

No. 7.—*New genera of Megapodagrioninae, with notes on the subfamily.*

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INTRODUCTION.

WHILE studying the Zygoptera of the Hagen Collection in the Museum of Comparative Zoölogy, in 1917, I noticed two males and two females of an undescribed Megapodagrionine dragonfly, which were labeled "West Australia," "Hagen." They were exceedingly interesting in that they were the smallest species of the Megapodagrioninae yet found, being of the size of the smaller Ischnuras. Further study shows that they are very generalized in both body and wing characters.

I wish to thank Mr. R. J. Tillyard of the Cawthron Institute, Nelson, New Zealand, for specimens of *Argiolestes minimus* Tillyard and *Argiolestes pusillus* Tillyard and the authorities of the Museum of Comparative Zoölogy for the privilege of describing the specimens in their charge.

DESCRIPTIONS OF GENERA AND SPECIES.

ARCHIARGIOLESTES, gen. nov.

TYPE.—*Archiargiolestes pusillissimus* Kennedy.

Megapodagrionine in that there are two antenodals, Rs and M₃ arise near the subnodus and there are various extra sectors between M_{1a} and Cu₁.

Wings with 10–12 postnodals, stigma short, surmounting two cells, an oblique stigmatic brace vein. Rs arises at the subnodus, M₃ arises before the subnodus, M₂ arises at postnodal 3 or 4, M_{1a} arises 3–4 costal cells before the stigma. Ac is at a level about midway between the two antenodals. The quadrangle has the anterior side 1–2 times as long as the outer side, the outer posterior angle acute. There are two postquadrangular cells and the area posterior to Cu₂ has a single row of 10–11 cells. Wing petioled to the middle level of the quadrangle.

In addition to the type species the genus includes *Argiolestes pusillus* Tillyard and *A. griseus* Selys; all confined to western Australia.

ARCHIARGIOLESTES PUSILLISSIMUS, sp. nov.

Plate, fig. 2.

TYPE.—M. C. Z. 15,356. ♂. West Australia. Thorey (Hagen Coll.). PARATYPE.—M. C. Z. 15,357. ♀. West Australia. Thorey (Hagen Coll.).

Holotype = male in Museum of Comparative Zoölogy which bears the labels "West Australia Thorey," "Hagen" and "penis drawn." Paratype = female with the holotype, labeled "West Australia Thorey" and "Hagen." Two other specimens accompany these, having similar labels, one, a male is undoubtedly conspecific but the other, a female, is so much more robust than the paratype that there is a remote possibility that she may belong to another species.

Colors largely black and creamy white. The striking feature of the coloration is the sharpness of the edges of the black areas on the head and thorax. There is no shading of black into creamy.

Head with base of mandibles brown, labrum creamy, broadly edged below with black. Clypeus creamy on its vertical surface, black on its horizontal surface. Genae creamy. The entire dorsal surface of the head black.

Prothorax with a large posterior lobe, the edge of which is divided into three hardly noticeable, subequal portions by two shallow notches. Entire dorsal and lateral surfaces black.

Meso- and metathorax with the dorsal surface black and the sides black except the following:—the lower one fourth of the mesinfraepisternum, the metaepisternum from the middle coxa to the spiracle and the mesepimeron. Coxae creamy. Legs pale brown with an outer and a dorsal row of minute spots on the femur; spines dark brown. Wings hyaline, stigma brown. Thorax sparingly covered with long coarse white pile.

Abdomen dark brown (black in the second male and the two females) with creamy on the under side and a narrow creamy basal ring around segments 3–8. Appendages brown. Dorsum of segments 1 and 2 pruinose.

Length:—abdomen (including appendages) 19 mm., hind wing 14 mm.

Superior appendages forcipate and notched at the apex, the inferiors rudimentary.

ARCHIARGIOLESTES PUSILLUS (Tillyard).

Plate, fig. 1.

Argiolestes pusillus Tillyard, Proc. Linn. soc. N. S. W., 1908, **32**, p. 736.

This was described as a variety of *Argiolestes minimus* Tillyard and as similar to *minimus* but smaller. No sufficient figure of wings or

appendages was published. Later Tillyard published figures of *minimus* (Proc. Linn. soc. N. S. W., 1913, 37, pl. 45, fig. 3, 4). My figures of M. C. Z. specimens did not agree with these in certain details, and on comparison with specimens of both *minimus* and *pusillus* received from Mr. Tillyard were so different in the male appendages that I separate the M. C. Z. specimens as a new species, *pusillissimus*, consider *pusillus* distinct from *minimus*, and describe the new genus *Archiargiolestes* for *pusillus* and *pusillissimus*, while *minimus* remains in *Argiolestes* because of the double row of cells in the Cu₂ area.

Mr. Tillyard states (Proc. Linn. soc. N. S. W., 1908, 32, p. 737) that *minimus* and *pusillus* occur with intergrades connecting them at "Bridgetown, Wilgarrup and probably other localities." It is probable that the intergrades are a third undescribed species, unless, of course, they are of unusual sizes. Mr. Williamson's recent work (Occ. papers Mus. zool. Univ. Mich., 1919, no. 68) on South American Megapodagrionines, as well as that of Ris (Archiv naturg., 1916, 82), shows that there are many close but distinct species in this subfamily.

In trying to place these generically, the described species of *Argiolestes* and related genera have been studied as carefully as could be from the literature and the few species represented in American collections, and a tentative revision of the subfamily has been made. The following new genera are described for certain unusual species.

CALEDARGIOLESTES, gen. nov.

Plate, fig. 3.

TYPE.—*Argiolestes uniseries* Ris, Nova Caledonia (Sarasin & Roux), Zool., 1915, 2, l. 1, p. 62, fig. 5, 6.

Megapodagrionine in general characters. Characterized by the following combination of characters:—Ac near the level of antenodal one; 14 postnodals; stigma short, surmounting two cells and having an oblique brace vein. M₃ arising the length of a small cell before the subnodus, Rs arising at the subnodus, M₂ beyond the fifth postnodal. M_{1a} arises two cells beyond the origin of M₂ or 6–7 cells before the stigma. Cu₂ 16–19 cells long with a single row of cells back of it. Petiolation to the level of the middle of the quadrangle which has its anterior side 2–3 times as long as the outer side so that the outer posterior angle is acute. Two postquadrangular cells. Extra sectors as follows:—M_{1a}–M₂ 1–2; M₂–Rs 2; Rs–M₃ 2; M₃–M₄ 2–3; M₄–Cu₁ 1.

Male inferior appendages nearly as long as the forcipate superiors.

Length:—abdomen 30 mm., hind wing 25 mm.

AUSTROARGIOLESTES, gen. nov.

Plate, fig. 4.

TYPE.—*Argiolestes icteromelas* Selys, Bull. Acad. roy. Belgique, 1862, p. 376. Melbourne, Australia.

This genus includes also *aureus* Tillyard,¹ *chrysoides* Tillyard,² *minimus* Tillyard,³ *amabilis* Forster⁴ and *alpinus* Tillyard.⁵ Probably several of Tillyard's "varieties"⁶ are good species when more material becomes obtainable for study.

Venation Megapodagrionine. Ac at the level of antenodal two. Rs arising at the subnodus, M₃ before the subnodus; 15–23 postnodals; stigma oblique, surmounting 1½–3 cells. Wing petioled to the base or the middle of the quadrangle, three postquadrangular cells. Cu₂ area with two rows of cells in its outer part. Extra sectors as follows: M_{1a}–M₂ 2; M₂–Rs 2; Rs–M₃ 2; M₃–M₄ 5–6; M₄–Cu₁ 2.

Male superiors forcipate and toothed while the inferiors are rudimentary. Length:—abdomen 26–34 mm., hind wing 20–30 mm.

This genus is more primitive than any of the Argiolestine genera of the Papuan region, except Podolestes and Caledolestes, in the position of Ac under antenodal two and in the Cu₂ area with its single extra row of cells.

ARGIOLESTES Selys.

Bull. Acad. roy. Belgique, 1862, p. 372.

TYPE.—*Agrion australis* Guérin, Voyage Coquille. Zool., 1831, 2, pt. 2, p. 196. Offak.

I include also *pallidistyla* Selys,⁷ *selysi* Forster,⁸ *rouxi* Ris,⁹ and *macrostylis* Ris,¹⁰ though, in the origin of M₃ and Rs, the last species appears to lie between Argiolestes and Wahnesia. Until the Selysian material is restudied the exact boundaries of this genus cannot be finally determined.

¹ Proc. Linn. soc. N. S. W., 1906, 31, p. 178, pl. 17, fig. 1. 1913, 37, p. 415, pl. 45, fig. 1, 2.

² Proc. Linn. soc. N. S. W., 1913, 33, p. 237, pl. 15, fig. 8, 9.

³ Proc. Linn. soc. N. S. W., 1908, 32, p. 735, pl. 35, fig. 11, 12.

⁴ Ann. Soc. ent. Belgique, 1899, 43, p. 71.

⁵ Proc. Linn. soc. N. S. W., 1913, 37, p. 417, pl. 44, fig. 7, 8.

⁶ *Argiolestes icteromelas* race *nobilis* Tillyard, Proc. Linn. soc. N. S. W., 1913, 37, p. 410.

⁷ Mitth. Zool. mus. Dresden, 1878, 3, p. 320.

⁸ Ann. Soc. ent. Belgique, 1899, 43, p. 70.

⁹ Nova Caledonia (Sarasin & Roux), Zool., 1915, 2, l. 1, p. 60, fig. 3, 4.

¹⁰ New Guinea (Lorentz), Zool., 1913, 9, l. 3, p. 475.

Argiolestes is thus restricted to that group of the Selysian *Argiolestes* in which M_3 arises shortly before the subnodus and Rs at or close to the subnodus. This is Selys's group C after the removal of *cincta* to *Celebargiolestes*.

Rs arising at the subnodus, M_3 arising shortly before the subnodus; postnodals 20–25;¹ quadrangle of moderate length, *i.e.*, there are 2–4 postquadrangular cells; Ac lies under antenodal one; the Cu_2 area has short sectors 2–4 cells long.

Male inferior appendages rudimentary ?

Length:— abdomen 28–43 mm., hind wing 25–29 mm.

Argiolestes rouxi Ris, isolated in New Caledonia, is probably also generically distinct from the other species.

CALEDOPTERYX, gen. nov.

TYPE.— *Argiolestes sarasini* Ris, Nova Caledonia (Sarasin & Roux), Zool., 1915, 2, l. 1, p. 58, fig. 1, 2.

Ac lies near the level of antenodal one; petiolation only to the base of the quadrangle; M_3 arises shortly before the subnodus and Rs at the subnodus; apex of quadrangle not reaching the level of the middle of the third antenodal space; 4 postquadrangular cells; about 30 postnodals; stigma oblique, surmounting 2–3 cells and with an oblique brace vein; M_2 arising near postnodal 11–12, M_{1a} arising 4 cells farther out; apex of Cu_2 reaching level of postnodal 18–20 with many short branches, many of which are 3–4 cells long; extra sectors as follows, M_{1a} – M_2 2, M_2 –Rs 2, Rs– M_3 2, M_3 – M_4 6, M_4 – Cu_1 2.

Male inferiors long.

Length:— abdomen 43–48 mm., hind wing 39–40 mm.

This genus is close to *Argiolestes*, but differs in having 30 postnodals, 4 postquadrangular cells and in the well-developed branches on Cu_2 . It differs from *Podopteryx* in having Ac under antenodal one, in the narrower stigma and in the shorter branches on Cu_2 . From *Celebargiolestes* it differs in having fewer postnodals.

CELEBARGIOLESTES, gen. nov.

Plate, fig. 5.

TYPE.— *Argiolestes cincta* Selys, Mem. Acad. roy. Belgique, 1886, 38, p. 86.

The following description is from a male collected in the Tokalla

¹ *Argiolestes selysi* Forster has 29–35 postnodals and because of its greater size, abd. 54 mm., may be generically distinct.

Mountains, Celebes Island by I. Rolle in 1915 and presented to Mr. Williamson by Dr. Ris whose label *Argiolestes cincta* ♂ is still on the pin.

Ac under antenodal one; wing petioled to middle of quadrangle; origin of M_2 and Rs normal; 35–40 postnodals, several double cells beyond stigma; M_2 arising at postnodal 13–15, M_{1a} at 15–19; stigma normal, surmounting 3–4 cells, no brace; postquadrangular cells 4; extra sectors, M_{1a} – M_2 4–, M_2 –Rs 2, Rs– M_3 2, M_3 – M_4 4–, M_4 – Cu_1 2; Cu_2 about 28 cells long with 8 or 9 branches 2–5 cells long. Male inferiors one half as long as the superiors.

Length:—abdomen 34–36 mm., hind wing 30–32 mm.

The great number of postnodals at once separates this genus from all other genera of the *Argiolestes* series. It is a moderate-sized species so its wings are more densely veined than are those of *Podopteryx* and *Caledopteryx*, both of which have fewer postnodals.

BURMARGIOLESTES, gen. nov.

Plate, fig. 6.

TYPE.—*Argiolestes melanothorax* Selys, Ann. Mus. civ. Genova, 1891, ser. 2, 10, p. 500.

Megapodagrionine with the following distinctive combination of characters: M_3 arises at the subnodus, Rs at the first postnodal, M_2 at postnodal 8–9, M_{1a} near postnodal 11–12. Ac lies under antenodal one. Petiolation to the middle level of the quadrangle. Quadrangle six times as long as wide, its apex reaching the level of the nodus so that the subnodus lies over the first of the one or two postquadrangular cells. About 24 postnodals (17–23 Selys); stigma surmounting one and one half cells and having an oblique brace vein. Cu_2 14–16 cells long with 5–14 cells of a second row which commences 4–5 cells distad of the quadrangle.

Length:—abdomen 30–38 mm., hind wing 25–27 mm. Male inferiors rudimentary.

This differs from *Wahnesia*, which also has M_3 arising at the subnodus, in that the quadrangle reaches to the level of the nodus. This character may relate it to *Allolestes* of the Seychelles, which also has a long quadrangle. It distinguishes it at once from all of the Papuan genera of the *Argiolestes* series.

Two new mainland species have been discovered recently.

OLIGOARGIOLESTES, gen. nov.

TYPE.—*Oligoargiolestes oligocenum* Kennedy.

I suggest *oligocenum* for the second fragment identified by Cockerell

and Andrews (Proc. Biol. soc. Washington, 1916, 29, p. 90, pl. 2, fig. 5) as *Megalestes anglicus*. It is from the Oligocene of the Isle of Wight and is too fragmentary to describe definitely. The tip is too rounded to be a Lestid, therefore the short stigma and extra sectors show that it is a Megapodagrionine. The strong stigmatic brace vein suggests relationship to the Argiolestine series of genera.

MIPODAGRION, gen. nov.

TYPE.—*Lithagrion optimum* Cockerell, Proc. U. S. N. M., 1916, 51, p. 101.

These fragments may not be even Megapodagrionine, but they are not *Lithagrion* as the petiolation is much less than in that genus. The fragment with double cells in the Cu_2 area suggests *Argiolestes*.

NOTES ON SOME GENERA.

ARCHIARGIOLESTES Kennedy, 1925. Western Australia. Three species.

Length:—abdomen 19–21 mm., hind wing 14–16 mm. Male inferiors rudimentary.

This is one of the very primitive and generalized genera of the Megapodagrioninae. The characters that indicate this are the simple Cu_2 area, the position of Ac basad of antenodal two, the normal origin of M_3 and Rs , the few sectors, and the simple stigma. Its primitiveness is further indicated by the small number of species and that it occurs in Western Australia, one of the oldest and most isolated regions, zoögeographically. *Archiargiolestes pusillissimus* with an abdomen only 19 mm. long is the smallest known Megapodagrionine. It is an interesting light on the size of the primitive ancestral Zygoptera that all the large Megapodagrionines are very specialized while the primitive and generalized Megapodagrionines are small. The very primitive and generalized Hemiphlebia is also a small insect.

This genus is specialized in the considerable petiolation, the short Cu_1 and Cu_2 , in the two postquadrangular cells and in the rudimentary inferior appendages of the male.

Archiargiolestes griseus Selys, and probably also *fontanus* Tillyard, the latter as yet unstudied, are included in this genus. This *griseus* is the species identified by Tillyard as *griseus* Selys. In Williamson's collection is another species labeled *griseus* Selys by Martin, but which

by the specialized penis, the spined male superiors, and the venation though the Cu_2 area is a single row of cells is an *Austroargiolestes*. This latter is an undescribed species, if Martin is mistaken. The *griseus* of Tillyard (and Selys?) belongs in *Archiargiolestes* by the generalized penis, the spineless male superiors, and the venation.

The species *minimus* has the venation of *Austroargiolestes*, but the male appendages are spineless and resemble those of the species of *Archiargiolestes*. The penis is also more generalized than is usually found in *Austroargiolestes* in that the apical lobes are unmodified as in *Archiargiolestes*. Thus *minimus* is intermediate between the two genera, if all characters are considered, but based on venation it is distinctly a species of *Austroargiolestes*.

CALEDARGIOLESTES Kennedy, 1925. New Caledonia. One species, *C. uniseries* (Ris) from New Caledonia, 900 miles east of Australia, one of the most isolated zoögeographic regions.

Length:— abdomen 30 mm., hind wing 25 mm. Male inferiors long.

Venationally this is close to *Podolestes*, *Trineuragrion*, and *Archiargiolestes*. It differs from all three in having Ac more nearly under antenodal one than under antenodal two. If this evidence is of value, it is intermediate between the Australian genera and the Papuan *Argiolestes*. On the other hand it is so similar to *Trineuragrion* in the simple Cu_2 area and the long inferior appendages of the male that the latter may have been derived from *Caledargiolestes*.

LITHAGRION Scudder, 1882. Miocene. Florissant, Colorado. One species.

Probable length of wing 33 mm.

Lithagrion umbratum and *optimum* have already been removed from this genus. Scudder's type had no distinct stigmatic brace vein. However Cockerell had what he thought was a second fossil of this species, which agreed with *hyalinum* otherwise but had a stigmatic brace. (Cf. Bull. Amer. mus. nat. hist., 1907, 23, p. 137, 1908, 24, p. 63). A stigmatic brace would make the fossil agree with the other Florissant Odonata, which are related to the Oriental genera rather than with the South American *Megapodagrionines*. If it has three antenodals as Cockerell's specimen appeared to have, it is close to *Trineuragrion* of New Caledonia which it resembles also in the position of Ac and in the irregular group of cells between the tips of M_3 and M_4 . It is evidently more primitive than the present-day *Argiolestes* (*australis*), *Wahnesia*, *Podopteryx*, and relatives with an enriched Cu_2 area.

Lithagrion is not closely related to *Thaumatoneura* and Para-

phlebia of modern Mexico and Central America. These differ in the short Cu_2 with numerous Cu_1 - Cu_2 sectors attached to its tip. *Lithagrion*, *Melanagrion*, and *Miopodagrion* appear to represent a stock entering from the Orient but which appears to be somewhat distinct from the *Paraphlebia*-*Thaumatoneura* stock. The latter may be an earlier stock yet, as their penes are so generalized that they might fit species in the Megapodagrioninae, Agrioninae, or Coenagrioninae.

MELANAGRION Cockerell, 1907. Miocene. Florissant, Colorado. One species.

Length of wing 34.5 mm.

This genus, based on *Lithagrion umbratum* Scudder, is close to *Austroargiolestes* as it has Ac under antenodal two, a conspicuous stigmatic brace vein, and a Cu_2 area with several double cells. This relates it to the more primitive Megapodagrionines of the Indo-Australian region rather than with the more specialized genera of the Papuan region. This suggests that the Old World genera with the rich Cu_2 areas may have developed since the Miocene.

EPODAGRION Cockerell, 1920. Eocene. Green River, Wyoming. Two species. Based on fragments of two wings, *Podagrion abortivum* Scudder and *Eopodagrion scudderi* Cockerell, suggested by Cockerell to have been perhaps the front and hind wing of the same species.

These are probably Megapodagrionine, if so they belong to the Old World series because of the distinct stigmatic brace vein. The simple Cu_2 area places this genus among the primitive genera. These fossils give us an Eocene horizon for the primitive Megapodagrionines though they probably arose before this.

OLIGOARGIOLESTES Kennedy, 1925. Oligocene. Isle of Wight, England. New name based on the second fragment of *Megalestes angelicus* Cockerell.

The shape of the wing apex is Megapodagrionine and not Megalestine. Because of its stigma with an oblique brace vein it falls among the relatives of *Argiolestes*, though it has the regular splitting of the marginal cells found in *Neurolestes* of the Cameroons.

MIPODAGRION Kennedy, 1925. Miocene. Florissant, Colorado. New name for *Lithagrion optimum* Cockerell.

This is so fragmentary that it may or may not belong here. Cockerell places it next *Lithagrion hyalinum* but, if his figure is correct, it is not petioled beyond Ac, which makes it necessary to give it a distinct generic name.

AUSTROARGIOLESTES Kennedy, 1925, Australia. Several species. Length:—abdomen 24–36 mm., hind wing 20–33 mm. Superior

appendages of the male with a large inferior subapical tooth, inferiors rudimentary.

This genus was erected to include *Argiolestes icteromelas* Selys and those other Australian species in which Ac lies nearer antenodal two, petiolation ceases near the base of the quadrangle; the male superior appendages have a large inferior subapical tooth and there are usually 2-3 rows of cells in the Cu₂ area. The penis usually has narrow lobes that are more or less united into a narrow tip. Besides *icteromelas*, it includes *amabilis* Forster, *alpinus* Tillyard, *chrysoides* Tillyard, *aureus* Tillyard, and *minimus* Tillyard. An unnamed species of *Austroargiolestes*, male and female, occur in Mr. Williamson's collection which were labeled by Martin *griseus* though they are close to the species identified by Tillyard as *icteromelas* Selys. They have a large subapical spine on the superior appendages of the male. In these the Cu₂ area is a single row of cells as in *Archiargiolestes*. Otherwise the wings are distinctly *Austroargiolestes* as is also the penis.

The Cu₂ area varies in this genus from a single row of cells as in the unnamed species noted above to specimens that have a few double cells in a simple Cu₂ area as in *Argiolestes icteromelas* on to species with three well-developed rows of cells in the Cu₂ area.

Argiolestes minimus is placed in this genus because its wings are distinctly *Austroargiolestine* though its penis and the superiors of the male are like those of the species of *Archiargiolestes*.

The genus is intermediate between the very primitive genera such as *Podolestes* and *Archiargiolestes* and the more specialized genera such as *Argiolestes*, *Podopteryx*, *Caledopteryx*, *Wahnesia*, etc. It is primitive in the position of Ac under antenodal two while it is only moderately specialized in the Cu₂ area. This genus and *Archiargiolestes* suggest that the *Argiolestine* series of genera beginning in these simply veined genera and ending in the very specialized *Burmargiolestes* and *Allolestes* may have arisen in Australia.

ARGIOLESTES Selys, 1862. For *Agrion australis* Guérin from the island of Offack near New Guinea. Several species.

Length:—abdomen 28-38 mm., hind wing 26-32 mm. (*A. selysi* Forster, abdomen 53-54 mm., hind wing 44 mm.).

The history of *Argiolestes* according to Dr. Calvert, follows:—Guérin (*Voyage de la Coquille. Zool.*, 2, p. 196), described the species, placing it in the genus *Agrion*. Rambur (*Histoire naturelle des insectes. Névroptères*, 1842, p. 256), described the same specimen, but referred incorrectly to "pl. 10," Guérin, on which there is no figure of this species. De Selys (*Synopsis des Agrionines*, Legion

Podagrion, described the same specimen, obtained from Dumont d'Urville, 1862, p. 39) but incorrectly refers the original description to Rambur.

The series of Australian species are included in Archiargiolestes and Austroargiolestes. After removing *sidonia* Martin, *aurantiaca* Ris, *obscura* Selys, and *ornata* Selys to Wahnesia, *sarasini* Ris to Caledopteryx, *melanothorax* Selys to Burmargiolestes, *cincta* Selys to Celebargiolestes and *uniseriis* Ris to Caledargiolestes there are left in Argiolestes, *australis* Guérin, *pallidistyla* Selys, *rouxi* Ris, *selysi* Forster, and *macrostylis* Ris. *Argiolestes selysi* Forster may be a Podopteryx as it has a slightly richer Cu₂ area than the others and is a giant in size. Forster's description is not detailed enough to settle the question. *Argiolestes macrostylis* Ris may be a Wahnesia. In the origin of M₃ and Rs it appears intermediate between the two genera. According to Ris all the Papuan species of the Selysian genus Argiolestes are congeneric with *australis*.

Wahnesia, which is specialized in the origins of M₃ and Rs, is an offshoot of Argiolestes, while Metagrion is an even more specialized offshoot of Wahnesia. Caledopteryx and Celebargiolestes are specialized offshoots of Argiolestes in other directions.

CALEDOPTERYX Kennedy, 1925. New Caledonia. One species based on *Argiolestes sarasini* Ris.

Length:—abdomen 48 mm., hind wing 39–40 mm. Male inferiors long.

Only Ris's very complete description is available for study. The penis has not been examined. This is a very large Argiolestes (*sensu strictu*) as is shown by the position of Ac under antenodal one. It is not closely related to Podopteryx because there Ac lies under antenodal two which relates Podopteryx to Austroargiolestes. The penes of Austroargiolestes and Podopteryx also show this relationship. The simple stigma also distinguishes it generically from Podopteryx, which has a dilated stigma, as well as the long inferiors of the male.

Caledopteryx sarasini is considered an independent development parallel with Podopteryx.

CELEBARGIOLESTES Kennedy, 1925. Celebes. For the single species *Argiolestes cincta* Selys.

Length:—abdomen 34–36 mm., hind wing 30–32 mm. Male inferiors half as long as superiors.

I have had the privilege of studying a male specimen determined by Ris (Williamson's collection). This is a beautiful insect with the wing developed by increased length between nodus and apex. It is special-

ized in the unusual squareness of all the cells in the apical half of the wing so that the long extra sectors are very evenly curved. The great number of postnodals, 34-40, indicates this development of the distal half of the wing. It belongs in the Papuan group of genera in which Ac lies under antenodal one.

WAHNESIA Forster, 1900. New Guinea and Bismarck Archipelago. Six species.

Length:—abdomen 30-38 mm., hind wing 28-30 mm. Male inferiors rudimentary.

This genus includes *kirbyi* Forster and *montivagans* Forster, the first of which is the type. From descriptions, it appears also to include *ornata* Selys, *obscura* Selys, *sidonia* Martin, all of New Guinea and all placed in *Argiolestes*; also *Argiolestes aurantiaca* Ris from the Bismarck Archipelago at the eastern end of New Guinea. All of these species are modified *Argiolestes* in which the wing has become specialized by the origins of M_3 and Rs having moved distad. *Argiolestes macrostylis* Ris appears to be intermediate in this character between *Argiolestes* (*sensu strictu*) and Wahnesia. Ris (Odonata Neu-Guinea, 1913) thinks these genera should not be separated.

Ris thinks also that Wahnesia cannot stand as a generic name because Forster's description is not adequate. However, Forster distinguished *kirbyi* from *montivagans* in his notes on the genus and deposited the types in the Hungarian National Museum. As the stability of a scientific name does not depend on the length or quality of the specific description, the genus will stand unless it is merged into *Argiolestes*.

This genus is close to *Metagrion* from which it differs in the less movement distad of the origins of M_3 and Rs. It is also close to *Burmargiolestes*, but differs in the normal quadrangle. It thus appears to be the stock from which have developed *Metagrion*, *Burmargiolestes*, and *Allolestes*.

BURMARGIOLESTES Kennedy, 1925. Northern British India and Burma. For *Argiolestes melanothorax* Selys.

Length:—abdomen 30-38 mm., hind wing 25-27 mm. Male inferior appendages short. Only the literature available.

This genus is a member of the *Argiolestes* series as is shown by the pronounced stigmatic brace vein. It is related to the Papuan genera, *Argiolestes*, Wahnesia, and *Metagrion* rather than the Australian genera *Austroargiolestes* and *Archiargiolestes*, because Ac is under antenodal one. It differs from Wahnesia in having only one post-quadrangular cell which brings the apex of the quadrangle to the level of the nodus.

It is related to *Allolestes* of the Seychelles in which the lengthening of the quadrangle has gone a step farther. As *Burmargiolestes* has two rows of cells in the Cu_2 area and *Allolestes* but one row, it would seem that the latter genus had derived its simple Cu_2 area by reduction from a double rowed *Burmargiolestes* type.

ALLOLESTES Selys, 1869. Seychelles, two species.

Length:— abdomen 25 mm., hind wing 20 mm. Male inferiors long.

A fragmentary male (Plate, fig. 7) in Williamson's collection has been studied.

This is undoubtedly related to *Burmargiolestes*, but with the same specialization of a long quadrangle more extravagantly developed. It is a Gondwana species sprung from India stock. When one of the most specialized species of the subfamily is stranded in the Seychelles by the sinking of Gondwana, it shows how old the subfamily really is.

The other possibility is that *Burmargiolestes* and *Allolestes* may be more closely related to *Neurolestes* and *Nesolestes* than to the *Argiolestes* series of genera. All four genera are similar in the retracted nodus which lies close to the apex of the quadrangle. All four have a Gondwana distribution from Africa and Madagascar to the Seychelles and India.

Paraphlebia is not related to these though it has a similarly retracted nodus; it differs in having a short Cu_2 , in extra sectors between M_1 and M_{1a} as well as between Cu_1 and Cu_2 .

The penis is the same as in *Podolestes*, *Archiargiolestes*, *Nesolestes*, *Neurolestes*, and *Riphidolestes*.

TATOCNEMIS Kirby, 1889. Madagascar. One species.

Length:— abdomen 50 mm., hind wing 34 mm. Male inferiors short.

This strange species has been associated with the *Platycneminae* because it has the complete suppression of all extra sectors other than M_{1a} , however it possesses the following characters which exclude it from that family:—

1. Ac lies at the level of the first antenodal. In all known *Platycneminae* it lies between the two.
2. Petiolation reaches to the apex of the quadrangle.
3. Male superior appendages semicircular, forcipate with widened apices, a type never found in the *Platycneminae*.
4. Penis shaft with long hairs or spines, which never occur in the *Platycneminae*.
5. Penis lobes directed caudad before turning cephalad. In the *Platycneminae* they are always directed cephalad.

This is too large a list of antagonistic characters to permit the retention of *Tatocnemis* in the *Platycneminae*. Curiously enough these characters are all just as positively *Megapodagrionine* characters as they are not *Platycnemine*. The answer to this riddle is that *Tatocnemis* belongs in the *Megapodagrioninae* near the South American group of genera. In the lack of sectors and the origin of M_3 and Rs *Tatocnemis* appears to be related to the *Heteropodagrion-Oxystigma* series, but it probable comes off this branch of the South American group of genera below any of the existing genera. Its normal stigma suggests great primitiveness, but the loss of sectors suggests relationship to *Heteragrion* and its relatives.

Tatocnemis is one of the genera that appear to show a former land connection between Africa and South America.

NESOCNEMIS Selys, 1891. Madagascar.

As *Ac* is under antenodal one, this is related to *Tatocnemis*, if it is not that genus, rather than to *Prionocnemis* as suggested by Selys. All three genera have the edge of the wing sinuate. As Selys, in his discussion of the relationships of *Nesocnemis*, does not mention Kirby's description of *Tatocnemis* (1889), he probably did not know of it. This is probably *Tatocnemis*.

PROTOLESTES Forster, 1899. Madagascar. One species, *fickei*. Known only from Forster's description.

Length:—Female, abdomen 27–28 mm., hind wing 24–25 mm. Male unknown.

Forster's description suggests a link connecting *Tatocnemis* with the other *Megapodagrionines*. His description mentions but one extra sector other than M_{1a} , this being one that begins two cells before the stigma and that lies between M_{1a} and M_2 . *Ac* lies under antenodal one as in *Tatocnemis*, but M_3 arises one cell before the subnodus and Rs 2–3 cells beyond the subnodus. These characters make this a *Megapodagrionine*, but a type slightly less specialized than *Tatocnemis* as it still has one extra sector other than M_{1a} and the origin of M_3 and of Rs is less modified. This is probably a genus intermediate between *Tatocnemis* and the less specialized genera of the subfamily.

The extremely oblique stigma may or may not show relationship to the oblique stigmaed *Megapodagrioninae* of South America.

LIMITS OF THE MEGAPODAGRIONINAE.

The Megapodagrioninae may be defined as follows:—

Zygoptera with two antenodals (except in *Trineuragrion*, *Neurolestes*, *Thaumatoneura*, *Phenacolestes*, *Dysagrion*, and *Neuragrion*); M_3 and R_s arise at or within one or two cells of the subnodus (except M_3 in *Riphidolestes*, *Phenacolestes* and *Dysagrion*); stigma short, surmounting 1–4 cells (except in *Melanagrion* 5 and *Thaumatoneura* 8); quadrangle with acute apex (except in *Thaumatoneura*); one or two extra sectors besides M_{1a} (except in *Tatocnemis*). Male appendages forcipate with dilated apices, inferiors frequently rudimentary. Tropical and subtropical species.

The limits of the Megapodagrioninae are thus much more closely drawn than previously. The key shows what genera have been included, and the more notable exclusions are noted below.

PHILOGANGA Kirby, 1890, for *Anisoneura* Selys (1859, p. 444), which stands between the Megapodagrioninae and the Amphipteryginae was given subfamily rank as the monogeneric subfamily *Philoganginae* of the Agrionidae, because of the unusual combination of venational characters. The long narrow wing of this curious Himalayan relic can be accounted for if we consider *Philoganga* as having developed from an ancestor like *Hypolestes* (*Ortholestes*) or *Podolestes*. *Philoganga* is very large, being one of the heaviest bodied Zygoptera known. To support this very heavy body the wing area had to be greatly increased. This appears most easily done by simply lengthening all the longitudinal veins. This makes a paddle-like, narrow, and awkward wing with none of the fine adjustments in curved veins, but it answered the purpose of support in the early history of the Zygoptera before modern birds compelled better flying organs in Odonata.

The lengthening of Sc has placed the nodus (apex of Sc) seven or eight cells distad. The lengthening of M_{1-2} has carried the base of R_s distad a cell or two, while the origin of M_2 has passed farther distad than the nodus itself. The many extra antenodals have been necessary to support the long Sc .

An alternate classification would be to place *Philoganga* in the Amphipteryginae. It does not belong there because M_3 and R_s do not arise close enough to the arculus.

This awkward giant has survived to the present day through some special mode of living or by the protection given by some very special habitat.

PHILOSINA Ris, 1917, from the Province of Fokien, China, which is considered more primitive than any living Amphipterygine, Polythorine, or Agrionine has been given subfamily rank as the Philosininae of the Agrionidae. It is another giant Zygopter that has developed a large wing, with but little modification or adjustment of the plan of the wing of its small ancestor.

The long Amphipterygine stigma removes it from the Megapodagrioninae. The origin of M_3 and Rs nearer the subnodus than the arculus removes it from the Amphipteryginae. The penis with slender, doubly curved, recurrent lobes is very much like that of the Polythorinae and that of Caliphaea, the most primitive Agrionine. With its short Cu_2 it looks like a Megapodagrionine wing in which the area between the nodus and stigma had been enriched to increase the area for the very heavy body. It is possible that the stigma was lengthened in this same process, otherwise it stands between the Megapodagrioninae and Amphipteryginae.

PERILESTES Selys, 1862, SYNLESTES Selys, 1869, and CHLOROLESTES Selys, 1862, and the genera EPISYNLESTES Kennedy, 1920, and EUCHLOROLESTES Kennedy, 1920, have been removed to the Lestidae on the ground of penis characters. The apical segment is lacking in all three as it is in all Lestidae. Tillyard, 1914, had already recognized the Lestid relationships of these on venational grounds.

The Lestidae may be revised as follows:—

Perilestinae Perilestes Selys.

Synlestinae Synlestes Selys, Episynlestes Kennedy, Euechlorolestes Kennedy, Chlorolestes Selys.

Megalestinae Megalestes Selys, Chalcolestes Kennedy.

Lestinae Lestes Leach, Africalestes Kennedy, Ceylonolestes Kennedy, Austrolestes Tillyard, Superlestes Williamson, Archilestes Selys, Cyptolestes Williamson, Sympycna Charp., Platylestes Selys.

The male appendages of Perilestes are very obviously Lestid. The penis of Perilestes lacks the apical segment, which is the main character of the family. The venation of Perilestes, though, needs some explanation to adjust it to this family. However, it does not conflict if we consider Perilestes the most primitive member of the Lestidae, and from it derive the type of venation found in the modern genera of the Lestinae. This reverses the older idea of specialization in Zygopterous venation, this derivation of a broad, richly veined wing with little petiolation from a narrow, "reduced" wing that has an extraordinarily

long petiole. However, this derivation of the modern *Lestes* wing from the greatly reduced wing of *Perilestes* appears to be our best explanation of the curious location of the "oblique vein" in the apex of the *Lestes* wing.

When the *Perilestine* wing developed to its modern breadth in the *Lestes* wing all the forks retreated basad as the wing widened except that of *Rs* which was left behind in the apical half of the wing as the oblique vein. It, of course, occurs normally in the apical half of the wing in the ancestral *Perilestes* because here is the original condition of the *Lestid* wing in which none of the forks have as yet moved basad. *Chlorolestes* and *Synlestes* represent an intermediate condition between *Perilestes* and *Lestes*.

LESTOIDEA Tillyard, 1913a, is a very aberrant Megapodagrionine, but is left entirely out in this study because it is so strange, its place cannot be stated with any degree of certainty until the penis is studied, and may be not then. Probably it is best to give it a separate subfamily as did Tillyard (Legion *Lestoidea*) the *Lestoidinae*. The apical half of the wing is distinctly Megapodagrionine in the short stigma and the extra sector. Except for the origin of *M*₃ and *Rs* the base of the wing could be also Megapodagrionine in which the *Cu*₁ and *Cu*₂ veins were greatly reduced. The male appendages are distinctly Megapodagrionine. With all the other characters against it the reduced *Cu*₁ and *Cu*₂ do not show any relationship to the *Proto-neurinae*. The appendages and the general appearance of the wing do not indicate any close relationship to the *Lestidae*.

HEMIPHLEBIA Selys, 1869, has been given full family rank as the *Hemiphlebidae* because it combines the characters of the *Anisozygoptera* with characters of the *Agrionidae*, *Lestidae*, and *Coenagrionidae*, wherefore it would appear to be one of our most primitive *Zygoptera*.

Selys, while noting the strange characters of this genus, placed it at the apex of his system of classification. Dr. Needham and Dr. Munz both discussed it, but each placed it high in the *Coenagrioninae* and attributed its venational peculiarities to reduction. It was not until it was necessary to determine the place of this insect among the *Coenagrionine* genera that its great primitiveness was recognized. This discovery meant a complete revision and readjustment of the organization of the *Zygoptera* and many days were spent in checking over the probable biological history of the group, the venation, and the fossil record.

The venation of *Hemiphlebia* is primitive in the very irregular arrangement of the crossveins and in the acute forks at the origin of

M_2 and M_3 . This is not the usual specialized Odonate fork in which the bases of M_2 and M_3 extend out from M_1 at nearly right angles and then curve outward, but it is a more primitive fork such as occurs in other Neuropteroid insects. The stigma shows no specialization, being merely a thickened cell. The nodus has a remarkably small amount of specialization, being flat and similar to that in the less specialized Anisozygoptera. The open quadrangle may or may not be a primitive character. If it shows relationship to Chorismagrion it may be primitive.

The genitalia of the male second segment are interesting in that the anterior hamules are less developed than in any other Zygopter. The penis is remarkable for the great abundance of shaft hairs which cover its whole ventral surface. A similar condition is found only in some Megapodagrioninae and in some Agrioninae. This character alone excludes Hemiphlebia from the Coenagrionidae. The penis is peculiar in having a fossa in the ventral surface of the second segment. This pocket is similar to that found in the Lestidae and is the only case where such a fossa occurs outside the Lestidae.

Tillyard (*in litt.*) places Chorismagrion next to Hemiphlebia in primitiveness. The following relationship of the two genera is suggested.

Hemiphlebidæ

Hemiphlebinae *Hemiphlebia mirabilis* Selys.

Chorismagrioninae *Chorismagrion risi* Morton.

CHORISMAGRION Morton, 1914, has a subfamily of its own, but it is difficult to decide where such a specialized insect should be classed without having first studied the insect itself. Only Morton's description is available. The placing of this as a member of the Hemiphlebidæ is only a suggestion with several facts against it. First the wing has none of the very primitive characters of Hemiphlebia such as the simple stigma, the acute forks of M_2 and M_3 , and the irregular cells. The open arculus may be only a convergence. The appendages indicate an insect among the more primitive families rather than a member of the Coenagrionidae.

PHENACOLESTES Cockerell, 1908, and DYSAGRION Scudder, 1878, have been included in the Megapodagrioninae as being distantly related to Paraphlebia and Thaumatonereura as well as to Lithagrion, Melanagrion, Miopodagrion, and Eopodagrion Cockerell, 1920. This whole group of North American genera is related to the Oriental genera rather than to the nearer South American genera.

TATOCNEMIS Kirby, 1889, and NESOCNEMIS Selys, 1891, which is probably a synonym of the former, have been included in the Megapodagrioninae. These are Megapodagrionines that have lost all extra sectors except M_{1a} .

Dr. Ris has kindly sent me photographs of two new genera of Megapodagrioninae from South China and a third new genus from Luzon. One of the new genera from South China is obviously related to Burmargiolestes while the other appears to be Amphypterygine, though it has characters that seem to place it between the two subfamilies. The species from Luzon is a generalized and primitive form of the Argiolestes series.

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