



A New Species of *Triaenodes* (Trichoptera: Leptoceridae), based on morphological and molecular data, from Kaeng Khoi Waterfall, Chumphon Province, southern Thailand

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Abstract

A new species of *Triaenodes tipmaneei* **sp. nov.** is described and illustrated based on the male and female genitalia. The mitochondrial DNA (mtDNA) cytochrome c oxidase subunit I (COI) of the new species and of the most similar species *T. themis* Malicky and Prommi 2006 were analyzed. The male genitalia of *Triaenodes tipmaneei* **sp. nov.** is distinguished from other species in the genus by the shape of inferior appendages. Inferior appendages of the new species are without recurved processes; the dorsal branch is divided into a dorsal lobe and two processes, with the upper process curved upward and bifid, and the lower process slender and with pointed apex; the main body of the appendage has a short slender apicolateral process, the mesal process is short and pointed, the ventral process is stout, and the apex is pointed. The genetic distance between *T. tipmaneei* **sp. nov.** and *T. themis*, based on the mtDNA COI region, was 8.5 percent, indicating a large genetic differentiation between the two species.

Key words: taxonomy, freshwater, Malay Peninsula, DNA sequencing, caddisflies

Introduction

Larvae of *Triaenodes* (Trichoptera: Leptoceridae) are case-makers, creating distinctive tube-like cases of longitudinal plant material arranged in a spiral that they carry for camouflage, physical protection, and enhanced respiration (Morse 2004; St Clair 1994; Wiggins 1996, 2004). The species belonging to *Triaenodes* can be found in various regions around the world, with many species adapted to specific local environments (Holzenthall & Andersen 2004; Manuel & Braatz 1984; Morse 2024). In North America, *Triaenodes* species are common in streams, rivers, and lakes throughout the United States and Canada, inhabiting diverse habitats from slow-moving streams to fast-flowing rivers (Manuel 2010; Wiggins 1996). In South America, the genus is widely distributed, inhabiting a variety of freshwater environments, including the Amazon basin and other river systems, and are present in countries such as Brazil, Argentina, and Colombia (Holzenthall & Andersen 2004; Holzenthall & Calor 2017; Pes *et al.* 2018). Europe hosts several *Triaenodes* species in its freshwater bodies, including rivers, lakes, and streams, ranging from northern Europe, including Scandinavia, to southern regions like Spain and Italy (Neu *et al.* 2018). In Africa, *Triaenodes* species are found in rivers, streams, and lakes across various regions, including East Africa, Southern

Africa, and the Congo basin. Several *Triaenodes* species inhabit freshwater systems in Australia, including streams and rivers in both temperate and tropical regions. They are also present in New Zealand and on other Pacific islands (Houghton *et al.* 2018; Tagliacollo *et al.* 2021).

Triaenodes spp. can be found in diverse aquatic habitats across Asia, and they are present in countries like China, Japan, India, and Southeast Asian nations, adapted to the local freshwater ecosystems (Morse 2004; Yang & Morse 2000). Sixteen species are found in Laos, Peninsular Malaysia, Sumatra, Vietnam, and Thailand (Morse 2004). In Thailand, eleven species have been reported, namely *Triaenodes pellectus* Ulmer 1908, *T. dusrus* Schmid 1965, *T. trivulcio* Schmid 1994, *T. qinglingensis* Yang & Morse 2000, *T. pentheus* Malicky 2005, *T. menestheus* Malicky 2005, *T. narkissos* Malicky 2005, *T. iphis* Malicky 2005, *T. grifo* Malicky 2005, *T. patroklos* Malicky & Chantaramongkol 2006 (in Malicky 2006), and *T. themis* Malicky & Prommi 2006 (Malicky & Chantaramongkol 2010; Morse 2024).

The new species belongs to genus *Triaenodes*, a genus reviewed by Hur (2006) and Yang & Morse (1993). The adults of the family are characterized by very long antennae, head without ocelli, pronotum consisting of a lateral pair of erect and plate-like warts separated by a deep and wide concavity anteromesally, a pair of longitudinal rows of setae dorsally on the mesonotum, the mesoscutellum short and usually with a pair of small scutellar warts, narrow forewings each lacking a thyridial cell, and male paramere spines absent. Other characteristics of many males include antennal scapes each having a hairy scent organ covered with a long flap; maxillary palpi each with five segments, the basal plate of the inferior appendages being very short and not articulating with the ventral lip of the phallic shield, paramere spines being absent, and the phalotheca being either absent or fused with the phallobase. Yang & Morse (1993) recognized three subgenera within the genus. These findings were later challenged by Neboiss & Wells (1997) who described 44 new species from Australia (Neboiss & Wells 1998). Pending further descriptions of numerous species from Africa and South America (e.g., Andersen & Holzenthal 1999, 2001, 2002) and a reassessment of the global fauna (e.g., Hur 2006), a subgeneric classification is not implemented here.

Chumphon is geographically located in Thailand on the narrow Kra Isthmus of the Malay Peninsula. There are no prior reports about the biodiversity of caddisfly species in this region. Kaeng Khoi Waterfall includes different habitats such as limestone waterfalls, large rock waterfalls, and gravel and soil waterfalls. Recently, species diversity of caddisflies was surveyed, and the new species *Triaenodes tipmaneei* (Trichoptera: Leptoceridae) was found and is here described based on morphological and molecular data.

Materials and methods

During September 2023 and February 2024, UV pan light traps were set to collect adult specimens from three waterfalls in Chumphon Province: Ka Po Waterfall, Sai-On Waterfall, and Kaeng Khoi Waterfall.

The male and female genitalia of the new species were dissected and macerated in 10% KOH solution at 60°C for 60 minutes. The genitalia structures were observed and drawn by hand under 100X magnification with a compound microscope (Olympus SZ) equipped with a drawing tube attachment. The pencil templates of the genitalia structures were digitized using Adobe Illustrator© software.

Terminology for describing the male and female structures of genitalia of the genus *Triaenodes* follows Yang & Morse (2000).

The holotype, stored in 80% ethanol, is deposited in the Laboratory of Fishery Science and Aquatic Resources, Department of Agricultural Technology, King Mongkut's Institute of Technology Ladkrabang, Prince of Chumphon Campus, Chumphon, Thailand (KMITL). Paratypes, also in 80% ethanol, are deposited in the same collection and in the collection of Dr Hans Malicky (CHM), Sonnengasse 13, A-3293 Lunz am See, Austria.

Genetic analysis of the mtDNA barcoding region was conducted to examine the degree of genetic differentiation between the new species and *Trichosetodes themis*, the most similar species. Total genomic DNA of *T. tipmaneei* sp. nov. and *T. themis* were extracted from ethanol-preserved tissues of their hind legs and purified using a DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. The mitochondrial DNA (mtDNA) cytochrome c oxidase subunit I (COI) and 16S rRNA regions were amplified by a polymerase chain reaction (PCR) using the primer sets LCO1490 (5'-GGTCAA CAA ATC ATA AAG ATA TTG G -3') and HCOoutout (5'-GTA AAT ATA TGR TGD GCT C -3') (Folmer *et al.* 1994) and AQdb-16S_F (5'-TRA CYG TRC AAA GGT AGC -3') and AQdb-16S_R (5'-CCG GTY TRA ACT CAR ATC ATG T -3') (Takenaka *et al.* 2023)

from extracted total genomic DNA. Regarding each reaction, 1.0 µL of 10 x Ex Taq buffer, 0.8 µL dNTP Mixture (including 25 mM MgCl₂), 0.05 µL of 5 U/µL Ex Taq polymerase (TAKARA, Shiga), 0.25 µL of each primer, and 1.0 µL of extracted DNA, for a total of 10 µL, were applied. The PCR protocol of both genetic regions was: 94°C for 2 min; 35× (94°C for 1 min, 50°C for 1 min, 72°C for 1 min); and 72°C for 3 min. The PCR products were purified using ExoSAP-IT Express (Thermo Fisher Scientific K.K., Tokyo, Japan). Purified DNA fragments were sequenced directly by an automated method using a BigDye Terminator v.1.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) on an automated DNA Sequencer (ABI 3130 or 3130xl DNA Analyzer; Perkin Elmer/Applied Biosystems). The sequence data of two species have been submitted to the DNA data bank of Japan (DDBJ database) (GenBank accession numbers: the mtDNA COI region: LC844839–LC844846; the mtDNA 16S rRNA region: LC844831–LC844838).

For our analysis, we added appropriate DNA sequence data for some Asian species of *Triaenodes* (*T. trivulcio* Schmid 1994: KX291078; *T. dusrus* Schmid 1965: KX293023; *T. pentheus*: KX104957, KX293793, KX103645, and KX103682; *T. qinglingensis* Yang & Morse 2000: NC_069289 and OL678054; *T. pellectus*: KX295376, KX105293; and North American *T. frontalis* Banks 1907: JX682380, JX682474, JX682379). With respect to the outgroups, we added appropriate DNA sequence data of the South American species *Achoropsyche duodecimpunctata* (Navás 1916) (FN601000, FN601021). All sequence data were aligned and edited using CLC Workbench software (CLC bio, Aarhus, Denmark) and MAFFT v7.222 (Kato & Standley 2013). Phylogenetic analyses were performed by the maximum likelihood (ML) method (Felsenstein 1981) using RAxML-NG v. 1.2.2 (Kozlov *et al.* 2019). The genetic distance (*p*-distance) between the new species and *T. themis*, the most similar species by male genitalia morphology, was calculated using MEGA v.7 (Kumar *et al.* 2016).

Taxonomy

Triaenodes tipmaneei Nannaphat and Malicky sp. nov.

(Figs 1A–1E)

Type material. Holotype, ♂: Thailand, Chumphon Province, Pathio District, Kaeng Khoi Waterfall, 10°41'05"N, 99°16'43"E, 150 m a.s.l., 23. xii. 2023, leg. Nannaphat Suwannarat (KMITL).

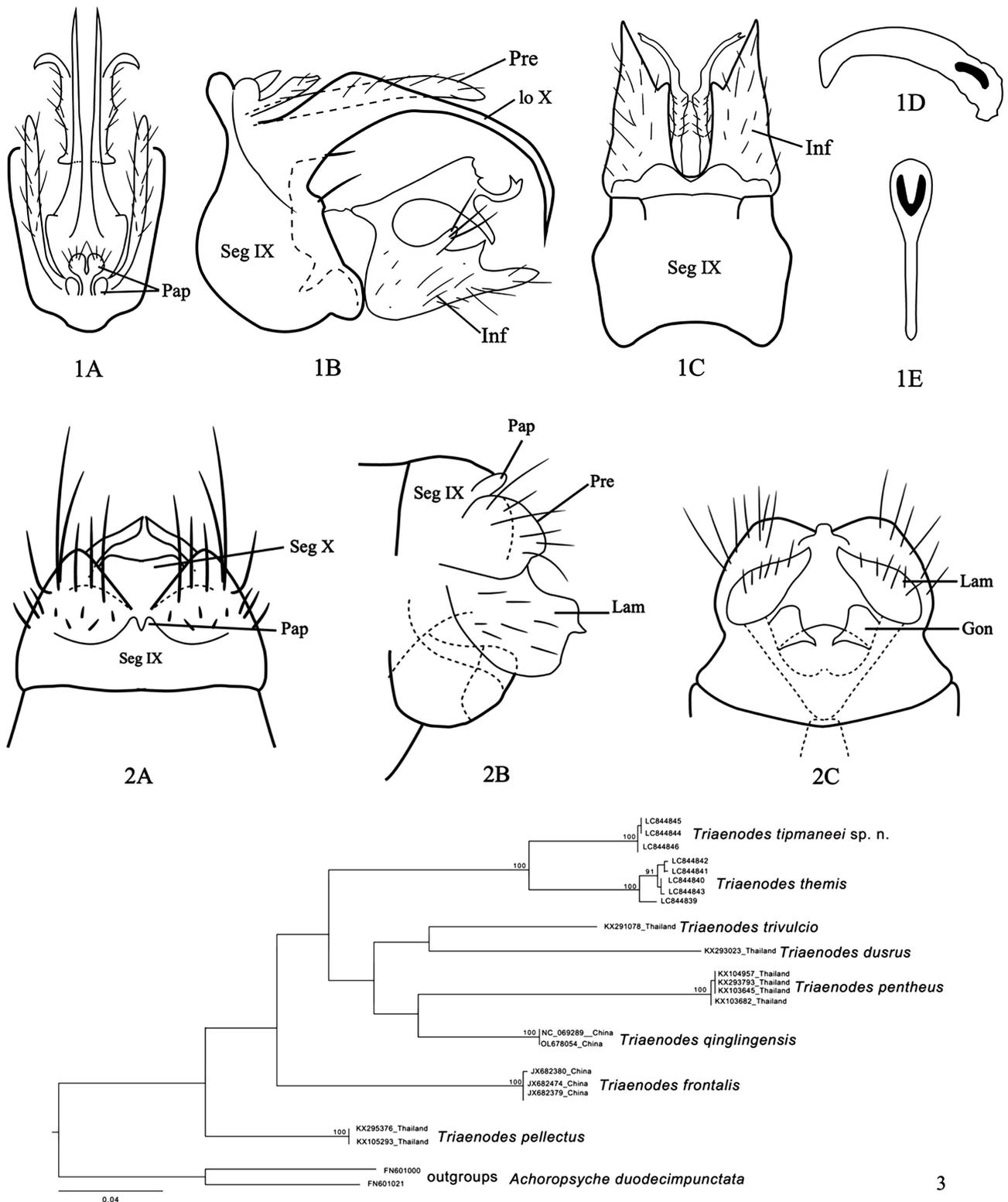
Paratypes: 7 ♂♂ and 6 ♀♀, same data as holotype (KMITL).

Paratypes: 4 ♂♂ and 2 ♀♀, same data as holotype (CHM).

Etymology. The species is named for Mr. Kamronwit Thipmanee, He is an executive vice president for the Chumphon Campus.

Description. Head, thorax, and legs yellow brownish. Body light yellowish brown. Forewings yellowish brown. Length of each male forewing 3.2–4.8 mm (N = 8), of holotype male forewing (4.8), of female forewing 3.0–4.2 mm (N = 6).

Male genitalia (Figs 1A–1E). Segment IX dorsal region in dorsal view (Fig. 1A) relatively short longitudinally and slightly convex anteriorly and with pair of short, bare papillae posteriorly; in lateral view (Fig. 1B, Seg IX) ventrolateral region five times as long as dorsal region and semicircular anteriorly, slightly concave posteriorly; in ventral view (Fig. 1C, Seg IX) subquadrate with shallow concavity anteriorly. Preanal appendages (Pre) slender with numerous setae, half as long as lower processes of segment X (Figs 1A, 1B). Upper part of segment X (up X) bilobed apically and setose, originating between pair of apicodorsal papillae of segment IX and pair of preanal appendages (Figs 1A, 1B). Lower part of segment X divided into pair of very long, sword-like processes slender and straight and parallel for most of their length in dorsal view (Fig. 1A), tall in basal 1/3 and slender and down-curved in lateral view (Fig. 1B, lo X). Inferior appendages in lateral view (Fig. 1B, Inf) without recurved processes; each with dorsal branch divided into subtriangular apicodorsal lobe and two slender apical processes, upper process curved upward and bifid, lower process downcurved, slender with pointed apex; main body of each appendage with short slender apicolateral process with long apical setae, apicomeral process short and triangular, apicoventral process stout with pointed apex directed caudad (Fig. 1B); in ventral view (Fig. 1C, Inf), main body of each inferior appendage somewhat long-triangular and covered with numerous setae, with short acute process at mid-length on mesal margin. Phallus slender, basal 3/5 laterally compressed and apical 2/5 spoon-like in dorsal view (Fig. 1E), with dark subapical phallotremal sclerite torch-like in lateral view (Fig. 1D), V-shaped in dorsal view (Fig. 1E).



FIGURES 1–3. *Triaenodes tipmaneei* sp. nov., 1A–1E, male genitalia: 1A, dorsal; 1B, left lateral; 1C, ventral; 1D, phallus, left lateral; 1E, phallus, ventral. 2A–2C, female genitalia: 2A, dorsal; 2B, left lateral; 2C, ventral. 3, Estimated phylogenetic relationships using the neighbor-joining clustering method for *Triaenodes* spp. based on the mtDNA COI region. The sequence of *Achoropsyche duodecimpunctata* was included as the outgroup. Gon = gonopod plate (paired), Inf = inferior appendage (paired), Lam = lamella (paired), lo X = lower part of segment X (paired), Pap = papilla (paired), Pre = preanal appendage (paired), Seg IX = segment IX, Seg X = segment X.

Female genitalia (Figs 2A–C). Segment IX (Seg IX) fused with setose preanal appendages and with pair of small papillae (Pap) apicodorsally in dorsal view (Fig. 2A); in lateral view (Fig. 2B, Seg IX), papillae somewhat oval and thumb-like. Preanal appendages setose, in dorsal view (Fig. 2A) triangular, more nearly circular in lateral view (Fig. 2A), in ventral view (Fig. 2C), scale-like and moderately large. Segment X in dorsal view (Fig. 2A, Seg X) short, fused with preanal appendages. Lamellae setose, in lateral view (Fig. 2B, Lam) subquadrate and beaklike apically, in ventral view (Fig. 2C, Lam) pear-like. Gonopod plates in ventral view (Fig. 2C, Gon) bird-head-like, concave mesally and acute anteromesally.

Diagnosis. *Triaenodes themis* Malicky & Prommi 2006 is the most similar species and lives also on the southern peninsula part of Thailand where the new species was found. The male genitalia of *T. tipmaneei* **sp. nov.** are distinguished from those of *T. themis* and the other species in the genus by the shape of inferior appendages. Inferior appendages of the new species are without recurved processes; the dorsal branch is divided into a dorsal lobe and two apical processes, the upper process curved upward and triangular apicodorsally and bifid apicoventrally, and the lower process slender with pointed apex; main body of the appendage is with short slender apicolateral process, mesal process short and pointed, ventral process stout, pointed apex. Each inferior appendages of *T. themis* has a dorsal branch that is not divided apicoventrally and the main body is without a mesal process.

The female genitalia of *Triaenodes* spp. found in Thailand and southeast Asia are mostly unknown. However, Yang & Morse (2000) described females of several species of *Triaenodes* from China such as those of *T. foliformis* Yang & Morse 2000, *T. qinglingensis*, and *T. unanimis* McLachlan 1877. However, these can be separated by the shapes of the lamellae. *Triaenodes* spp. found from China have lamellae that are spoon like, but the new species has sack-like lamellae, each with a beak-like apex in lateral view. According to the molecular analysis, *Triaenodes tipmaneei* **sp. nov.** has a close genetic relationship to *T. themis* with 8.5 percent difference between these two.

Molecular analysis. As shown in Figure 3, *Triaenodes tipmaneei* **sp. nov.** was genetically differentiated from all analyzed species in the same genus. The closest phylogenetic relationship was with *T. themis*, and genetic differentiation between these two species was also confirmed (Fig. 3). The genetic distance (*p*-distance) based on the mtDNA COI region between *T. tipmaneei* **sp. nov.** and *T. themis* was 8.5 percent.

Discussion

Triaenodes species are found in diverse freshwater habitats globally across both temperate and tropical regions (Tagliacollo *et al.* 2021; Houghton *et al.* 2018). Sixteen species are found in Laos, Peninsular Malaysia, Sumatra, Vietnam, and Thailand (Malicky & Chantaramongkol 2010). Moreover, Yang and Morse (2000) described several *Triaenodes* spp. species found in various environments, generally at waterfalls in China.

Like the latter species, this species, *Triaenodes tipmaneei* **sp. nov.** was found at a waterfall that is a picturesque natural attraction renowned for its serene environment and lush tropical surroundings (Figs 4A–4B). Kaeng Khoi Waterfall at Chumphon is geographically located in Thailand on the narrow Kra Isthmus of the Malay Peninsula. The habitat characteristics include moist, shaded environment around the waterfall and supporting lush vegetation, ferns, moss, liverworts, and various epiphytic plants. The riparian zone was characterized by dense forest with species such as bamboo, palms, and tropical hardwoods (Figs 4A–4B) (Suwannarat *et al.* 2020; Kalaninova *et al.* 2014).

The results of the phylogenetic analysis and the genetic distance (*p*-distance) indicate that the new species, *T. tipmaneei* **sp. nov.**, is genetically differentiated from *T. themis*, the species most closely related based on male genitalia morphology and is an independent species from all other described species. In this study, we analyzed the mtDNA and the 16S rRNA region; however, due to the absence of sequences of most described species of the genus, especially of the 16S rRNA region, we were unable to conduct a more comprehensive phylogenetic analysis. Since the mtDNA 16S rRNA region is valuable as a DNA barcoding marker, we registered it in the database for future use in conjunction with the mtDNA COI region (Takenaka *et al.* 2024), so that the inclusion of molecular data could be used in future research. Takenaka *et al.* (2024) reported that mtDNA COI and 16S rRNA regions analysis have proven useful to supplement taxonomy and diversity studies of Trichoptera. Molecular analysis by Laudee *et al.* (2023) revealed that the mtDNA and rRNA regions consistently reflected the morphological differences observed among the newly identified species of Trichoptera.



FIGURES 4A–4B. Study sites from Kaeng Khoi Waterfall, Chumphon Province.

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References

- Andersen, T. & Holzenthal, R.W. (1999) The genus *Allosetodes* Banks, 1931, a junior synonym of *Triaenodes* McLachlan, 1865 (Trichoptera: Leptoceridae). *In*: Malicky, H. & Chantaramongkol, P. (Eds.), *Proceedings of the 9th International Symposium on Trichoptera, Chiang Mai, Thailand, 5–10 January 1998*, pp. 7–16.
- Andersen, T. & Holzenthal, R.W. (2001) West African *Triaenodes* McLachlan (Trichoptera: Leptoceridae). 1. Introduction and subgenus *Triaenodella* Mosely. *Tidschrift voor Entomologie*, 144, 225–246.
<https://doi.org/10.1163/22119434-900000088>
- Andersen, T. & Holzenthal, R.W. (2002) West African *Triaenodes* McLachlan (Trichoptera: Leptoceridae). 2. Subgenus *Triaenodes sensu stricto*. *Tidschrift voor Entomologie*, 145, 61–88.
<https://doi.org/10.1163/22119434-900000100>
- Banks, N. (1907) Descriptions of new Trichoptera. *Proceedings of the Entomological Society of Washington*, 8 (3 & 4), 117–133, pls. 8–9.
- Felsenstein (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution*, 17, 368–376.
<https://doi.org/10.1007/BF01734359>
- Folmer, R.H.A., Nilges, M., Folkers, P.J. M., Konings, R.N.H. & Hilbers, C.W. (1994) A model of the complex between single-stranded DNA and the single-stranded DNA binding protein encoded by gene V of filamentous bacteriophage M13. *Journal of Molecular Biology*, 240 (4), 341–357.
<https://doi.org/10.1006/jmbi.1994.1449>
- Holzenthal, R. W. & Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa*, 511 (1), 1–80.
<https://doi.org/10.11646/zootaxa.511.1.1>
- Holzenthal, R.W. & Calor, A.R. (2017) Catalog of the Neotropical Trichoptera (Caddisflies). *ZooKeys*, 654, 1–566.
<https://doi.org/10.3897/zookeys.654.9516>
- Houghton, D.C., DeWalt, R.E., Pytel, A.J., Brandin, C.M., Rogers, S.E., Ruiter, D.E., Bright, E., Hudson, P.L. & Armitage, B.J. (2018). Updated checklist of the Michigan (USA) caddisflies, with regional and habitat affinities. *ZooKeys*, 730, 55–72.
<https://doi.org/10.3897/zookeys.730.21776>
- Hur, J-M. (2006) *World Revision of the genus Triaenodes (Trichoptera: Leptoceridae)*. Unpublished Ph.D. Dissertation, Clemson University, Clemson, South Carolina, 455 pp.

- Kalaninová, D., Bulánková, E. & Šporka, F. (2014) Caddisflies (Trichoptera) as good indicators of environmental stress in mountain lotic ecosystems. *Biologia*, 69, 1030–1045.
<https://doi.org/10.2478/s11756-014-0405-5>
- Kato, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular biology and evolution*, 30 (4), 772–780.
<https://doi.org/10.1093/molbev/mst010>
- Kozlov, A.M., Darriba, D., Flouri, T., Morel, B. & Stamatakis, A. (2019) RAxML-NG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics*, 35 (21), 4453–4455.
<https://doi.org/10.1093/bioinformatics/btz305>
- Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33 (7), 1870–1874.
<https://doi.org/10.1093/molbev/msw054>
- Laudee, P., Malicky, H., Kong, C., Takenaka, M. & Tojo, K. (2023) New species of the genus *Trichosetodes* Ulmer, 1915 (Trichoptera, Leptoceridae) from Ratanakiri province, Cambodia, based on morphological and molecular data. *ZooKeys*, 1182, 153–164.
<https://doi.org/10.3897/zookeys.1182.105716>
- Malicky, H. (2005) Beiträge zur Kenntnis asiatischer *Triaenodes* McLachlan 1865 (Trichoptera, Leptoceridae). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, 57 (1 & 2), 33–46.
- Malicky, H. (2006) Beiträge zur Kenntnis asiatischer Leptoceridae (Trichoptera: *Adicella*, *Athripsodes*, *Ceraclea*, *Leptocerus*, *Oecetis*, *Parasetodes*, *Tagalopsyche*, *Triaenodes*, *Trichosetodes*). *Linzer Biologische Beiträge*, 38 (2), 1507–1530.
- Malicky, H. (2010) *Atlas of Southeast Asian Trichoptera*. Biology Department, Science Faculty, Chiang Mai University, Chiang Mai.
- Malicky, H. & Prommi, T.-o. (2006) Beschreibungen einiger Köcherfliegen aus Süd-Thailand (Trichoptera) (Arbeit Nr. 42 über thailändische Köcherfliegen). *Linzer Biologische Beiträge*, 38 (2), 1591–1608.
- Manuel, K.L. (2010) *Longhorn Caddisfly Genus Triaenodes in North America*. The Caddis Press, Columbus, Ohio, vi + 109 pp.
- Manuel, K.L. & Braatz, D.A. (1984) The life cycle and fifth instar larval description of *Triaenodes taenia* (Leptoceridae). In: Morse, J.C. (Ed.), *Proceedings of the 4th International Symposium on Trichoptera, Clemson, South Carolina, 11–16 July 1983*, pp. 213–217.
- McLachlan, R. (1877) *A Monographic Revision and Synopsis of the Trichoptera of the European Fauna. Part 6*. John van Voorst, London, pp. 281–348, plates 32–37.
- Morse, J.C. (2004) Insecta: Trichoptera. In: Yule, C.M. & Yong, H.S. (Eds.), *Freshwater Invertebrates of the Malaysian Region*. Academy of Sciences Malaysia, pp. 501–539.
- Morse, J.C. (2024) *Trichoptera World Checklist*. Available from: <https://trichopt.app.clemson.edu/> (accessed 17 October 2024)
- Navás, L. (1916) Neurópteros Sudamericanos. Tercera Série. *Brotéria*, Série Zoológica, 14, 14–35.
- Neboiss, A. & Wells, A. (1997) Australian *Triaenodes* species: An overview. In: Holzenthal, R.W. & Flint, O.S. Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera, Minneapolis and Lake Itasca, Minnesota, U.S.A., 9–15 August 1995*, pp. 373–378.
- Neboiss, A. & Wells, A. (1998) Review of Australian species of *Triaenodes* McLachlan (Trichoptera: Leptoceridae). *Memoirs of the Museum of Victoria*, 57 (1), 89–132.
<https://doi.org/10.24199/j.mmv.1998.57.06>
- Neu, P.J., Malicky, H., Graf, W. & Schmidt-Kloiber, A. (2018) *Distribution Atlas of European Trichoptera*. Conchbooks, Harxheim, 891 pp.
- Pes, A.M., Holzenthal, R.W., Sganga, J.V., Santos, A.P.M., Barcelos-Silva, P. & Camargos, L.M. (2018) Order Trichoptera. In: Hamada, N., Thorp, J.H. & Rogers, D.C. (Eds.), *Keys to Neotropical Hexapoda: Thorp and Covich's Freshwater Invertebrates. Vol. III*. Elsevier: Academic Press, London, San Diego, Cambridge and Oxford, pp. 237–324.
<https://doi.org/10.1016/B978-0-12-804223-6.00010-X>
- Schmid, F. (1965) Quelques trichoptères de Chine II. *Bonner Zoologische Beiträge*, 16 (1 & 2), 127–154.
- Schmid, F. (1994) Le genre *Triaenodes* McLachlan en Inde (Trichoptera, Leptoceridae). *Faberies*, 19 (1), 1–11.
- St Clair, R. (1994) Some larval Leptoceridae (Trichoptera) from south-eastern Australia. *Records of the Australian Museum*, 46, 171–226.
<https://doi.org/10.3853/j.0067-1975.46.1994.13>
- Suwannarat, N., Malicky, H. & Laudee, P. (2020) Four new species of caddisflies (Trichoptera: Polycentropodidae, Psychomyiidae, Hydropsychidae, Odontoceridae) from Khao Nan and Tai rom Yen National Parks, southern Thailand. *Zootaxa*, 4801 (3), 577–583.
<https://doi.org/10.11646/zootaxa.4801.3.10>
- Tagliacollo, V.A., Dagosta, F.C.P., Pinna, M.D., Reis, R.E. & Albert, J.S. (2021) Assessing extinction risk from geographic distribution data in Neotropical freshwater fishes. *Neotropical Ichthyology*, 19, e210079.
<https://doi.org/10.1590/1982-0224-2021-0079>
- Takenaka, M., Hasebe, Y., Yano, K., Okamoto, S., Tojo, K., Seki, M., Sekiguchi, S., Jitsumasa, T., Morohashi, N., Handa, Y. & Sakaba, T. (2024) Environmental DNA metabarcoding on aquatic insects: Comparing the primer sets of MtInsects-16S based on the mtDNA 16S and general marker based on the mtDNA COI region. *Environmental DNA*, 6 (4), e588.

<https://doi.org/10.1002/edn3.588>

Ulmer, G. (1908) Japanische Trichopteren. *Deutsche Entomologische Zeitschrift*, 1908, 330–355.

<https://doi.org/10.1002/mmnd.48019080304>

Wiggins, G.B. (1996) *Larvae of the North American Caddisfly Genera (Trichoptera), Second Edition*. University of Toronto Press, Toronto, 472 pp.

<https://doi.org/10.3138/9781442623606>

Wiggins, G.B. (2004) *Caddisflies: The Underwater Architects*. University of Toronto Press, Toronto, 304 pp.

<https://doi.org/10.3138/9781442623590>

Yang, L. & Morse, J.C. (1993) Phylogenetic outline of Triaenodini (Trichoptera: Leptoceridae). In: Otto, C. (Ed.), *Proceedings of the Seventh International Symposium on Trichoptera, Umeå, Sweden, 3–8 August 1992*, pp. 161–167.

Yang, L.-F. & Morse, J.C. (2000) Leptoceridae (Trichoptera) of the People's Republic of China. *Memoires of the American Entomological Institute*, 55, i–viii + 1–309.