

AGRION

NEWSLETTER OF THE WORLDWIDE DRAGONFLY ASSOCIATION

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AGRION is the Worldwide Dragonfly Association's (WDA's) newsletter, which is normally published twice a year in January and July. Occasionally a special issue may be produced. The WDA aims to advance public education and awareness by the promotion of the study and conservation of dragonflies (Odonata) and their natural habitats in all parts of the world. AGRION covers all aspects of WDA's activities; it communicates facts and knowledge related to the study and conservation of dragonflies and is a forum for news and information exchange for members. AGRION is freely available for downloading from the WDA website at [<https://worlddragonfly.org/about/agrion/>]. WDA is a Registered Charity (Not-for-Profit Organization), Charity No. 1066039/0. A 'pdf' of the WDA's Constitution and byelaws can be found at its website link at [<https://worlddragonfly.org/about/>].



Editor's notes

Keith Wilson [kdpwilson@gmail.com]

WDA Membership

Membership signing up and renewal process is achieved directly through the WDA website [<https://worlddragonfly.org/>]. There are three kinds of WDA membership available, either **Regular** or single (£50/year), which is the standard category, **Family** (£75/year) or **Reduced** (£25/year). The latter is a reduced membership category for students (grade school, undergraduate, graduate, etc.), and anyone (student or not) residing in a developing nation (see [UN list](#)). For further information consult the WDA website at: [<https://worlddragonfly.org/new-changes-in-2021/>]. You can sign up for membership using the WDA's website [<https://worlddragonfly.org/membership-account/membership-levels/>] or by contacting the WDA secretary directly [wda.secretary@gmail.com]. Sponsored memberships are also available for those who cannot afford the cost due to currency restrictions or other reasons. Prior to 2021, membership options were with or without the WDA's journal (*The International Journal of Odonatology*)—in electronic form or hard copy, but as from January 2021 the *IJO* has only been available in electronic form and is now freely accessible through Open Access [<https://worlddragonfly.org/ijo/>]. For member benefits see WDA web page under Member Resources [<https://worlddragonfly.org/resources/member-resources/>].

WDA Membership Renewal

Automatic renewal is in place for existing members so they do not have to worry about their membership renewal. A reminder email, notifying members of their upcoming membership payment, will be sent seven days prior to the debit.

Conference news

Seventh European Congress of Odonatology (ECOO2024)

The Iberian Group of Odonatology (*Grupo Ibérico de Odonatología - GIO*) has announced on its Facebook website that the seventh *European Congress of Odonatology* (ECOO2024) will be held in Sevilla, Andalusia, Spain during the last week of June (25th - 28th) in the historical building of Casa de la Ciencia in collaboration with La Estación Biológica de Doñana (EBD-CSIC) [Doñana Biological Station, Spanish National Research Council]. A post-congress field trip will explore the best Andalusian rivers near Ronda in search of southwest Palearctic endemics and African 'new comers'. For more information consult the ECOO website [[Link](#)].



Cover. Mixed species pairing of lested damselflies in the UK. Southern Emerald Damselfly (*Lestes barbarus*) male paired with female Willow Emerald (*Chalcolestes viridis*), Canvey Island, Essex, 11 September 2023. Both these damselflies are relative newcomers to the UK having colonised many sites in south and southeast England in recent years. Photo credit: Keith D.P. Wilson.

International Congress on Odonatology (ICO2025)

ICO2025 is scheduled to be held in the Colombian National Heritage Town town of Villa de Leyva, located in Ricaurte Province, which is part of the Boyacá Department of Colombia. Villa de Leyva is a three-hour drive from the capital city of Bogota.

Members news

Sadly, the passing of four prominent members of the WDA was announced in the July 2023 issue of *Agrion*; Kiyoshi Inoue (1932-2023), Jillian D. Silsby (1925-2023), Richard J. Rowe (1948-2023) and Mike L. May (1946-2023). In Memoria were provided for Kiyoshi-san, Richard Rowe and Jill Silsby in the July 2023 *Agrion* but Mike May passed away just before publication on the 16th June 2023. A brief account of Mike's contributions to the WDA and our understanding of Odonata is given below. The December 2023 issue of *Odonatologica* (volume 52, issue 3/4) was dedicated to the memory of Kiyoshi Inoue, Michael L. May and Richard J. Rowe with In Memoria provided for each of them including comprehensive odonatological bibliographies. The *Odonatologica* 52(3/4) abstracts can be found at the journal's website [\[Link\]](#). An In Memoriam has also been published in the December 2023 issue of *Argia*, the *News Journal of the Dragonfly Society of the Americas* [\[Link\]](#).

Mike L. May 2 September 1946 - 16 June 2023

Mike was an avid supporter of the WDA and became WDA's President for a period of two years at the *International Symposium of Odonatology* held at Beechworth, Victoria, Australia in January 2003. He served on the WDA's Board of Trustees for a total period of 14 years from 2001 to 2015. He also served as Editor-in-Chief of WDA's *International Journal of Odonatology* from 2010 to 2015. As recently as 2020 he wrote an informative article for a Covid-19 Special Issue of *Agrion* titled: A quick tour of some libelluloid naughty bits [*Agrion* 24(2): 155-161]. Mike was also an active member of the *Dragonfly Society of the Americas*, for whom he served as President from 2001-2002.

Mike was a graduate student at the University of Florida during the late 1960s and early 1970s studying under the tutelage of Dr. Minter J. Westfall, Jr. (coauthor of the *Dragonflies of North America*, published in 1955), and assisting with his fieldwork. After gaining a Ph.D in 1974 Mike became a postdoctoral fellow at the University of Florida and from January to September 1974 he was based at the Smithsonian Tropical Research Institute on Barro Colorado Island in Panama where, *inter alia*, he worked on thermoregulation in Odonata and light signalling patterns in fireflies. In 1978 Mike took up a post at Rutgers University, in New Brunswick, initially working on beetles, but dragonflies and damselflies soon became one of Mike's main research subjects. During a long academic career at Rutgers, as Professor of Insect Behavior and Structure and Function, he published many important contributions to our understanding of odonate thermoregulation. Mike's varied interests also included numerous publications (>80) on odonate systematics, taxonomy, ecology, behaviour, migration and distribution. He extensively revised the two manuals covering North America Odonata, namely the 1955 *Dragonflies of North America* (revised edition 2000) and the *Damselflies of North America*, first published in 1996 (revised edition 2006).

Mike was born in Quincy, Florida and grew up in Gainesville, Florida where he developed a strong Floridian accent that he never lost. His colleagues and postgraduate students all speak very fondly of Mike's gentle demeanour, warmth, kind nature and endless enthusiasm for the study of Odonata and entomology in general. Jessica Ware (WDA President 2021-23) and John LaPolla, who both studied for their Ph.Ds at Rutgers under Mike, wrote a glowing tribute to him published in *Organisms, Diversity & Evolution* in 2012 [\[Link\]](#).

Mike is survived by his wife Leslie, his son Jamie, daughter-in-law Lauren and his two grandchildren.



Mike & Linda May attending 6th International Congress of Odonatology mid-symposium lunch at Alex Cordoba-Aguilar in-law's summer home, Xalapa, Mexico, 10th June 2009.

WDA and social media

WDA has an active social media team coordinated by Social Media Coordinator, Rhema Dike [<https://worlddragonfly.org/about/social-media-team/>]. Rhema is a student and research assistant at the University of Lagos in Nigeria. Rhema studies the diversity, distribution, and taxonomy of Odonata in Southwestern Nigeria. He also studies odonates as indicators of water quality. The Social Media Team regularly posts information on Facebook, Twitter, Instagram and the WDA website about Odonata related news and research. WDA's Facebook group can be found at [<https://www.facebook.com/WorldwideDragonflyAssociation>], its Twitter presence at [<https://twitter.com/worlddragonfly?lang=en>] and Instagram at [<https://www.instagram.com/worlddragonfly/>].

Next issue of AGRION

For the next issue of *AGRION*, to be published at the beginning of July 2024, please send your contributions to Keith Wilson [kdpwilson@gmail.com]. All articles, information and news items related to dragonflies or of interest to WDA members are most welcome and will be considered for publication. Please send all text and figure captions in a Word file by email. Please do not include artwork with the text but provide a separate file or files, ideally in a compressed format (e.g. 'tiff', 'jpeg' or 'gif'). Do not make up plates of multiple photos but send the original photo images as separate files.

If you have an odonate photo illustrating any rarely observed aspect of dragonfly biology, or an unusual species, or simply a stunning dragonfly shot, please submit it for consideration for publication on the front cover of *AGRION*.

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Observations on the breeding behaviour of *Austroargiolestes alpinus* (Zygoptera: Argiolestidae)

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Abstract

Observations of *Austroargiolestes alpinus* on oviposition, emergence, copulation, female mating refusal, adult season length, and aggression, made at montane swamps/bogs in northeast New South Wales, are described, illustrated and discussed.

Introduction

Austroargiolestes alpinus (Tillyard, 1913) was originally described from Ebor in northeast New South Wales. Historically, it appeared to be a very localised species recorded within a 15 km radius around Ebor, including one record each from New England National Park and the Cathedral Rocks National Park, and a further record collected from Boonoo Boonoo State Forest on the 9th of January 1988. There have been no published records outside the Ebor area until recently when it was recorded from Deer Vale. The larva of *A. alpinus* was described by Theischinger & Coy (2023). The species is IUCN red-listed as near-threatened (Dow 2017).

The male's thoracic markings, which vary in colour from blue, mauve to maroon, and the shape of its anal appendages distinguish this species (Fig. 1) from the closely related *A. brookhousei* Theischinger and O'Farrell, 1985. The female may have brown or blue thoracic markings with the blue variant also changing through mauve to purple on cool days. The particular shape of some elements of the thoracic colour pattern and the structure of the male secondary genitalia and anal appendages as described by Theischinger & O'Farrell (1986) make *A. alpinus* and *A. brookhousei* a very distinctive group within *Austroargiolestes*.



Figure 1. Male *Austroargiolestes alpinus*.

Observations,

All observations were made by the author (RC) on a property located at Deer Vale in north east New South Wales, Australia. There are three main swampy areas that *A. alpinus* inhabits on this property, but most observations referred to in this paper were made at a montane swamp, which was completely burnt on the 10th of December 2019 (Fig. 2). This particular swamp is 1,225 metres above sea level, and a little less than one hectare in area. The main shrubs in the swamp are *Callistemon pallidus* and *Baeckea omissa*. A very thick cover of Pouched Coral Fern (*Gleichenia dicarpa*) made the swamp very difficult to access prior to the 2019 fire. The surface water of the swamp dried-up in the winter and early spring of 2021, leaving only a few puddles in the tiny rocky creek that runs out of it. RC made 25 trips to this swamp from October 25th 2020 to March 16th 2023.



Figure 2. An orthomosaic image of the burnt swamp, Deer Vale, northeast New South Wales, Australia, December 2019. Credit: Danni Coy.

Oviposition

16 Nov 2020. A brown marked damselfly, which looked like an *A. alpinus* female, was observed laying eggs alone at the edge of one bare, then a second bare freshwater crayfish hole.

It was only active for a short time, then disappeared. No male was observed nearby.

02 Jan 2021. RC startled a brown female *A. alpinus* on the ground next to a row of three freshwater crayfish holes (9:43 am). This female flew onto nearby grass before returning two minutes later to the ground near one of the holes. RC left temporarily to look for teneral *A. alpinus*. Upon RC's return at 10:07 am, the female took flight, and landed on a *Callistemon* bush. Within two minutes, the female had flown back down to the grass and in another three minutes, the female was perched on a stick overlying the mossy hole where it remained for at least fifteen minutes. RC left the scene returning at 10:36 am to witness the female laying eggs around the edge of the mossy hole (Fig. 3A). At 10:47 am, while attempting to get a better view, RC unintentionally scared the female, which flew away. The female laid eggs for a minimum of eleven minutes. Notably, no males were seen in the vicinity.

14 Jan 2022. A pair of *A. alpinus* was observed copulating from 12.58 to 1.05 pm, in which time they moved perches twice (Fig. 3B). Following separation (1:06 pm), the female flew down next to a freshwater crayfish hole behind the bush on which they had been copulating (1:06:54 pm). The male flew off. The female appeared to begin laying eggs (1:07:09 pm) near the hole, then flew inside the hole (1:07:40 pm) and commenced laying eggs in the hole (Fig. 3C). Thirty minutes later the female came out of the hole, perhaps laid a few eggs amongst the grass next to the hole, crawled across the hole, turned around and resumed laying eggs in the hole. The female stopped laying at 1:45 pm and flew behind the hole where it perched for about three and a half minutes before flying off. This female laid eggs almost non-stop for 38 minutes. The water level in the crayfish hole was about 3 cm below the rim of the hole. A link to a video of this female laying eggs is provided here [[Link](#)].

Adult season length

25 Oct 2020. Nearly 11 months after the fire, RC counted eight *A. alpinus* at the burnt swamp. Most of these individuals had their wings spread, indicating that they had not recently emerged.

10 Oct 2021. RC checked the burnt swamp which was very dry with only a few small puddles of water in the tiny creek that runs out of it. No *A. alpinus* were seen.

17 Oct 2021. After rain in the preceding week, RC photographed about 13 individual *A. alpinus* of which three were male. These were all teneral.

17 Oct 2022. One female and two teneral males of *A. alpinus* were observed.

28 Oct 2022. One teneral female, one teneral male and one young female *A. alpinus* were observed.

01 Jan 2021. At least 14 individuals were seen of which 12 were male, one being teneral, and two were females.

05 Jan 2021. Two teneral *A. alpinus* were observed, one male and one female.

17 Feb 2021. Four male and one female *A. alpinus* were observed.



Figure 3. (A) Female *A. alpinus* laying eggs in an old crayfish hole, 2 Jan 2021. (B) Pair of *A. alpinus* damselflies copulating in front of a crayfish hole, 14 Jan 2022. (C) Female *A. alpinus* laying eggs in a crayfish hole, 14 Jan 2022.

26 Feb 2023. Three male *A. alpinus* were observed

16 Mar 2023. No *A. alpinus* were observed

Larva and exuvia

01 Jan 2021, 05 Jan 2021 and 22 Jan 2021. RC sieved the sediment in some of the shallow pools of water in different sections of the swamp looking for *A. alpinus* larvae. No larvae were found, only tadpoles.

25 Oct 2021. RC found an exuvia near a teneral *A. alpinus*. RC noted that there were three freshwater crayfish holes close to the base of the *Baeckia* bush, which an *A. alpinus* larva had climbed to emerge (Fig. 4A).

09 Nov 2021. At 8.23 am RC found an exuvia 90 cm up a *Callistemon* bush from which a newly emerged female *A. alpinus* had just flown. There were two grass surrounded holes overflowing with water next to this bush.

22 Jan 22. RC observed water funnelling down some of the freshwater crayfish holes after abundant rain, indicating that there would most likely be a pool of water beneath, which connected some of the freshwater crayfish holes (Fig. 4B).

Copulation

18 Dec 2013. RC observed a pair of *A. alpinus* copulating for at least 17 minutes from 3:38-3:55 pm. After separation the female rested for about five minutes before disappearing. The male stayed for another minute before leaving. This observation was made between a creek and sphagnum bog at an altitude of 1,110 m — not at the burnt swamp.

29 Dec 2020. RC observed a pair of *A. alpinus* copulating, which flew down behind a *Callistemon* bush startling a second pair also mating. This second pair landed low down in another *Callistemon* bush and mated for a further 43 minutes (10:23-10:01 am). RC had to leave due to a thunderstorm. A handheld video of the mating *A. alpinus* pair was recorded [[Link](#)].

05 Jan 2021. RC observed a male and female *A. alpinus* in close proximity for about 15 minutes (Fig. 4C). The female was young with very pale markings and holding its wings together over its abdomen. The male showed no interest in the female. Both appeared to be hunting.

Female mating refusal

05 Jan 2021. RC found a female perched on a horizontal stick less than a metre from the ground. The female had pale blue upper thoracic markings and pale pink pterostigmata (the pterostigmata are white at emergence and darken with age). A male *A. alpinus* landed close to the opposite end of the stick (10:00 am) in a position such that both damselflies faced each other. The female had her wings held at a backwards angle. Within two minutes the female slipped her body, with wings mostly spread, over the side of the stick so you could just see her eyes peeping over the stick (10:02 am). This female, with wings angled backwards, curved its abdomen up until the tip touched the underside of the stick, curling it back and forth for about one and a half minutes (10:04 am). The female then straightened her abdomen and held it at an oblique angle to the stick with her wings mostly spread. The male moved within approximately two body



Figure 4. (A) Crayfish hole under a bush where an exuvia of *A. alpinus* was found, 25 Oct 2021. **(B)** Water funnelling down a crayfish hole. **(C)** Male *A. alpinus* in close proximity to a young female *A. alpinus*.

lengths of the female (10:05:12 am). The female crouched on the side of the stick with a straight abdomen and with wings held back over her body (Fig. 5A). The male moved back away from the female (10:05:37 am). The female curved her abdomen under the stick again (10:06 am) then straightened it and held her wings parallel to her body. The male moved back within about two body lengths of the female (10:06:22 am). The female had her abdomen curled under when the male launched himself at the female and grabbed her (10:07:17 am) (Figs 5B-C). Over the next five seconds the male, while clasping the female, circled the stick until both were back on top of the stick, then the male tried to fly off with the female in tandem. The male pulled in several different directions, but the female held on to the stick tenaciously (Fig 5D). The male then released the female and flew off.

About one minute later a male landed on the stick behind the female and tried to grab the female. However, a second male intervened, and both males flew off fighting. Neither male returned. The female flew to the opposite end of the stick (10:10:32 am), then moved into a *Baeckia* bush adjacent to the stick (10:11:17). RC went to look for teneral *A. alpinus*, and when RC returned the female had left (10:15:41 am).

Aggression

22 Jan 2021. RC observed a male *A. alpinus* having a territorial dispute with a male *Austroargiolestes icteromelas* (Selys, 1862).

09 Dec 2021. RC observed a male *A. alpinus* chasing off a mating pair of *A. alpinus* as well as two males having a head-on confrontation.

05 Jan 2021. The previously described two males (mating refusal) were fighting after one grabbed or tried to grab the female.

6 Nov 2022. RC observed in a different area on the same property, an *A. alpinus* male fly towards an individual *Austrolestes* species. The *Austrolestes* sp. damselfly flew up from the ground and a short head to head confrontation ensued between the two species. Following the encounter, the *A. alpinus* male landed on nearby vegetation while the *Austrolestes* damselfly returned to the ground near its original location.



Figure 5. (A) Male *A. alpinus* showing interest in a female. (B) Male *A. alpinus* flying in to grab the perched female. (C) Male *A. alpinus* grabbing the female. (D) Male *A. alpinus* trying to fly off with the female.

Freshwater crayfish burrows

16 Jul 2023. An excavation was carried out on a burrow with a 7 cm diameter entrance hole (Fig. 6). The burrow rapidly narrowed to about 4 cm in diameter then gently sloped until it opened up into a chamber. Here one branch went up under a *Baeckea* bush and a second branch went down to a second chamber that was filled with water. The water surface was 32 cm beneath the ground and 42 cm deep overall. The burrow was approximately one metre long from the entrance to the end of the second chamber. No crayfish were seen. Another burrow with a 7 cm diameter entrance was also partly excavated. The excavation process was halted by a layer of rocks between which the burrow kept going. The depth of this section of burrow was 43 cm.



Figure 6. Water-filled crayfish hole, July 2023 (a crayfish is known as a yabby in Australia). The tunnels are mostly full of water in late spring, summer, and autumn, but a lot drier in winter to early spring.

Discussion

Kalkman and Theischinger (2013) commented regarding Argiolestidae that: 'Detailed notes on territoriality, aggressive behaviour, courtship, mating and oviposition are not available for any species' and that: 'For most species only some general information on habitat is available'. Observations on the breeding behaviour of the argiolestid *A. alpinus* provided here may begin to fill the gap in our knowledge on this group of damselflies.

The following Deer Vale site observations indicate that the larvae of *A. alpinus* may live in and benefit from old crayfish holes in swamp/bog habitat:

1. *A. alpinus* females were observed laying eggs in and around freshwater crayfish holes.
2. Freshwater crayfish holes were found at the base of bushes that larvae had climbed to emerge.
3. Due to very dry conditions in early spring of 2021 there was no open surface water for larvae to live in at the bog. However, water was observed in the bottom of a freshwater crayfish burrow in the middle of winter 2023 (winter and early spring are the driest times of the year in this area).
4. No larvae were found when sieving the pools of water which lay on the surface of the swamp after rain.

Crayfish holes provide a wet refuge from fire, and perhaps predators, for *A. alpinus* larvae to develop. Another advantage to living in burrows is that there would be less temperature variation in winter especially in an area that is subject to heavy frosts.

In the three instances that RC observed oviposition, no male guarding was observed.

Watson & Dyce (1978) documented the larvae of the argiolestid *Podopteryx selysi* (Förster, 1899) living in phytotelmata containing 2-3 litres of humified water and 60-80 cm up from the ground. *A. alpinus* larvae also appear to live in water-filled or partly water-filled holes, but these are in the ground and some may connect to underground pools.

Tillyard (1911) found *Griseargiolestes griseus* (Hagen in Selys, 1862) close to entrances of tunnels of *Petalura gigantea* Leach, 1815 but didn't find them in the tunnels. *G. griseus* is a food source for *P. gigantea*, which would make it unlikely for the *G. griseus* larvae to live there. It would be interesting to find out whether *A. alpinus* larvae come out of the tunnels to feed as *P. gigantea* have been observed to do, or if they have enough prey underground.

Murray (1992) observed *Austroargiolestes isabellae* Theischinger & O'Farrell, 1986 laying eggs in soggy bark of a fallen tree limb in a creek. RC has observed *A. christine* laying eggs in old wood and dirt in the bank of a creek, as well as wood in a spring, *A. icteromelas* laying eggs in old wood in a creek and *A. amabilis* laying eggs on mossy rocks next to a creek but this is the first time crayfish holes have been documented as an oviposition site for an argiolestid in Australia.

The flying season for *A. alpinus* in this location is from mid-October to late February (and perhaps early March as the latest observation by RC was 26 February 2023). That is four and a half to five months of activity. The latest seasonal observation of a teneral *A. alpinus* was on 05 January 2021 indicating that individuals might live as long as two months.

Although a full mating was not observed, *A. alpinus* may copulate for a long time, over 43 minutes

in one instance. RC watched a pair of *A. icteromelas* in the wheel position for about 30 minutes (not the entire mating) but this pair seemed to be just resting in contrast to the active 43 minute mating of *A. alpinus*. In the instance where a mature male was in close proximity to a teneral/young female for at least New 15 minutes, the male showed no interest in the female.

The only courtship-like behaviour observed in *A. alpinus*, occurred during an instance of female mating refusal. The male watched the female intently for around seven minutes before attempting to mate. (RC has also observed a male *A. christine* staring at a female *A. christine* in a similar manner before trying to grab her, though the male was watching the female from behind.)

Corbett (2004) describes female zygopteran refusal behaviour being usual in a perched position with wing spreading, abdomen raising and abdomen curling ventrally, as the main documented cues. Hiding (sidling around a stem) and gripping the substrate tightly are also mentioned. Corbett noted an exception to wing spreading in *Lestes rectangularis* Say, 1840 that closes its wings instead. On the approach of a male, a perched *A. alpinus* female was observed to sidle around a stick and press her body against the perch. The female partly closed or closed her wings instead of spreading them, possibly a first record of this behaviour in Argiolestidae. The female had her abdomen curled under signalling her unwillingness to mate when the male grabbed her. The female held on to the stick so tightly that the male could not dislodge her from it. Perhaps this female had already mated and wasn't ready to do so again. The second time a male tried to grab this female, another male flew in and both flew off fighting showing that *A. alpinus* males can be aggressive.

A. alpinus are quite capable of defending their territory from their own kind and other damselflies. It is not often necessary for them to be aggressive due to their low density in their breeding habitat as well as the rarity of finding other damselfly species there.

Acknowledgements

Günther Theischinger for the many relevant papers he sent to me and Danni Coy for producing the photo orthomosaic.

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A review of the Indomalayan genera *Onychogomphus*, *Lamelligomphus* and *Ophiogomphus* (Odonata: Onychogomphinae) and a redescription of *Onychogomphus thienemanni* Schmidt, 1934

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Abstract

In recent years there have been many taxonomic revisions to members of the odonate subfamily Onychogomphinae, especially species found within the Indomalayan biogeographical realm. The majority of Indian and Burmese *Onychogomphus* species, that were treated by Fraser (1934), have been transferred to other genera by various authors, sometimes without explanation. The taxonomic changes to the Indian and Burmese members of *Onychogomphus* and *Lamelligomphus*, since the publication of Fraser (1934), are catalogued here with brief explanations. It had also been noted by several authors that Chinese gomphid species treated by Hsiu-fu Chao (1990) in the genus *Ophiogomphus* did not belong to this genus. The recent subsequent changes in nomenclature to the Asian tropical and subtropical *Ophiogomphus* are detailed and briefly explained. A brief review is given for the remaining Indomalayan species of *Onychogomphus* and their close congeners. A redescription is also provided for the poorly known *Onychogomphus thienemanni* Schmidt, 1934.

Keywords: dragonfly; systematics, taxonomy; India, China, South Asia; Gomphidae

Introduction

Asian members of the Onychogomphinae Chao 1984 were first treated comprehensively in two important publications; the first for Indian and Burmese Odonata by Fraser (1934) and the second for Chinese Gomphidae by Chao (1990). Following many changes in gomphid taxonomic nomenclature it can prove an onerous task to follow the reasoning behind many of the subsequent name changes. For example, how did *Onychogomphus m-flavum* Selys, 1894 in Fraser (1934) become known as *Scalmogomphus bistrigatus* (Hagen in Selys, 1854)?—(see Fig. 1). This account attempts to provide brief explanations for all the name changes to the species treated by Fraser (1934) in the genera *Onychogomphus* Selys 1854 and *Lamelligomphus* Fraser 1922 and species of *Ophiogomphus* (*Ophionurus*) treated by Chao (1990).

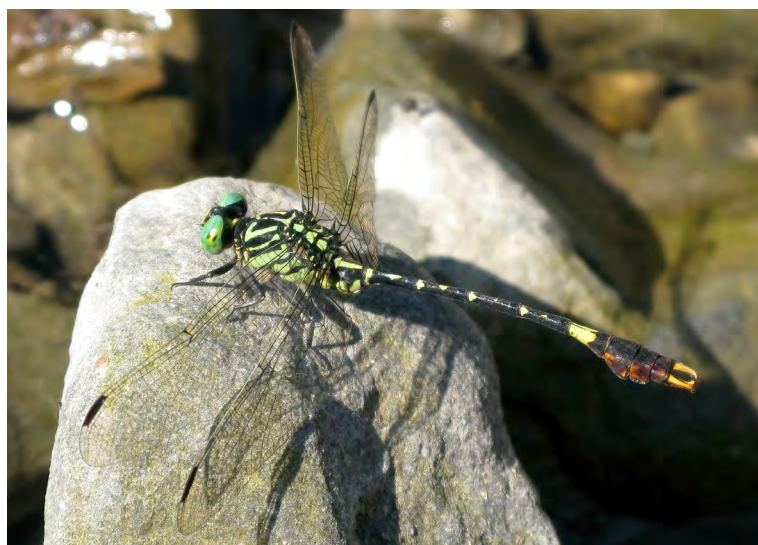


Figure 1. *Scalmogomphus bistrigatus*, Nepal, 2010. Photo credit: Gary Feulner.

The placement of many gomphid species, named from the Indomalayan region, within the *Onychogomphus* genus has hitherto been very much a conservative approach due to the difficulties in identifying reliable generic characters (Müller & Hämäläinen, 1993; Dow, 2014). No definitive phylogeny of Gomphidae has yet been published. To date the most significant contributions to the classification of Gomphidae—focusing on Asian gomphids—have been provided by Carle (1986), Chao (1990) & Carle *et al.* (2015). Seventeen years ago the World Odonata List (WOL) listed 45 species under *Onychogomphus* (Schorr *et al.*, 2007). The numbers of species listed in this genus in the latest WOL (Paulson *et al.*, 2023) has been reduced to thirty-four. The transfer of many Indomalayan *Onychogomphus* species to genera such as *Lamelligomphus*, *Melligomphus* Chao, 1990, *Nychogomphus* Carle 1986, *Orientogomphus* Chao & Xu, 1987 & *Scalmogomphus* Chao 1990 indicates a gradual acceptance of Chao's new genera and Carle's comprehensive onychogomphine classification. However, recent descriptions of new onychogomphine species in Indonesia have blurred the distinction between *Phaenandrogomphus* Lieftinck, 1964 and *Nychogomphus*. For example: Dow *et al.* (2018) apparently overlooked *Nychogomphus* in describing *Phaenandrogomphus safei* and remarked:

'In fact the closest relative to *P. safei* now appears to be *Onychogomphus duaricus* Fraser, 1924, which is often placed in *Nychogomphus*.' See discussion below under paragraph titled: *Phaenandrogomphus* Lieftinck, 1941 and *Nychogomphus* Carle, 1986.

Background

Most gomphids have cryptic coloration usually comprised of camouflage patterns of pale green, pale yellow and black. They tend to be infrequently observed and appear to be poorly represented at most site inventories in any continent, especially in terms of sightings and collections of odonates. In contrast colourful libellulids are usually highly visible and well represented at most freshwater wetland sites in all continents bar Antarctica. Given the apparent contrast in libellulid and gomphid sightings and published records for many sites it would be reasonable to assume that the total number of described species of extant Libellulidae would greatly exceed the number of described gomphid species. Surprisingly, the actual number of libellulids described is only very slightly more than the total number of gomphid species. According to the current WOL (Paulson *et al.*, 2023) the total number of libellulid species is 1,037, whereas the total number of gomphids is 1,009. These two families are the most species-rich Anisopteran families and together they represent more than one-third of the 6,409 total number of described Odonata species that are currently accepted as valid (Paulson *et al.*, 2023). Gomphids tend to spend a lot of their time as adults being relatively inactive; either sitting on stones, logs or bankside foliage or perched high up in the forest canopy. Furthermore, since male gomphids are not so conspicuously coloured as the majority of male libellulids they are more easily overlooked. In consequence gomphids are infrequently observed and usually under-represented in odonate collections. Many gomphids in Asia are poorly known and some species are only represented by one or two, often damaged, specimens belonging to just one sex. When only gomphid females are known from the original description it can be very difficult to place the taxon in the correct genus.

Although there are a similar number of species within each of the Libellulidae and Gomphidae families the number of genera in each of these families is significantly different. There are currently 140 accepted genera in Libellulidae listed in the WOL compared with just 103 genera in Gomphidae (Paulson *et al.*, 2023). The average number of species within each genus for Libellulidae is *ca.* seven whereas the average number of species within Gomphidae genera is *ca.* ten. Both species and family level taxonomic classification are reasonably objective and stable over time whereas classification at generic level tends to be a far a more subjective process with more frequent changes. Given their respective number of genera it would appear that libellulids have received far more attention from systematists than gomphids.

Brief history of the subfamily Onychogomphinae Chao 1984

Dr Chao, Hsiu-fu [Zhao, Xiufu] moved from China to Massachusetts, USA in 1948 where he gained Master's and Doctorate degrees for his studies on Gomphidae. Chao (1953a) published: *The external morphology of the dragonfly Onychogomphus ardens* Needham and became very familiar with wing venation and the caudal and secondary sexual genitalia of the Gomphidae. Over the next three a series of important publications followed on the Classification of Chinese Gomphidae (Chao, 1953b; 1954a; 1954b; 1954c; 1955). Chao (1984) established the subfamily Onychogomphinae and the onychogomphine genus *Amphigomphus* Chao (1954c). Chao (1990) referred to China as the headquarters of Gomphidae. There are currently 37 gomphid genera represented in China, which is 36% of the total number of gomphid genera known globally.

Unlike other Anisopteran families, gomphids display very little variation in wing venation yet early classification of gomphids relied almost entirely on wing venational characters. Early attempts to establish gomphid subfamily groups often produced polyphyletic groupings. Tillyard and Fraser (1940) raised four of Williamson's (1920) six gomphid groupings to subfamily rank based on venational characters but the present subfamily classification of Gomphidae was not established until the taxonomic studies of Chao Hsiu-fu and Frank Carle were published. Carle (1986) created the subfamilies Austrogomphinae and Phyllogomphinae and recognised six additional subfamilies, namely: Epigomphinae, Gomphinae, Hageniinae, Lindeniinae, Octogomphinae and Onychogomphinae.

Lieftinck (1964) established the onychogomphine genus *Phaenandrogomphus*, which is closely related to *Onychogomphus*, to receive his new species *Phaenandrogomphus asthenes* from the Malay Peninsula. Seven Asian species are now recognised in this genus including the Indian *Phaenandrogomphus aureus* (Laidlaw, 1922) and Indian and southeast Asian *Phaenandrogomphus dingavani* (Fraser, 1924), which were both treated under *Onychogomphus* by Fraser (1934).

Following a phylogenetic analysis based on character state polarities from out-group comparisons and the establishment of monophyletic groups from the distribution of derived character states (synapomorphies) Carle (1986) proposed a revised classification of the Gomphidae. Carle (1986) accepted the monophyly of Chao's Onychogomphinae and divided the subfamily into the tribes Onychogomphini

and Crenigomphini, the latter containing the Asian and African *Paragomphus* Cowley, 1934 and African *Crenigomphus* Selys, 1892. Carle (1986) provided detailed morphological descriptions of the various Onychogomphini genera but did not provide a key to the genera. He did, however, provide a key to the *Onychogomphus* subgenera and established the subgenus *Nychogomphus* with *N. geometricus* Selys, 1854 as the genotype species. Carle (1986) also established two additional subgenera of *Ophiogomphus* Selys 1854 comprising *Ophionuroides* and *Ophionurus*; all based on sexual characters of the male and female. Needham et al (2000) and Garrison et al (2006) did not adopt the *Ophionuroides* and *Ophionurus* subgenera and treated all North American species within the *Ophiogomphus* genus. Carle (1986) commented that: ‘As presently defined, the subgenus *Onychogomphus* does not occur in China or India, the *Onychogomphus* of Chao (1954) being *Lamelligomphus* and the remaining *Onychogomphus* of Fraser (1934) being placed in the new subgenus *Nychogomphus*’. This statement is only partially correct as the nominate taxon *Onychogomphus forcipatus* (Linnaeus, 1758) is known from temperate Xinjiang in northwest China (Zhang, 2019). *Nychogomphus* is now accepted at generic level following Chao (1990).

Chao & Xu (1987) established the Onychogomphini genus *Orientogomphus* when describing the new species *O. armatus* and Chao (1990) transferred two species, formerly treated by Fraser (1934) in *Onychogomphus*, to this new genus, namely *Orientogomphus circularis* (Selys, 1894) and *O. earnshawi* (Fraser, 1924). Chao (1990) also transferred *Onychogomphus aemulus* Lieftinck, 1937, known from Indonesia and Peninsular Malaysia, to *Orientogomphus*. Wilson (2008) subsequently transferred *Acrogomphus minor* (Laidlaw, 1931) and *Acrogomphus naninus* (Förster, 1905) to *Orientogomphus*. Wilson & Xu (2009) also transferred *Nihonogomphus indicus* Lahiri, 1987 to *Orientogomphus*.

Chao (1990) responded to Carle’s (1986) comment that no members of the subgenus *Onychogomphus sensu stricta* occur in India or China by closely examining and figuring the penile organ of the genotype species *Onychogomphus forcipatus* (Fig. 2D-E) and examining its close ally *O. uncatus* (Charpentier, 1840). Chao deduced: ‘there is a prepuce [prepuce = preputial fold, posterior lobe or ventro-lateral lobe], produced dorsally from the middle segment and a pair of spine-like processes at the base of the distal segment, both directed anterodorsally. The prepuce is partially covered by the spine-like process in lateral view of the penis’ (Fig. 2A-B). Chao (1990) commented that none of the Chinese species possess a penis with a similar structure and concluded that it was justified to say that the nominate subgenus *Onychogomphus* does not occur in China. Chao was also unaware of the presence of *Onychogomphus forcipatus* in temperate Xinjiang, China.

Chao (1990) raised Carle’s *Nychogomphus* subgenus to generic status and transferred three species treated by Fraser (1934) within *Onychogomphus* to *Nychogomphus*, viz. *Nychogomphus duaricus* (Fraser, 1924), *N. saundersii* (Selys, 1854) and *N. striatus* (Fraser, 1924).

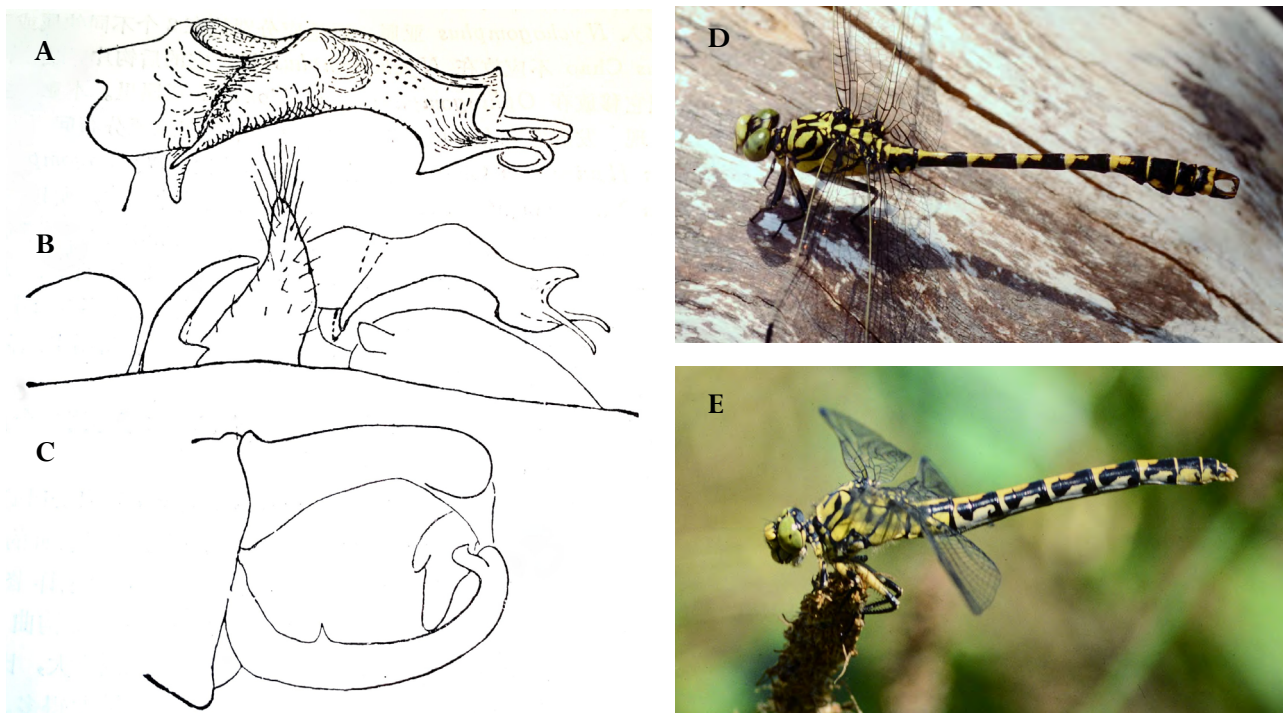


Figure 2. *Onychogomphus forcipatus* (Linnaeus, 1758). (A) Penile organ, lateral view. (B) Penile organ and secondary genitalia, lateral. (C) Caudal appendages, lateral. (A-C) from Chao, (1990). (D-E) Male & female, La Brenne, France, 1983. 1983. Photo credits: Keith D.P. Wilson.

***Onychogomphus* and *Lamelligomphus* species from India and Myanmar treated by Fraser (1934)**

Fraser (1934) selected the wing venation of *Onychogomphus saundersii* Selys, 1854 to serve as the template for characterising Indian and Burmese members of the genus *Onychogomphus*. His selection of *O. saundersii* rather than the genotype species *Onychogomphus forcipatus* (Linnaeus, 1758) to represent the genus was not appropriate since several of Fraser's venational characters for *Onychogomphus* do not apply to the genotype species *Onychogomphus forcipatus*. This can be seen in the list of Fraser's (1934) wing characters for both species provided in Table 1. It wasn't until 56 years later, after the work of Carle (1986), that Chao (1990) transferred *saundersii* to the genus *Nychogomphus* Carle 1986.

Table 1. List of Fraser's (1934) wing characters given for *O. saundersii* (now *Nychogomphus saundersii*) compared with the genotype *Onychogomphus forcipatus*.

Wing characters	<i>Onychogomphus forcipatus</i>	<i>Nychogomphus saundersii</i>
Pterostigma rather short and swollen at its middle, braced, equal to slightly less than one-third the distance from node to the proximal end of the pterostigma.	Yes	Yes
1A in fore-wing pectinated.	No	Yes
3 rows of cells between 1A and hind-wing border.	Yes	Yes
Cuii and 1A in hind-wing closely parallel.	No	Yes
Only 1 cubital nerve in all wings.	Yes	Yes
Subtrigones and hyertrigones entire in all wings.	Yes	Yes
Discoidal field with 2 rows of cells to level of node.	No	Yes

Fraser's (1934) list of Indian and Burmese *Onychogomphus* and their subsequent systematic treatment are tabulated in Table 2. All the species treated in the genus *Onychogomphus* by Fraser (1934), except two taxa of uncertain generic status, *O. annularis* and *O. grammicus*, have been moved to other genera. Fraser (1934) also treated six species within *Lamelligomphus* which are also included in Table 2. Details of the history and characterisation of the now generally accepted genus *Lamelligomphus* are provided below.

***Lamelligomphus* Fraser (1922) syn *Lamellogomphus* Fraser (1923)**

Fraser (1922a) thought that several of the larvae he had found associated with his newly described subspecies, *Onychogomphus biforceps nilgiriensis* Fraser 1922, belonged to this taxon, but we now know the larvae were those of *Heliogomphus* Laidlaw 1922. Fraser (1922b) established the genus *Lamelligomphus* conditionally, stating: 'If the breeding out of these larvae prove the correctness of the diagnosis, I propose to remove the group *biforceps* from *Onychogomphus* and erect a new genus for it with the name of *Lamelligomphus*'. Fraser (1923) then made the genus name *Lamellogomphus* available in the form of a key (he spelt *Lamelligomphus* as *Lamellogomphus* and designated the genotype species as *Lamellogomphus biforceps biforceps*). Fraser (1924) formerly erected the genus *Lamellogomphus*, still using the spelling with an 'o' rather than 'i'. He took this action despite apparently not being successful in rearing out the larvae with the fan-shaped antennae, which actually belong to *Heliogomphus*, since he erroneously included the description of these larvae in the characterisation of *Lamellogomphus*. Regarding the name validity of *Lamelligomphus* versus *Lamellogomphus*—under the International Code of Zoological Nomenclature (ICZN, 2020: 15.1 Conditional proposal)—a new name or nomenclatural act proposed conditionally and published after 1960 is not thereby made available but a new name or nomenclatural act proposed conditionally and published before 1961 may be available for species-group names first published at the same time as conditionally proposed generic names. Therefore, *Lamelligomphus* is valid, although published conditionally, as it was made available first before 1961 in Fraser (1922b: 426), which is before Fraser's (1923: 64) key as *Lamellogomphus* and formal description also as *Lamellogomphus* in Fraser (1924: 983).

Notwithstanding the larval identification error, Lieftinck (1941) did not consider the genus sufficiently well characterised and commented: 'It has since been found that the different species of *Onychogomphus* show extreme variability in the colour of the body as well as in the shape of the male anal appendages and genital organs'. While that may well have been true for the other members of *Onychogomphus* in 1941 it was not true for *Lamelligomphus*, which, for species currently included in the genus, all have consistent and remarkably hook-shaped caudal appendages. Fraser (1924) stated of *Lamelligomphus*: 'Anal

appendages of great length, the inferior usually overlapping the superior which, except in *acinaces* are strongly hooked downwards so that the dorsal surface of their apices comes into contact with the dorsal surface of the inferior appendage'. In Fraser (1934) he remarked that *Lamelligomphus* anal appendages were: 'forcipate, remarkably curled, so that the tips are directed forwards (except in *L. acinaces*); the inferior bifid almost to base, the two branches very closely apposed and curled almost as much as the superiors, which they overlap at the apices, so that the two sets of appendages come to enclose a large cordate space'. Fraser (1934) also noted: 'the distance from node to proximal end of pterostigma, braced; IA in fore-wing markedly pectinate, 3 rows of cells between it and margin of wing; Cuii and IA in hind-wing barely divergent at wing-border.' *L. acinaces* was eventually transferred to *Melligomphus* by Kalkman *et al.* (2020). *Lamelligomphus* is now well-accepted as a valid genus and there are currently 19 species listed in the WOL (Paulson *et al.*, 2023).

Lamelligomphus bitorceps is the genotype species for *Lamelligomphus* established by Fraser (1922). Five additional species were treated by Fraser (1934) in *Lamelligomphus* (*L. acinaces*, *L. cacharicus*, *L. malabarensis*, *L. nilgiriensis* & *L. risi*). All five species were returned to *Onychogomphus* by Lieftinck (1941)—a treatment adopted by Davies & Tobin (1985) and Bridges (1994). As mentioned above *L. acinaces* was transferred to *Melligomphus* by Kalkman *et al.* (2020). Two of these species (*nilgiriensis* & *risi*) were returned to *Lamelligomphus* in the WOL (Paulson *et al.*, 2023) in accordance with Kalkman *et al.* (2020). Although, only known from female descriptions, *L. cacharicus* and *L. malabarensis* are still listed in *Onychogomphus* in the latest WOL. These two poorly known Indian species should also be returned to *Lamelligomphus*, which was their original combination genus, given that it is highly improbable that they would belong to *Onychogomphus*.

Since Fraser (1934) one further *Onychogomphus* species has been described from India, namely *Onychogomphus meghalayanus* by Lahiri (1987). It is known only from the female holotype collected at Rongregiri, Garo Hills, Meghalaya, India (Lahiri, 1987). As commented by Kalkman *et al.* (2020), based on its morphology it is not possible to determine which genus this species belongs to.

Table 2. Fraser's (1934) original list of Indian and Burmese *Onychogomphini* (*Onychogomphus* and *Lamelligomphus*) species and their current status.

Species treated in the genus <i>Onychogomphus</i> and <i>Lamelligomphus</i> by Fraser (1934).	Current combination WOL (Paulson <i>et al.</i> , 2023).	New combination author or possible genus combination.
<i>Lamelligomphus acinaces</i> (Laidlaw, 1922). Treated within <i>Onychogomphus</i> by Davies & Tobin (1985) & Bridges (1994). Now accepted as a species of <i>Melligomphus</i> by WOL (Paulson <i>et al.</i> , 2023) following Kalkman <i>et al.</i> (2020).	<i>Melligomphus</i>	Kalkman <i>et al.</i> , 2020
<i>Lamelligomphus bitorceps</i> (Selys, 1878) was established as the genotype species for <i>Lamelligomphus</i> .	<i>Lamelligomphus</i>	Fraser (1934)
<i>Lamelligomphus cacharicus</i> Fraser, 1924. Only known from holotype female from Assam. No spines on occiput. Fraser (1934) maintained <i>cacharicus</i> in <i>Lamelligomphus</i> , which was before the establishment of the genera <i>Melligomphus</i> and <i>Nychogomphus</i> . Davies & Tobin (1985) followed Lieftinck (1941) and moved <i>cacharicus</i> to the genus <i>Onychogomphus</i> . But, since no <i>Onychogomphus sensu stricto</i> are known from Assam or the Indian & Burmese biogeographical region it is preferable to leave <i>cacharicus</i> in <i>Lamelligomphus</i> in accordance with Fraser (1934). There is a record of a male from Arunachal Pradesh identified as belonging to this species (Prasad, 1997) but the identity of this specimen requires confirmation.	<i>Onychogomphus</i>	Lieftinck (1941). Preferable to revert this species combination to the original genus <i>Lamelligomphus</i> as originally described by Fraser (1924).

Species treated in the genus <i>Onychogomphus</i> and <i>Lamelligomphus</i> by Fraser (1934).	Current combination WOL (Paulson <i>et al.</i> , 2023).	New combination author or possible genus combination.
<i>Lamelligomphus malabarensis</i> Fraser, 1924. Only known from female holotype from Kerala, Western Ghats. Fraser (1934) maintained <i>malabarensis</i> in <i>Lamelligomphus</i> . It was placed in <i>Onychogomphus</i> by Lieftinck (1941), Davies & Tobin (1985) & Bridges (1994). This taxon may belong to another genus, other than <i>Lamelligomphus</i> , and may also be a synonym, but is extremely unlikely to belong to <i>Onychogomphus</i> , where it is currently placed in WOL (Paulson <i>et al.</i> , 2023)	<i>Onychogomphus</i>	As above for this <i>cacharicus</i> this taxon should be returned to <i>Lamelligomphus</i> in accordance with the original description Fraser (1924).
<i>Lamelligomphus nilgiriensis</i> (Fraser, 1922b). Fraser originally described <i>nilgiriensis</i> as a subspecies of <i>Onychogomphus biforceps</i> Selys, 1878. Lieftinck (1941), based in part on the fact that Fraser (1922b) had mistaken a <i>Heliogomphus</i> larvae for the larvae of <i>Lamelligomphus biforceps nilgiriensis</i> , did not recognise Fraser's <i>Lamelligomphus</i> genus, and transferred all Fraser's (1934) <i>Lamelligomphus</i> to <i>Onychogomphus</i> . As pointed out by Kalkman <i>et al.</i> (2020): 'Both <i>Lamelligomphus risi</i> and <i>L. nilgiriensis</i> have been placed by many authors in <i>Onychogomphus</i> but should be included in <i>Lamelligomphus</i> following Fraser (1934), based on the shape of the male anal appendages'.	<i>Lamelligomphus</i>	Fraser (1934)
<i>Lamelligomphus risi</i> (Fraser, 1922). Originally described by Fraser within <i>Gomphus</i> Leach in Brewster, 1815 but placed in <i>Lamelligomphus</i> in Fraser (1934). <i>L. risi</i> was treated within <i>Onychogomphus</i> by Davies & Tobin (1985) and Bridges (1994) but now accepted in <i>Lamelligomphus</i> by WOL (Paulson <i>et al.</i> , 2023) following Kalkman <i>et al.</i> (2020).	<i>Lamelligomphus</i>	Fraser (1934)
<i>Leptogomphus</i> (?) <i>maculivertex</i> Selys, 1891. Only female known from Myanmar. Lieftinck (1969) pointed out that he had erroneously synonymised <i>Onychogomphus aureus</i> Laidlaw 1922 with <i>maculivertex</i> in Lieftinck (1960; 1964) and noted the two species actually belonged to different genera. He moved <i>aureus</i> to <i>Phaenandrogomphus</i> and left <i>maculivertex</i> in <i>Onychogomphus</i> . However, Selys (1891) described <i>maculivertex</i> with a vulvar scale tapered and deeply divided by two very narrow blades reaching to the end of S10, which is identical in form to female <i>Scalmogomphus bistrigatus</i> (Hagen in Selys, 1854) and it is quite possible that <i>maculivertex</i> is a synonym of <i>S. bistrigatus</i> . Kalkman <i>et al.</i> (2020) dismissed a female record of <i>Onychogomphus? maculivertex</i> (Selys, 1891) from Khasi hills, Meghalaya by Lahiri (1987) as not belonging to this taxon and refrained from including <i>maculivertex</i> in their list of Indian odonates.	<i>Onychogomphus?</i>	Possibly a synonym of <i>Scalmogomphus bistrigatus</i> (Hagen in Selys, 1854)
<i>Onychogomphus annularis</i> Selys, 1894. <i>Onychogomphus annularis</i> is known only from two males collected in 1907 from Myanmar. Fraser (1934) was of the opinion that <i>O. annularis</i> might be a variety of <i>Onychogomphus saundersii</i> Selys, 1854, which is now treated in <i>Nychogomphus</i> .	<i>Onychogomphus?</i>	Possibly a synonym of <i>Nychogomphus saundersii?</i> Fraser (1934)

Species treated in the genus <i>Onychogomphus</i> and <i>Lamelligomphus</i> by Fraser (1934).	Current combination WOL (Paulson <i>et al.</i> , 2023).	New combination author or possible genus combination.
<i>Onychogomphus earnshawi</i> Fraser, 1924	<i>Orientogomphus</i>	Chao, 1990
<i>Onychogomphus echinoccipitalis</i> (Fraser, 1922)	<i>Paragomphus</i>	Davies & Tobin (1985)
<i>Onychogomphus grammicus</i> (Rambur, 1842). The original description of the holotype female states it is from an unknown locality. However, Fraser (1934) found an incomplete female specimen, labelled as Rambur's type 'India, Stevens', in the Pusa Museum, Bihar. According to Rambur it resembles <i>Stylurus flavipes</i> . Laidlaw (1922) described a male from Agra, Uttar Pradesh with caudal app. entirely yellow, sup. app. 2 x length of inf. app., very like those of <i>O. lineatus</i> [now in <i>Paragomphus</i>] but flattened and truncate apically. According to Laidlaw his Agra male is closely allied to <i>Onychogomphus flexuosus</i> (Schneider, 1845). Fraser (1934) reported another female collected from Pusa, Bihar in July 1920. Bose & Mitra (1975), recorded a male <i>O. grammicus</i> from Chittorgarh, Rajasthan remarking it had a greenish thorax. Listed in Kalkman <i>et al.</i> (2020) as <i>Onychogomphus grammicus</i> but without comment. Possibly a little known, perhaps genuine <i>Onychogomphus</i> . Habitat unknown. Distribution: northern India.	<i>Onychogomphus?</i>	
<i>Onychogomphus maclachlani</i> Selys, 1894. Only known from type female from Myanmar. Selys (1894) commented that it may be the female of <i>O. annularis</i> known from two males from Myanmar.	<i>Nychogomphus?</i>	Possible synonym of <i>O. annularis</i> see Fraser (1934)
<i>Onychogomphus m-flavum</i> Selys, 1894. Fraser (1937) synonymised <i>O. m-flavum</i> with <i>O. bistrigatus</i> . Chao (1990) subsequently established the genus <i>Scalmogomphus</i> with <i>bistrigatus</i> as the type species. <i>Onychogomphus garhwalicus</i> Singh & Baijal, 1954 is a junior synonym of <i>S. bistrigatus</i> (Hämäläinen, 1988). <i>S. bistrigatus</i> is known from north India, Nepal and West Bengal (Dow, 2010).	<i>Scalmogomphus</i>	Fraser (1937) & Chao (1990)
<i>Onychogomphus pulcherrimus</i> Fraser, 1927 known from Myanmar and Thailand. Female unknown. Transferred to <i>Nihonogomphus</i> by Chao (1954c).	<i>Nihonogomphus</i>	Chao (1954)
<i>Onychogomphus saundersii</i> Selys, 1854 Kalkman <i>et al.</i> (2020) overlooked Chao (1990) when they transferred <i>saundersii</i> to <i>Nychogomphus</i> , supposedly as a new combination, as Chao (1990: 309) had already transferred <i>saundersii</i> to <i>Nychogomphus</i> some 30 years earlier but credited Carle (1986) for the new combination.	<i>Nychogomphus</i>	Chao (1990)
<i>Onychogomphus striatus</i> Fraser, 1924. When Chao (1990) elevated <i>Nychogomphus</i> to species level he also transferred <i>striatus</i> to <i>Nychogomphus</i> .	<i>Nychogomphus</i>	Chao (1990)

Indomalayan *Ophiogomphus*

After moving several Chinese species listed in *Onychogomphus* by Davies & Tobin (1986) to *Nychogomphus* and *Lamelligomphus* Chao (1990) also established the genera *Melligomphus* and *Scalmogomphus* to receive the remaining Chinese *Onychogomphus* species apart from *O. sinicus* Chao 1954. Chao (1990) moved this species

to the genus *Ophiogomphus* (*Ophionurus*). The genotype *Ophiogomphus* (*Ophiogomphus*) *cecilia* (Geoffroy in Fourcroy, 1785) from Europe and Russia and its Palaearctic congeners all look very similar to their Nearctic *Ophiogomphus* counterparts with predominantly bright green thorax and yellow-marked black abdomens—with a snake-like pattern, hence the name *ophis* = snake—and relatively short, stout caudal appendages (Needham *et al.*, 2000; Lam, 2010). In contrast *Ophiogomphus* (*Ophionurus*) *sinicus* looks nothing like *O. cecilia* and closely resembles *Lamelligomphus* and *Melligomphus*.

When Carle (1986) created the subgenera *Ophiogomphus Ophionurus* and *Ophiogomphus Ophionuroides*, he characterised the subgenus by: ‘Posterior hamulus elongate with a hook-like apex, male epiproct with a well-developed dorsolateral spine, female postocellar ridge well-developed medially’ and the nominate subspecies characterised by: ‘Posterior hamulus without elongate hooklike apex, male epiproct without well-developed dorsolateral spine, female postocellar ridge typically vestigial medially’. Vogt and Smith (1993) pointed out that the North American species they described as *O. susbehcha* had characteristics of both *Ophionurus* and *Ophionuroides*. As previously mentioned, neither Needham *et al.* (2000) nor Garrison *et al.* (2006) adopted these subgenera, but treated all North American species within *Ophiogomphus*. These authors all considered that Carle’s sexual characters of male and female *Ophiogomphus* were inconsistent and applicable at species rather than generic level.

Arising from Chao’s (1953a) very detailed study of the external morphology of *Onychogomphus ardens* Chao (1990) selected *ardens* as the genotype species for his new Oriental genus *Melligomphus*. According to Chao’s characterisation, *Melligomphus* appears to be very close to *Ophiogomphus*; it has superior appendages shorter than inferior appendage and the superiors are not markedly hooked apically as in *Lamelligomphus*. Chao (1990) separated *Ophiogomphus* from *Melligomphus* in couplet (8) of his key to Chinese Onychogomphinae genera as follows:

Superior anal appendages slightly shorter than inferior anal appendage; anal loop 1 or 2-celled, A_2 arising from subtriangle *Melligomphus*.
 - Superior anal appendages slightly longer than inferior anal appendage, or subequal in length; anal loop 3-celled, A_2 arising between cu-a and subtriangle..... *Ophiogomphus*.

Wilson & Xu (2009) pointed out that all *Melligomphus* do indeed have superior appendages slightly shorter than inferior appendage [including *Ophiogomphus guangdongensis* which Wilson & Xu (2009) transferred to *Melligomphus*], but also showed that the wings of the genotype *M. ardens* figured in Chao (1953) and by Wilson & Xu (2009) clearly illustrate A_2 arising from the anal vein between the anal crossing (= cu-a) and the subtriangle and not from the subtriangle. Moreover, Wilson & Xu (2009) noted that Chao’s (1994) own drawings of *O. guangdongensis* showed the superior appendages were clearly shorter than the inferior appendage. The anal loop is 3-celled, but this character is inconsistent as Wilson & Xu (2009) noted that three *guangdongensis* specimens (syn *Melligomphus moluami* Wilson, 1995) examined from Hong Kong had 2-celled anal loops.

Chao (1994) placed his new Chinese species *Ophiogomphus guangdongensis* in the subgenus *Ophiogomphus* based on: ‘posterior hamulus produced into a short finger-like process and the inferior anal appendage with a well-developed dorsolateral spine’. The former is actually a trait seen in all other described *Melligomphus* but it would be more appropriate to consider these relatively minor character traits at species level rather than at generic level. Apart from *sinicus* and *guangdongensis* all other members of the *Ophiogomphus* genus, both in North America and Eurasia, are very similar in appearance. Schröter (2010) noted that members of the genus *Ophiogomphus* were the most cold tolerant gomphid dragonfly species worldwide, even reaching the Arctic Circle. No true *Onychogomphus* reaches the subtropics and the placement of Oriental *guangdongensis* in *Ophiogomphus* was not supported by Wilson & Xu (2009) who transferred the species to *Melligomphus* and synonymised *Melligomphus moluami* Wilson, 1995 as a junior synonym.

Although *O. sinicus* has a posterior hamulus and epiproct broadly in agreement with Carle’s (1986) characterisation of the subgenus *Ophiogomphus Ophionurus* (i.e. posterior hamulus elongate with a hook-like apex, male epiproct with a well-developed dorsolateral spine), since these are relatively weak characters at generic and subgeneric level, and given the aforementioned reasoning, *sinicus* more appropriately belongs in *Melligomphus*. Based on general colouration, colour pattern and molecular genetic analysis Kalkman *et al.* (2022) formally transferred *Ophiogomphus sinicus* together with three species described from Vietnam, *Ophiogomphus longihamulus* Karube, 2014, *Ophiogomphus minimus* Karube, 2014, *Ophiogomphus phantoani* Ngo & Nguyen, 2021 to *Melligomphus*.

Melligomphus sinicus is known to be common across a wide range of south and southwest China from Zhejiang through Jiangxi, Fujian, Guangdong, Hong Kong, Guangxi (Wilson & Xu, 2009; Tong, 2013; Zhang, 2019) and northern Vietnam (Kompier, 2014).

There are two species of *Ophiogomphus* listed in the checklist of dragonflies and damselflies for Bangladesh, Bhutan, India, Nepal, Pakistan and Sri Lanka (Kalkman *et al.*, 2020): *Ophiogomphus caudoforcipis* Yousuf & Yunus, 1977 and *Ophiogomphus reductus* Calvert, 1898. *Ophiogomphus caudoforcipis* is only known from the holotype male collected at Mingora in Pakistan in 1966 at an elevation of 910 m (Yousuf & Yunus, 1977). Based on a comparison between the description and material of *O. reductus* at the Rijksmuseum van Natuurlijke Historie (RMNH) Kalkman (2022) concluded that *O. caudoforcipis* is a junior synonym of *Ophiogomphus reductus*. *O. reductus* is known from Afghanistan, China, India, Kazakhstan, Kyrgyzstan, Mongolia, Pakistan, Tajikistan, Turkmenistan, Turkey, and Uzbekistan in montane areas of central Asian bordering arid plains up to 1700 m (Kalkman, 2014). *O. reductus* is a typical *Ophiogomphus sensu stricta*, known as snaketails, with predominantly bright green thorax and yellow-marked black abdomens.

***Phaenandrogomphus* Lieftinck, 1941 and *Nychogomphus* Carle, 1986**

Lieftinck (1941) established and characterised the genus *Phaenandrogomphus* in fine detail. In comparison with *Onychogomphus* the body is slender with more drawn-out terminal segments. The key features of Lieftinck's characterisation of the genus include: (i) legs short, third femur reaching just caudad of S1, (ii) abdomen very slender with elongated segments, S8 only a little shorter than S7, (iii) male secondary genitalia projecting strongly, (iv) hamuli well-developed, long and slender, (v) vesicle large and complex and projecting ventrally, (vi) median and distal penile segments elongate and distal segment slender, dorsoventrally flattened and bilobed with cornua, (vii) subgenital plate of female large, (viii) male caudal appendages well-developed, superior appendages forcipate, inferior appendage deeply cleft, both caudal appendages of similar size slightly less than equal to length of S9+S10 combined.

All currently described *Nychogomphus* share the same characterisation as detailed above. In Carle's (1986) key to the subgenera of *Onychogomphus* he separated *Onychogomphus sensu stricto* from *Onychogomphus* (*Nychogomphus*) based on *Onychogomphus s. str.* having: (i) male cerci directed medially, (ii) penile organ with spine-like prepuce, (iii) anterior hamule with elongate shoulder, and (iv) anterior lamina raised hood-like as opposed to *Nychogomphus* that has (i) cerci directed posteroventrally, (ii) prepuce absent, (iii) anterior hamuli without shoulder and (iv) anterior lamina low and not hood-like as in *Nychogomphus*. Again, these *Nychogomphus* characters are also shared with *Phaenandrogomphus*. *Phaenandrogomphus* does not have its superior appendages directed medially, it lacks a prepuce and the anterior lamina is not prominent.

Continental Asia species currently treated in both *Phaenandrogomphus* and *Nychogomphus* in the WOL (Paulson *et al.*, 2023) are very much alike and all have similar general body form with slender elongate bodies, yellow '7'-shaped dorsal stripes or narrow oblique dorsal stripes not connected to collar stripe on black thorax and yellow marked superior appendages, caudal appendages which are long and of similar length, *ca.* two times length of S10, both have penile organs lacking a prominent prepuce with very large protruding vesicles. *Nychogomphus* differs only slightly from *Phaenandrogomphus*. Continental *Phaenandrogomphus* can be differentiated from the former by entirely yellow male caudal appendages as opposed to black-tipped superior appendages and black inferior appendages seen in *Nychogomphus* and females with narrowly divided flat, truncated subgenital plates, as opposed to those of *Nychogomphus* with flat, W-shaped, acutely pointed branches of subgenital plate. *Nychogomphus* also have abdominal patterns with isolated yellow oval spots along the dorsal carina centres of S3-S5/S6, whereas the dorsal abdominal colour pattern in *Phaenandrogomphus* is much more developed.

Chao (1990) separated *Phaenandrogomphus* from *Nychogomphus* based on the former's inferior appendage that strongly bends upward at about its apical third with its apex horizontally truncated as compared to uniformly curved inferior appendage not truncated apically in *Nychogomphus*. However, now that *Nychogomphus lui* Zhou, Zhou & Li, 2005 and *Nychogomphus yangi* Zhang, 2014 have been described from Yunnan, China, both having inferior appendages that strongly upturn at about their apical half with their distal half expanded and truncated, this distinction is no longer clear.

When Muller & Hämäläinen (1993) described *Onychogomphus treadawayi* from Busuanga Island, Coron, Palawan, Philippines the authors stated: 'Our generic combination of the new species is conservative, since we feel that the recent splitting of *Onychogomphus* Selys 1854 to several genera remains unsatisfactory unless all known species of this widespread group are treated simultaneously'. In terms of 'recent changes' Muller & Hämäläinen (1993) were presumably referring to Lieftinck (1941), Carle (1986) and Chao (1990) but they made no specific mention of any author. Certainly the distinction between *Phaenandrogomphus* and *Nychogomphus* was vague in 1993 when far fewer species belonging to these two genera were known.

Dow & Luke 2015 described *Phaenandrogomphus safei* from Sabah and also moved *O. treadawayi* to the genus *Phaenandrogomphus*. When Dow *et al.* (2018) recorded the second record of *P. safei* from Sarawak the first author Dow had second thoughts and stated that he: '...may have been premature in placing this species and *Onychogomphus treadawayi* in *Phaenandrogomphus*: in doing so he overlooked, for instance, *Nychogomphus* Carle, 1986, which has a very similar penile organ. In fact the closest relative to *P. safei* now appears to be

Onychogomphus duaricus Fraser, 1924, which is often placed in *Nychogomphus* [as in the WOL (Paulson *et al.* 2023)]. With hindsight it would have been better to take a conservative approach and describe this species in *Onychogomphus* pending a thorough genus level revision of the Asian Onychogomphinae'.

Dow's hesitation is understandable since *Nychogomphus* and *Phaenandrogomphus*, as previously noted, both share similar body shape, penile organs with no well-developed prepuce and large vesicle and general form of caudal appendages. Both *P. safei* and *P. treadwayi* have inferior appendages which strongly bend upward at about their apical third and are horizontally truncated apically, similar to the genotype *Phaenandrogomphus asthenes* Lieftinck, 1941. *Phaenandrogomphus safei* and *P. treadwayi* appear to be correctly placed in *Phaenandrogomphus*. The principal differences between continental *Nychogomphus* and *Phaenandrogomphus* are relatively minor species level characters and some of these distinctions don't apply to Philippine *P. treadwayi* and Bornean *P. safei* that both have different body and caudal appendage colour patterns to their mainland counterparts. The very close structural similarity of *P. safei* and *Nychogomphus duaricus*, noted by Dow *et al.* (2018), further indicates the close similarity between *Nychogomphus* and *Phaenandrogomphus* species. From the perspective of continental Asia it is easy to separate *Nychogomphus* from *Phaenandrogomphus* but the presence of many shared characters in Philippine *P. treadwayi* and Bornean *P. safei* indicates the paraphyletic nature of species within *Nychogomphus* and *Phaenandrogomphus*. Given the general similarity in body form, especially the structure of the penile organs, and general form and structure of the caudal appendages, *Nychogomphus* may prove to be a junior synonym of *Phaenandrogomphus*.

Review of *Onychogomphus thienemanni* Schmidt, 1934 and its allies

Onychogomphus thienemanni Schmidt, 1934 (Figure 3A-F)

Onychogomphus thienemanni Schmidt: (1934: 369-371, figs 78-80, holotype male thorax, genitalia & app., W. Java); Lieftinck (1954: 93, Sumatra, Java); Norma-Rashid & van Tol (1995: 102, Selangor, P. Malaysia); Orr (2005: 69, 3 Figs, dorsal view, lat. caudal app., lat. thorax, P. Malaysia, Sumatra & Java); Wilson & Gibert (2006: 4-9, Fig. 6, common, Endau Rompin, Pahang, P. Malaysia); Novelo-Gutiérrez & Che Salmah (2013: larva description, Kelantan, P. Malaysia).

Redescription of male *O. thienemanni*

Specimens: 2 males, Endau Rompin, Pahang, P. Malaysia, 13 v 2006, coll. K.D.P. Wilson.

Male. Head: Labium pale yellow. Labrum black with pair of very large yellow spots extending to the lateral border in the upper corners. Mandibles yellow and genae pale brownish-yellow. Anteclypeus yellow with fine black lateral margins. Postclypeus black with large yellow spots laterally occupying lateral third except dorsal margin. Face of frons black. Dorsal surface of frons black with a frontal margin broadly yellow divided at centre. Vertex black and occiput dark brown and smooth with margin of fine hairs. Ocelli pale and dorsal margin of basal segment of antennae ringed pale yellow. Rear of head black. Prothorax black. Synthorax black with pair of narrow slanted greenish-yellow dorsal stripes slightly thicker above and not connected to narrowly divided collar stripe. Antealar triangle greenish-yellow. Sides of thorax black with broad greenish-yellow stripe across mesepimeron. Metepimeron bordered black along margins except base, otherwise yellow; metepisternum entirely black. Trochanter and coxae greyish-black, legs entirely blackish-brown. Wings: Veins black including costa. Anal triangle 4-celled, anal loop 2-celled, 1A and CuP parallel to wing border. Discoidal field with two rows of cells from origin to slightly beyond level of nodus in fore-wings not in hind-wing which forms three rows before level of nodus. Sectors of arcus well separated at origin with 3 crossveins before first bifurcation of superior sector in fore-wings and 1 in hind-wings. Pterostigma dark brown, braced covering 5 cells. Abdomen: Predominantly black with yellow pattern. S1-2 relatively broad with central, dorsal narrow yellow stripe not quite reaching the distal border. S1-2 laterally black above yellow below with basal margin of S2 ringed dark brown. S3 with pair of narrowly divided basal yellow spots extending laterally to mid-point. S4-6 with similar pattern to S3 but smaller yellow spots. S7 basal third yellow, dorsal carina very finely black. S8-9 black with dusky-orange lateral spots occupying lower basal half. S10 black. Superior appendages dark brownish-orange, forcipate, >2 x length of S10, with prominent dorsal pointed prominence at distal two-thirds. Inferior appendage, almost as long as superiors, deeply divided almost to the base with two parallel branches, markedly upcurved at apical third, and two pairs of prominent raised pegs at basal half. Penile organ without a well-developed prepuce, anterior lamina not especially prominent, vesicle large and distal segment bilobed with each lobe bearing finely tipped cornua.

Measurements (mm): abdomen = 32-33, app. 2.5, hw 25-27.

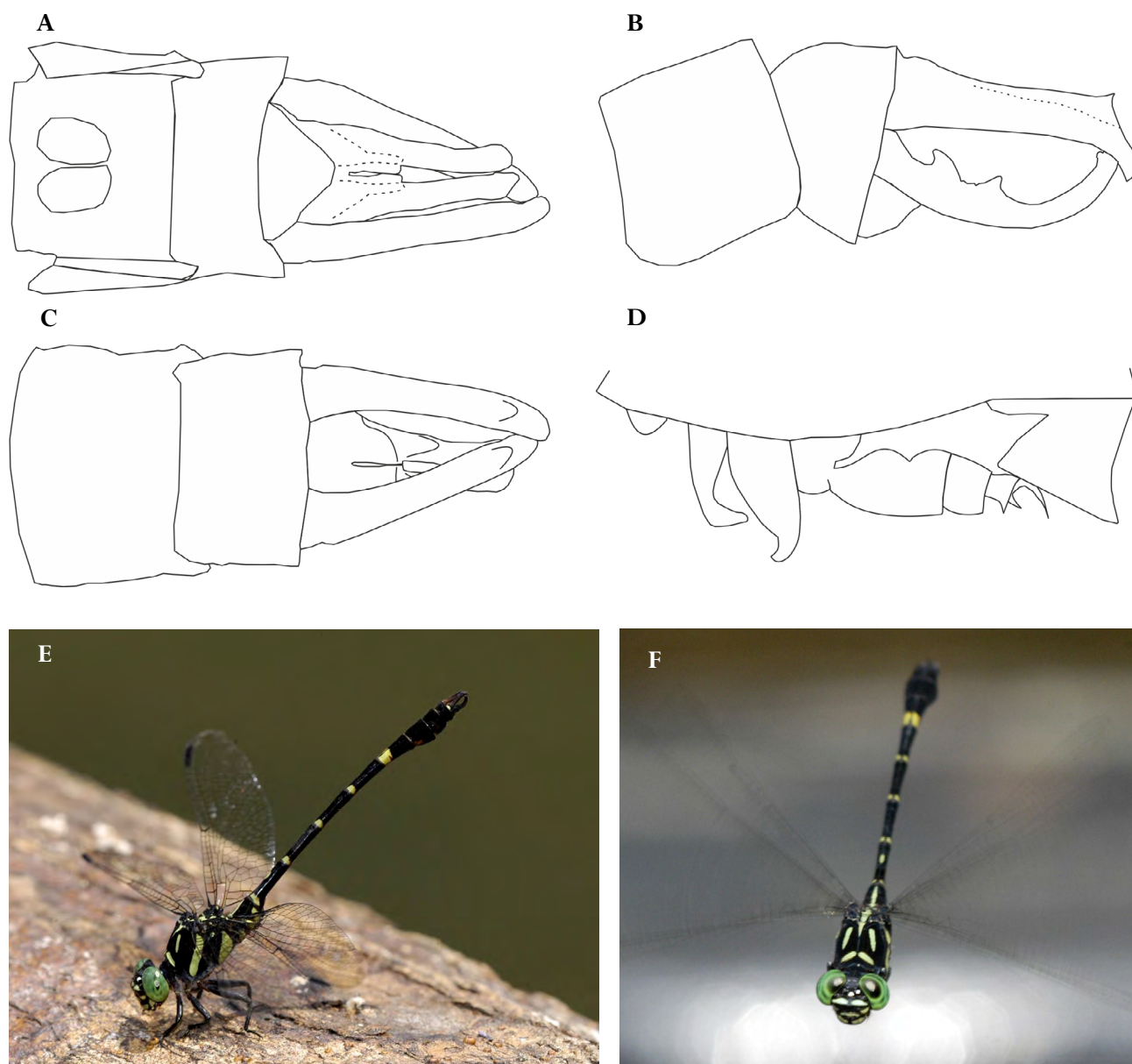


Figure 3. *Onychogomphus thienemanni* Schmidt, 1934, male, Endau Rompin, Pahang, Peninsular Malaysia, 13 May 2006. (A-C) Caudal appendages. (A) Ventral view. (B) Lateral view. (C) Dorsal view. (D) Penile organ and secondary genitalia. (E) Male perched on fallen log mid-stream next to a broad stream riffle in open forest. (F) Male in flight hovering over shallow stream riffle in open forest. Photo credits: Keith D.P. Wilson.

Close allies of *Onychogomphus thienemanni*

Onychogomphus marijanmatoki Dow, 2014

Dow (2014) noted, when describing the small gomphid *Onychogomphus marijanmatoki* from Sarawak, that: 'A number of genera have been erected within the Asian Onychogomphinae over the decades, but many of these have not been accepted by all authors. I prefer to follow the same conservative course as Müller & Hämäläinen (1993) and place the new species in *Onychogomphus* pending a thorough revision of the entire subfamily'. Presumably Dow (2014) considered *Nepogomphus* Fraser (1934), although he made no specific mention of the genus in his differential diagnosis other than an oblique reference that his new species possessed: 'a large seminal vesicle but not very large'.

The known *Nepogomphus* are immediately recognised by their diminutive size, notably smaller than *Onychogomphus*, with characteristic forcipate caudal superior appendages of similar length to inferior appendage *ca.* 2 x S10, basal segment of penile organ (vesicle) extremely swollen, anterior lamina projecting strongly and arched, and penile organ with an extended prepucce. All three species currently named

under *Nepogomphus*, namely *Nepogomphus fruhstorferi* (Lieftinck, 1934), *N. modestus* (Selys, 1878) and *N. walli* (Fraser, 1924) all have similar body dorsal thoracic patterns and hind-wing less than 25 mm in length. *O. marijanmatoki* is marginally larger with a hind-wing length of 25.5 mm and as stated by Dow (2014) has a large seminal vesicle but not very large. *O. marijanmatoki* doesn't have a prominent anterior lamina or a penile organ with a well-developed prepuce so it probably doesn't belong in *Nepogomphus* or *Onychogomphus* and appears to be closest to *Phaenandrogomphus*.

O. marijanmatoki has a lot in common with *Onychogomphus thienemanni*. Both are small-sized onychogomphines that have caudal appendages of similar length $> 2 \times S10$, with an unusual raised peg on the distal dorsal margin of superior appendages and well-developed low projections on the dorsal base of inferior appendage. The inferior appendages in both species are deeply divided into a pair of long parallel branches. Moreover, both species lack a well-developed prepuce and have large seminal vesicles. They also share the same head proportions, thoracic dorsal and lateral pattern, black with oblique greenish-yellow dorsal stripes not connected to a narrowly divided collar stripe and metepisternum entirely black. Hitherto, the secondary genitalia for *Onychogomphus thienemanni* have not been described or figured. A brief description including figures of the caudal and secondary genitalia are provided here (Fig. 3A-D).

***Onychogomphus (Siriusonychogomphus) louissiriusi* Fleck (2020)**

Fleck (2020) established the subgenus *Onychogomphus Siriusonychogomphus* to receive his new species *Onychogomphus louissiriusi* reared from larvae collected from Thailand. The new subgenus was characterised by Fleck using both adult and larval morphology as follows:

- peculiar shape and disposition of larval antennae meeting for a long distance medially thus completely covering labrum and clypeus;
- unique triangular shape of larval frons;
- larval abdominal dorsal hook well developed only on second segment and directed anteriorly;
- hindwing lacking anal loop;
- vesica spermalis lacking flagellae and instead with pair of oreillets; prepuce rounded and not directed backwards;
- male caudal appendages strongly developed, of same length and not overlapping, with cerci almost straight in dorsal view, and with epiproct having closely appressed branches and bearing long molar ridge at base.

The larvae of *O. louissiriusi* described by Fleck has the same unusual antennae shape and general morphology as the larvae of *O. thienemanni* described by Novelo-Gutiérrez & Che Salmah (2013). Moreover, the adult has similar wing venation and there are similarities in the secondary genitalia and caudal appendages. *O. thienemanni* is clearly closely related to *O. louissiriusi*. Fleck considered the Bornean species *O. marijanmatoki* and *O. thienemanni* were possibly closely allied to his new species.

A further species *Onychogomphus kerri* Fraser, 1933 was briefly described from two specimens collected in 1932 from Khon Khaen in north-east Thailand by Fraser (1933) in a discussion of *O. saundersii*, without giving the type locality. Kimmins (1966) designated the type and its locality from one of the specimens in the Natural History Museum London. Dow (2009) commented that: 'It is questionable whether Fraser's one paragraph treatment of this species even constitutes a proper description'.

Discussion

This review of Indian and Chinese Onychogomphinae thus far has indicated that no true *Onychogomphus* species occur in continental tropical and subtropical south, southeast and southwest Asia. The taxonomic status of the three *Onychogomphus* detailed above, *O. (Siriusonychogomphus) louissiriusi*, eastern Malaysian *Onychogomphus marijanmatoki* and *Onychogomphus thienemanni*, also from Southeast Asia, do not belong in *Onychogomphus* and in their general appearance bear no resemblance to *Onychogomphus sensu stricta*. They are all small onychogomphines differentiated from other genera of the Onychogomphinae by (i) inferior appendages of similar length to superior appendages, deeply divided with both branches parallel, or slightly divaricate, ca. two \times length of S10 or slightly longer, (ii) inferior appendage with raised baso-dorsal peg structures and superior appendages with ridged dorsal peg at apical half, (iii) penile organ with moderately large vesicle, without a prominent prepuce (posterior lobe), with or without cornua, (iv) hamuli well-developed, long and slender with gently curved tips, and (v) anterior lamina not especially raised. Both *O. louissiriusi* and *O. thienemanni* also share the same unique shape of the larval antennae; the larvae of *O. marijanmatoki* being unknown.

***Onychogomphus* from Borneo and Indonesia**

Four *Onychogomphus* species are listed in the WOL (Paulson *et al.*, 2023), that were all described by Lieftinck from Indonesia. Three species from Sumatra; *O. perplexus* Lieftinck, 1935, *O. rappardi* Lieftinck, 1937, and *O. pollux* Lieftinck, 1941. A further species, *O. banteng* Lieftinck, 1929 was described from west Java. *O. perplexus* was originally described as a subspecies of *Onychogomphus geometricus* Selys, 1854, but treated as full species by Lieftinck (1954). *O. kerri* is now the genotype species of *Nychogomphus*. *O. perplexus* should be moved to *Nychogomphus*. *O. pollux* has strongly hooked superior appendages identical in form to *Lamelligomphus* and it clearly belongs in this genus. *O. rappardi* and *O. banteng* both have inferior appendages with no baso-dorsal teeth that are slightly shorter than superiors. They both key out at *Melligomphus* in Chao's (1990) key.

***Borneogomphus* Karube and Sasamoto, 2014**

Karube and Sasamoto (2014) described the new genus *Borneogomphus* with *B. teramotoi* as the genotype species from specimens collected from Kinabalu, east Malaysia. Karube & Sasamoto (2014) considered *Phaenandrogomphus* to be the closest congener to *Borneogomphus* stating their new genus: 'is likely to be closest to the genus *Phaenandrogomphus*, both of which share several characteristics, such as yellowish orange coloured body and female with a pair of conical horns on post-ocellar part. However they are significantly different in the morphology of accessory genitalia and the penile organ'. Karube and Sasamoto (2014) dismissed the likeness of their new species to *Nychogomphus*: 'by the shapes of accessory genitalia, penis and epiproct'. But, there are closer similarities to the hamuli and caudal appendages of *B. teramotoi* to *Nychogomphus*. The tip of the penile organ, which is broadened apically, without cornua, does appear to differ significantly from described *Nychogomphus* and *Phaenandrogomphus*.

Conclusion

It is clear that the systematic treatment of Indomalaya onychogomphines is in need of a thorough taxonomic review and further analysis. Hitherto, authors have relied mostly on morphology but a thorough revision of the Onychogomphinae is required based on a combination of both morphology and comprehensive molecular genetic analysis.

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New book

Dragonflies and Damselflies of Tasmania

Authors: Michael Driessen and Günther Theischinger

Publisher: Tasmanian Field Naturalists Club - Paperback Nov 2023
 132 pages, 74 colour photos, b/w line drawings, colour distribution maps
 A5 size, NHBS £49.99 [[Link](#)]
 Also available from Tasmanian Field Naturalists Club bookshop [[Link](#)]

This field guide is dedicated solely to Tasmanian species of dragonflies and damselflies and includes information on their conservation and scientific significance. It also includes the most recent consensus of dragonfly and damselfly taxonomy. The beautiful images, detailed descriptions, identification keys and distribution maps will help the reader identify the dragonflies and damselflies in Tasmania. By taking an interest in this group of animals and reporting identifications we can help build our understanding of their distribution and ecology and help better conserve and manage Tasmania's unique fauna.

This book caters for the beginner providing clear images of each species (both male and female) and for more experienced people who will find the illustrated keys to adults and larvae valuable. The book has a comprehensive illustrated glossary that explains all terms used in the book that may not be familiar to all readers, something that is often lacking in other guides.

Biography

Michael Driessen is a zoologist with over 30 years of experience researching a variety of animal species and their threats and raising awareness about Tasmania's special fauna. While undertaking his Ph.D on the resilience of moorland invertebrates to fire, he became fascinated with dragonflies. Michael works for the Tasmanian Government and is an adjunct Senior Researcher at the University of Tasmania.

Günther Theischinger has had a life-long interest in aquatic insects and is the foremost authority on Australian dragonflies and damselflies. He has published more than 300 scientific papers, and over the years has described more than 60 new species and several new genera of Australian dragonflies. He has been a visiting scientist at the Australian National Insect Collection in Canberra and is a Research Associate of the Australian Museum and a Visiting Fellow at the Smithsonian Institution, USA.

You can listen to the ABC Radio Hobart radio interview with author Michael Driessen promoting the book, which as broadcast 25 November 2023, at the following link [[Link](#)].



