The nymph of *Atopopus tarsalis* Eaton, 1881 (Ephemeroptera, Heptageniidae): first description, ecology and behaviour

MICHEL SARTORI¹, PASCALE DERLETH¹ & J. M. WEBB²

¹Museum of zoology, Palais de Rumine, Place Riponne 6, CH-1014 Lausanne, Switzerland.
E-mail: michel.sartori@vd.ch, pascale.derleth@vd.ch
²Department of Entomology, Purdue University, West Lafayette, Indiana 47907-2089, USA. E-mail: jmw975@yahoo.com

Abstract

The nymph of *Atopopus tarsalis* Eaton, 1881, type species of the genus, is described in detail for the first time. The egg stage is also presented. Endemic to Borneo, *A. tarsalis* nymphs exhibit a peculiar behaviour, being able to climb boulders and stay out of the water for periods of at least 20 minutes without dehydration. Hypotheses for such behaviour are briefly discussed such as drift and predation avoidance.

Key words: Borneo, nymph, egg, first description, behaviour, dehydration

Introduction

The genus *Atopopus* Eaton was proposed by Eaton for an unusual heptageniid species from Borneo (Eaton 1881). The male imago of *A. tarsalis* Eaton presents tarsi much longer than the tibiae on all legs, but especially on the hind ones. This species was described from Labuan, an island (Wilayah Persekutuan Labuan) located some miles off the shores of Sabah (Malaysia). Later, another species was described under the name *A. tibialis* Ulmer from the Philippines (Ulmer 1920), based also on male imagos. The species described under the name *Atopopus spadix* Harker (Harker 1950) from Australia is in fact most probably a member of the family Leptophlebiidae (Hubbard & Campbell 1996). A third species, *A. edmundsi* Wang & McCafferty, was described from Sabah by Wang and McCafferty (1995) who also provide the first account of the nymph of the genus with the description of those of *A. tibialis* and *A. edmundsi*. In his recent monograph, Kluge partly illustrated the nymph of *A. tarsalis* (Kluge 2004, fig. 59A). Finally, *A. meyi* Braasch was recently described in the imaginal and larval stages from material collected in the Philippines (Braasch 2005).

Herein, we describe the nymph of the type species of the genus, *Atopopus tarsalis*, based on abundant material collected in East Kalimantan (Indonesia) during the PhD thesis of the second author (Derleth 2003). The first description of the eggs is also presented. Moreover, information on the ecological requirements of this species, as well as its very unusual behaviour is also presented.

Description

*Atopopus tarsalis* Eaton, 1881

Nymph. Size: male, body length up to 12.3 mm, cerci length up to 14.8 mm; female, body length up to 14.9 mm, cerci length up to 15.5 mm.
Head: Broader than the pronotum, antennae short, at most reaching the margin of the cephalic capsule. Hind margin smoothly concave, lateral emargination behind the eyes strongly developed (Fig. 1). Fore margin above the labrum thickened.

FIGURES 1–10. *Atopopus tarsalis* nymph. Fig. 1: shape of the head; Fig. 2: labrum in ventral view; Fig. 3: left mandible; Fig. 4: right mandible; Fig. 5: dentisetae on the inner margin of the galea-lacinia (pd: proximal dentiseta; dd: distal dentiseta); Fig. 6: left side of the hypopharynx (ventral view); Fig. 7: outline of the fore leg; Fig. 8: lateral expansions of abdominal segments 2–8 (ventral view); Fig. 9: gill I; Fig. 10: gill IV.
Labrum expanded laterally, about 5 times broader than long, slightly bent backwards (Fig. 2). Anterior margin with a V-shaped incision densely covered with long and thin setae. Ventral surface with submarginal row of stout setae arranged in V-shape.

Mandibles slender and elongated, outer margin densely and regularly covered with long setae. Left mandible with well developed inner incisor; outer incisor serrated on its entire inner face; tuft of 5–7 somewhat plumose setae below the inner incisor; 3–5 hair-like setae below the mola (Fig. 3). Right mandible with shorter inner incisor, ending with two setae-like teeth; outer incisor serrate on its inner face, except the apical fourth; tuft of 7–9 plumose setae below the inner incisor; tuft of numerous, short setae above the mola, and a row of 7–9 hair-like setae below it; mola ending posteriorly with a hook (Fig. 4).

Ventral surface of the galea-lacinia covered with scattered simple setae; proximal dentiseta forked near apex; distal dentiseta composed of a bunch of forked and simple setae (Fig. 5); crown of the galea-lacinia covered with 15–19 comb-shape setae, the median ones composed of ca 10–12 teeth; first segment of the maxillary palp with numerous long setae on its outer margin, and with scattered and thinner setae on its inner one.

Lingua of hypopharynx thick and with a tuft of setae apically; superlingua well developed, outer margin folded one or two times, apex pointed and strongly bent backwards (Fig. 6).

Labium with glossae widely separated by a large and angular emargination; inner face of glossae covered with long setae; paraglossae extended laterally, with rounded apex and slightly turned backwards.

Thorax: Lateral margin of the pronotum rounded, without postero-lateral expansions; posterior margin slightly concave.

Legs unusually short and stout; ratio length/width of the fore, middle and hind femora ca 2.0, and ratio femur/tibia lengths ca 1.3 (Fig. 7). Dorsal margin of femora covered with long and stout setae, ventral margin with scattered small spine-like setae, increasing in number from the fore- to the hind femora; upper face covered with numerous small spine-like setae, rounded at the apex, slightly longer than wide. Dorsal margin of tibiae covered with long and thin setae, ventral margin with few spine-like setae. Tarsi with dorsal margin covered with long and thin setae, except the fore tarsi which bear only minute thin setae. Presence of a well developed spine-like seta on the ventro-distal part of the hind tarsi. Tarsal claws without apical denticle.

Abdomen: Colour pattern very characteristic and as in Fig. 11. Abdominal sternite I with lateral sclerites quadratic to pentagonal, and reaching almost the posterior margin. Postero-lateral extensions increasing in size from sternite II to VIII (Fig. 8).

Gills present on segments I–VII. Gill I attached dorsally and composed of a well developed tuft of fibrillae and a minute, almost invisible lamella (Fig. 9). Gills II–VI alike, attached laterally and composed of a lamella with well marked tracheation, and a tuft of purple fibrillae (Fig. 10). Gill VII with a well developed lamella but without fibrillae. All lamellae with some kind of strengthening subparallel to the outer margin.

Posterior margin of the sternite IX of female nymphs slightly concave.

Cerci and well developed terminal filament with whorls of spine-like setae, without hair-like setae.

Egg. Shape ovoid, ca 110 μm x 75 μm (Fig. 13). Chorionic surface covered with small granulations (ca 1 μm in diameter), as well as with medium size knob-terminated coiled threads (KCT’s) approximately 2–3 μm in diameter. Two polar caps with numerous KCT’s of the same size as those on the other part of the chorion. Four micropyles situated in the equatorial area; margin of the micropyle with irregularly placed granulations (Fig. 14).

Material examined. All the material listed below comes from the Island of Borneo and is deposited in the Museum of Zoology, Lausanne, Switzerland and in the Museum of Zoology, Bogor (LIPI), Indonesia.

INDONESIA, East Kalimantan: Malinau Basin
Rian River tributaries
Belakau, Langap Sud (1997-petak 6),116°30’26’’E, 3°04’04’’N, 13.06.2000 (B0110), Derleth, P., 10 nymphs; same locale but 05.07.2000 (B0111), Derleth, P., 7 nymphs; same locale but 20.04.2001, (B0113),
Derleth, P. & Sartori, M., 10 nymphs; same locale but 07.07.2000, (0121), Derleth, P., 10 nymphs; same locale but 18.04.2001 (B0123), Derleth, P. & Sartori, M., 10 nymphs

Ngayo, Langap Sud (1995), 116°31'11''E, 3°04'41''N, 14.06.2000 (B0410). Derleth, P., 5 nymphs; same locale but 08.07.2000, (B0411), Derleth, P., 12 nymphs;


**FIGURES 11–12. Atopus tarsalis** Fig. 11: abdominal pattern of three different nymphs; Fig. 12: wings pattern of the male imago.
**Seturan River tributaries**

Temalat (Sungai Guang), Seturan (1999-petak 39-40), 116°32'24"E, 3°00'10"N, 01.07.2000, (B0211), Derleth, P., 1 nymph; same locale but 27.03.2001, (B0213), Derleth, P., 2 nymphs;

Seturan River main stream, Bulungan camp, 116°30'36"E, 3°00'20"N, 13.07.2000, (B0431), Derleth, P., 12 nymphs

Tamulang, Seturan (2001-petak 57), 116°30'29"E, 2°59'22"N, 10.04.2001, (B0513), Derleth, P., 1 nymph;

Bengahau, Seturan (2001-petak 57), 116°30'46"E, 2°59'22"N, 08.08.2000, (B0531), Derleth, P., 2 nymphs; same locale but 11.04.2001, (B0533), Derleth, P. & Feldmeyer, B., 7 nymphs

Wok (Sungai Guang), Seturan (2000-petak 45), 116°33'29"E, 2°59'09"N, 16.06.2000, (B0611), Derleth, P. & Gattolliat, J.-L., 1 nymph;

Wok (Sungai Guang), Seturan (2000-petak 45), 116°33'30"E, 2°59'11"N, 29.06.2000, (B0631), Derleth, P., 11 nymphs

Wok (Sungai Guang), Seturan (2000-petak 44-45), 116°33'11"E, 2°59'12"N, 17.06.2000, (B0711), Derleth, P. & Gattolliat, J.-L., 8 nymphs; same locale but 05.04.2001, (B0713), Derleth, P. & Feldmeyer, B., 29 nymphs;


Unnamed tributary, Seturan (unexploited), 116°33'29"E, 2°58'54"N, 24.04.2001, (B1413), Derleth, P., Sartori, M. & Feldmeyer, B., 1 male imago, 8 nymphs;


MALAYSIA — **Sabah**: Penampang River, Crocker Range National Park, 15.08.2003, (B2001), M. Whiting’s lab., 5 nymphs.

**Figures 13–14.** *Atopopus tarsalis* egg. Fig. 12: general shape; Fig. 13: detail of the micropyle area.

**Affinities.** The nymphs of *A. tarsalis* are more similar to those of *A. edmundsi* than to those of *A. tibialis* or *A. meyi* based on the similarities in the number of comb-like setae on the galea-lacinia, the shape of the coxae and the shape of the 9th sternite of mature females. Based on the figures present by Wang and McCafferty (1995), there are distinct differences between *A. edmundsi* and *A. tarsalis* in the shape of the hypopharynx, the shape of the pronotum, the setation of the mandibles, and the relative size of the femora. In order to confirm these differences, we examined the type series of *A. edmundsi* and found that all of the differences indicated by the Wang and McCafferty (1995) figures are the result of inaccurate illustrations or poor speci-
mens. Their figure of the hypopharynx does accurately represent the specimen from which it was drawn, but the specimen was killed in the process of moulting and the hypopharynx is distorted; we have also observed this distortion in mature larvae within large series of specimens that all have the typical posteriorly directed, sharply pointed lobes of the superlingua, so is it not likely a specific, but rather an artifact of moulting. In all examined characters, the paratype nymphs of *A. edmundsi* appear to be identical to those of *A. tarsalis*. Neither the association of the nymphs and adults of either *A. edmundsi* nor *A. tarsalis* was confirmed through rearing. We believe, however, that the nymph of *A. tarsalis* described herein is correctly associated with the adult as it was collected at essentially the same location as an adult male, whereas the nymphs and holotype male of *A. edmundsi* were collected from different locations. It is likely that the association made by Wang and McCafferty (1995) is incorrect and they inadvertently described the nymph of *A. tarsalis*.

The adult male of *A. edmundsi* appears to be a good species, and differs from males of *A. tarsalis* in having the first segment of the hind tarsus shorter than the hind tibia. Additionally, the fore wing is approximately 3.5 times longer than wide, whereas in *A. tarsalis* the fore wing is less than 3 times longer than wide (Fig. 12). The narrow hind wing described and illustrated by Wang and McCafferty (1995) is inaccurately drawn; the wing from which the drawing was made is folded, making it appear narrower than it actually is. The other hind wing of the holotype is not folded and has the same shape as those of *A. tarsalis*. The female subimago described by Wang and McCafferty (1995) as *A. edmundsi* has fore wings that are 2.8 times longer than wide, so is unlikely to actually be *A. edmundsi*. It is probable that this specimen is *A. tarsalis*, but because the female of *A. tarsalis* is unknown, we cannot confirm this. Until *A. edmundsi* becomes better known, the species concept should be restricted to that of the holotype.

**Distribution and ecology.** *Atopopus tarsalis* is endemic to Borneo and is herein reported for the first time from Indonesia (East Kalimantan) although its presence was expected, based on its occurrence in Malaysia (Sabah).

Nymphs of this species have been found in small to medium size streams as well as in rivers in lowland dipterocarp forests. The watercourses ranged from 0.5–15 m wide, 2–80 cm deep, had current speeds between 0.2–1.4 m/s and water temperatures between 23.8–26.5°C. Despite this wide range of habitats, *A. tarsalis* has been shown to be a sensitive species, mainly present in pristine habitats (reference sites “group green” according to Derleth 2003).

A striking characteristic of this species is that 94% of all specimens were collected during qualitative prospecting whereas only 6% were collected with a Surber net. Detailed field observations show that *A. tarsalis* microhabitats are not located in small to medium size substrata where quantitative samples have been performed, but rather on and around large rocks and boulders (see below).

No adults of *A. tarsalis* were collected in light traps at either dusk or at dawn. The single male imago was caught resting under a leaf in the forest around noon. Nuptial flight probably occurs during the afternoon.

**Behaviour.** Nymphs of *A. tarsalis* have been mainly found scraping periphyton on large boulders. They generally are located a few centimetres below the water surface and, when disturbed, they move like crabs around the stone and are difficult to catch. What seems unique, to our knowledge, is that *A. tarsalis* nymphs, when not disturbed, are frequently found on rocks above the water surface. They can be found up to 20 centimetres above the water surface and in some occasions they were found at the top of the rock. As soon as they are approached too closely, they return to the water.

As far as we know, this behaviour has never been reported for any mayfly nymph. A South American mayfly, *Cloedodes hydation* McCafferty & Lugo-Ortiz, 1995, a rock pool colonizer, has been reported to resist up to 9 hours out of the water (Nolte et al.1996). It seems to be an extreme adaptation to frequent drought in this peculiar habitat, and seems to be a passive behaviour. *A. tarsalis* behaviour is quite different since this species actively leaves the water and returns to it periodically, obviously to avoid dehydration. Our preliminary field observations, based on modest research facilities, indicate that *A. tarsalis* nymphs can spend up to 20 minutes out of the water, even in open streams and rivers with direct sunlight.
We have then to conclude that nymphs of *A. tarsalis* are able to retain a film of water around them to avoid complete dehydration. In that sense, the special shape of the head, with a thickened cephalic capsule, as well as the reinforcement of the gills may play a role in maintaining this water film and/or avoiding a total dehydration.

Reasons for this peculiar behaviour are not clear. Two hypotheses can be put forward. The first is that this behaviour allows *A. tarsalis* nymphs to avoid fish predation. The general behaviour of macroinvertebrates in the presence of carnivorous fishes is drifting (see e.g. Huhta *et al.* 1999; Huhta *et al.* 2000; McIntosh *et al.* 2002). This should be especially the case in rivers where fish composition is more diversified than in small streams (but see Melo & Froehlich 2004 for contrasting results). Climbing out of the water may be a less risky behaviour than drifting for avoiding predation for *A. tarsalis*.

Another hypothesis is that this behaviour may prevent *A. tarsalis* nymphs from being dislodged by the frequent and sudden spates that occur in the study area (pers. obs). When it is raining, the water level in streams and rivers increases rapidly, as do discharge and turbidity, inducing drift among macroinvertebrates and mayflies in peculiar (see e.g. Brittain & Eikeland 1988; Lancaster 1992).

But it is also possible that both hypotheses may be involved in this behaviour, as suggested by Dudgeon (1993). This will require complementary field studies in the future.

Finally it is worth mentioning that *A. tarsalis* is not the only mayfly that exhibits this behaviour. The baetid nymph *Platybaetis probus* Müller-Liebenau has been found generally together with *A. tarsalis* and is also frequently found above the water level. The morphological adaptation of this species will be discussed elsewhere.

**Acknowledgements**

Our sincere thanks are addressed to our partners in Indonesia who make this research possible: CIFOR (International Centre for Forestry Research, Bogor) for the field camp infrastructure on the study site in East Kalimantan, and LIPI (Lilik Priyono, Museum Zoology, Research and Development, Bogor) for permission, collection and exportation of the macroinvertebrates. Fieldwork and collecting in East Kalimantan was possible thanks to financial support from the ZIL (Swiss Center for International Agriculture) through a research fellow grant to P. Derleth. Jean-Luc Gattolliat (Lausanne) and Barbara Feldmeyer (Germany) offered precious help in the field. The SEM photographs have been taken by Geneviève L’Eplattenier (Lausanne) at the Electronic Microscopy Center of Lausanne University.

**References**


Australian Society of Limnology, Special Publication, 11, 1–43.
McIntosh A.R., Peckarsky B.L. & Taylor B.W. (2002). The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. Freshwater Biology, 47(8), 1497–1513.