotised as lateral and ventral surfaces. S10 without distinct armature 5

4 Posterior margin of S10 with single large raised spine or a tightly packed bundle of smaller spines (fig. 5e). Posterior margin of S10 never serrated. The spine is absent in *W. saltator* but in this species S8-9 are expanded and about twice as broad as S10, a condition never found in *Metagrion* ..... *Wahnesia*
– Posterior margin of S10 never with single raised spine. Posterior margin of S10 serrated, forming a series of teeth (fig. 5b). The serrations on S10 are absent in *M. fornicatum* and *M. verrucatum* but these have the apex of the genital ligula reduced to a whip-like structure lacking apical lobes, while in *Wahnesia* the apical lobes are always present .. .. *Metagrion*

5 Postocular lobes strongly bulging, clearly extending beyond level of compound eyes; head, thorax and abdomen never with bright blue, red or orange colours ..... *Luzonargiolestes*
– Postocular lobes not strongly bulging and not extending beyond level of compound eyes ... 6

6 Cerci and apical half of S10 whitish and contrasting with darker S9 (fig. 4, 9b); two apical lobes of genital ligula at least four times as long as broad ..... *Argiolestes*
– Cerci and S10 dark, not contrasting with S9, two apical lobes of genital ligula absent or less than four times as long as broad 7

7 Large species. Fw with 28 (rarely 25) or more Px 8
– Medium to small species. Fw with fewer than 28 Px 9

8 Hw with up to three rows of cells between CuA and hind border. Terminal segment of genital ligula not reduced to a long whip (fig. 12e, f) ..... *Celebargiolestes*
– Hw with four or more rows of cells between CuA and hind border. Terminal segment of genital ligula reduced to a long whip that is round in basal cross section (fig. 20a) .... *Podopteryx*

9 Cerci with ventrally pointing spur. Generally three or more cells in discoidal field between discoidal cell and level of subnodus..... ..... *Austroargiolestes*
– Cerci never with large ventrally pointing spur. Generally one or two, sometimes three (*Podopteryx*), cells in discoidal field between discoidal cell and level of subnodus 10

10 Paraprocts more than half as long as cerci ... 11
– Paraprocts less than half as long as cerci 12

11 Ground colour of body metallic green (fig. 24a, b). Wings with 3 Ax, sometimes one or two wings with 2 Ax. Lateral horns of ligula without distinct inflated base ("heel") (fig. 20d, e) ..... *Trineuragrion*
– Ground colour of body brown to black, not metallic (fig. 9d). Wings with 2 Ax. Lateral horns of ligula with inflated base ("heel") armed with minute spines (fig. 12a, b) .... *Caledargiolestes*

12 Legs and thorax without bright orange, red or blue colours 13
– Legs and thorax with bright orange, red or occasionally blue colours 15

13 Hind rim of S8-9 with conspicuous white annulus (fig. 19a) ..... *Miniargiolestes*
– Hind rim of S8-9 without conspicuous white annulus 14

14 Interior of base of cerci flattened and beset with long pale hairs. Dorsum of thorax without or with very small pale stripe .... *Archiargiolestes*
– Interior of base of cerci not flattened or beset with long pale hairs. Dorsum of thorax with pale stripe along humeral suture for at least half the length of thorax ..... *Griseargiolestes*

15 Labrum deeply metallic throughout. Dorsum of synthorax dark ..... *Pyrrhargiolestes*
– Labrum not metallic. Dorsum of synthorax with orange or blue pattern ..... *Solomonargiolestes*

DISCUSSION

Taxonomy

The classification presented here forms a thorough framework for the family Argiolestidae and at present it does not seem likely that further genera are needed in this family. Possible exceptions are the genera *Metagrion*, of which future taxonomic work might show that it should be further divided, and the genus *Argiolestes* where *A. tuberculiferus* stands apart both on morphology and molecular characters. The morphology of the larvae has contributed strongly to the recognition of this group as a family on its own, yet the larvae of many genera are still unknown (*Allolestes*, *Argiolestes*, *Luzonargiolestes*, *Neurolestes*, *Wahnesia*, *Pyrrhargiolestes*), whereas in some other genera (eg *Nesolestes*, *Metagrion*, *Podolestes*, *Podopteryx*) only the larvae of a few of the species have been described or only pictures are available (*Celebargiolestes*). Probably all species occurring in Australia and New Caledonia have been described. It is however likely that in the other areas several dozens of species still await description. At present at least half a dozen undescribed species belonging to each of *Metagrion* and *Wahnesia* are available in the RMNH. Other genera in which new species are likely to be found are *Argiolestes*, *Nesolestes*, *Podolestes*, *Pyrrhargiolestes* and probably also *Neurolestes* and *Luzonargiolestes*. It seems likely that the family holds between 150 and 180 species.

Distribution

Argiolestidae is confined to the eastern hemisphere and is found on Madagascar, the Comoros and the Seychelles (two genera, 17 species), mainland West Africa (one genus, two species), South-East Asia and Borneo and Sumatra (one genus, eight species) and in the Australasian region from the Philippines, over Sulawesi, the Moluccas, New Guinea, the Solomon Islands to Australia and New Caledonia (16 genera and 83 species) (fig. 1). The distribution of all genera is reasonably well known and the maps presented here are likely to give a proper estimate of the true distribution of the genera. The distribution of many species is poorly known and many species, especially on New Guinea and Madagascar, are known from one or two records only. A review of the biogeography of the family will be published elsewhere.

Life history

It is remarkable how little has been published on the life history of the species belonging to Argiolestidae. For most species only some general information on habitat is available. Detailed notes on territoriality, aggressive behaviour, courtship, mating and oviposition are not available for any species. The species belonging to Argiolestidae generally tend to show very little behaviour, with adults sitting motionless most of time. Many of the species have striking patterns on the face or brightly coloured legs and in some genera males can widen their abdominal tip (eg *Wahnesia*, *Metagrion*, *Eoargiolestes*) all of which suggests that courtship and aggressive behaviour do take place regularly. As far as is known, all species are limited or largely limited to running waters or seepages. The only marked exception is the genus *Podopteryx* with probably all of its species breeding in phytotelmata. To our knowledge this is the only example of an odonate genus belonging to a running-water dependent family which has become adapted to phytotelmata. Information on larval behaviour and larval microhabitat is likewise scarce, with a more detailed account only available for *Podolestes* (Choong & Orr 2010). The suggestion by Lieftinck (1976) that the horizontal position of the gills "probably serve to anchor the insect to rocks" still remains to be tested. A basic study on the life history of one of the Australian species or of *Podolestes* would provide a valuable framework for further data collection on the life history.

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