Received 01 July 2010; revised and accepted 13 July 2010

The larva of *Tetracanthagyna plagiata*, with notes on its biology and comparisons with congeneric species (Odonata: Aeshnidae)

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Key words: Odonata, dragonfly, Anisoptera, Aeshnidae, *Tetracanthagyna*, *plagiata*, Singapore, Sundaland, larva.

Abstract

The F stadium larva of both sexes of *Tetracanthagyna plagiata* is described and figured based on exuviae from which confirmed adult specimens had been reared. Larvae were originally collected in small, slow forest streams in Singapore, and in captivity were fed on local shrimp and small fish species. The known larvae of *Tetracanthagyna* species, *T. degorsi*, *T. plagiata* and *T. waterhousei* are compared and characters for separating the three species are tabled and figured. *T. plagiata* larvae reared in captivity exhibited obligate ambush predation and ballistic defaecation.

Introduction

The genus *Tetracanthagyna* Selys, 1883, includes some of the largest of all Odonata. *T. plagiata* (Waterhouse, 1877) is generally considered the heaviest living odonate (Tillyard 1917) and in wingspan the female is exceeded only by the slightly built, giant, neotropical zygopteran, *Megaloprepus coerulatus* (Drury, 1782) of the Pseudostigmatidae (Wilson 2009). The genus includes just five species and is centred on Sundaland, with up to four species occurring in parts of Borneo, namely: *T. brunnea* McLachlan, 1898, *T. degorsi* Martin, 1895, *T. plagiata* and *T. waterhousei* McLachlan, 1898 (Lieftinck 1954; Orr 2003). Elsewhere, *T. waterhousei* is widely distributed in tropical Asia from Bengal in the west (Fraser 1936) to Hong Kong (Wilson 1995) in the east. *T. bakeri* Campion in Campion & Laidlaw, 1928, is known only from the Philippines (Hämäläinen & Müller 1997).

The larvae of *T. degorsi* and *T. waterhousei* have been known for many years. That of *T. degorsi* was recorded by Lieftinck (1954), with its habits briefly noted, and a drawing of the habitus from Lieftinck's archives was published by Corbet (1999: 151). Larvae were also reared in Brunei by Orr (2001), who described the larva, its habitat, and behaviour. Larvae were observed perching nocturnally with much of the body out of the water and only the head submerged, capturing surface swimming fish. The larva of *T. waterhousei*, was described in detail by Matsuki (1988), who compared Hong Kong and Thai specimens. Wilson (1995: 100) also published a spectacular photograph of a *T. waterhousei* larva catching fish. From these sources it is clear that the general form of the larvae of these two species is similar, with short, strong, thigmotactic legs, angular sculpturing on the head and a thin abdomen, becoming triangular in cross-section caudally. The form of the labial palps is unlike that of any other aeshnid larva, being produced into a sharp hook with serrate inner margin. Compared with other large aeshnids, such as *Anax* spp., the F stadium larvae and exuviae are not remarkably large in relation to the adult size.

Occasionally, exuviae have been found, which, because of their large size and distinctive sculpturing on the head seemed very probably to belong to *T. plagiata* but this supposition could not be taken as certain. Recently however, RWJN succeeded in rearing a male and TML a female, both from advanced larvae collected from streams in the Central Catchment Nature Reserve, Singapore, where the insect is comparatively common (Leong & Tay 2009) and from where no other *Tetracanthagyna* species are known (Tang et al. 2010). In this paper we describe the larvae of both sexes of *T. plagiata*, compare its morphology with that of *T. degorsi* and *T. waterhousei* and discuss its ecology and behaviour.

Material and methods

Specimens of *Tetracanthagyna plagiata* were collected using a tray net, by searching streamside vegetation for exuviae and by sieving through dense stream leaf litter. The male larva (F-1) was found within the Macritchie Reservoir streams system while the female larva (F) was found in a clear, slow-flowing forest stream at Nee Soon swamp forest. Both locations are in the Central Catchment Nature Reserve, Singapore. The male larva was reared to emergence in a glass aquarium tank (60 x 40 x 40 cm), the substrate being small aquarium pebbles with a scattering of leaf litter. A large piece of wood was placed in the middle of the tank, partially submerged in water of about 6 cm depth. The female larva (Plate Ia) was reared in a plastic aquarium (30 x 20 x 20 cm), half-filled with water and provided with a substrate of dead leaves. Water was partially changed weekly but not aerated. A branch was positioned diagonally on which the larva perched. Both were fed mainly on a diet of shrimps, *Macrobrachium lanchesteri* and/or small fish. Tubifex worms, *Tubifex tubifex* were also offered to the male.

Specimens of *T. waterhousei* were collected as exuviae from streamside vegetation in Hong Kong. One male exuvia was obtained from streamside vegetation at Doi Suthep, near Chiang Mai, northern Thailand. Specimens of *T. degorsi* larvae were collected by searching along a small, shallow, forest stream at Bukit Patoi, Brunei, by torchlight, then bred to maturity in an open container and provided with small fish for food (see Orr 2001).

All specimens were examined as exuviae (except for one F stadium larva of *T. degorsi*) using a Leitz stereomicroscope with illustrations prepared with the aid of a drawing tube. Terminology used follows Watson & O'Farrell (1991).

Larva of *Tetracanthagyna plagiata*
(Figs 1, 2, 3b, f, g, 4b, e, Plate Ia)

Specimens examined

Tetracanthagyna plagiata: 1 ♂ exuvia (reared), collected as F-1 larva, 09 xi 2009, Singapore, stream along Sime Track within Macritchie Reservoir forest, RWJN leg., emerged 26 i 2010; 1 ♀ exuvia (reared), collected as F larva, 23 iii 2010, Singapore, Nee Soon swamp forest, in stream, H.H. Tan leg., emerged 20 iv 2010; 1 ♂ exuvia, Singapore, Nee Soon end stream, 27 vii 2008, H.B. Tang leg.

Other *Tetracanthagyna* species: *T. degorsi*: 1 ♂ F larva, collected as F-1 larva, Brunei, Bukit Patoi, stream, AGO leg.; 1 ♀ exuvia (reared), collected as F larva, same data as ♂. *T waterhousei*: 1 ♂ exuvia, Thailand, stream at Doi Suthep, near Chiang Mai, IV 2003, AGO leg.; 2 ♀ exuviae, Hong Kong, one Hock Tau stream, 23 iv 2003, the other without further data, both G.T. Reels leg.

Diagnosis

A large, elongate aeshnid larva, with a generally angular outline and distinctive, pronounced, sculpturing on head, thorax and abdomen (Fig. 1a). Generally dark in colour with some banding on legs. Posterior segments of abdomen triangular in section. Legs short and robust, adapted for grasping. At rest upper surface of head strongly depressed so as to form an angle of ca 40° to the substrate (Fig. 1c). Mask with prementum robust and expanded distally with labial palps thin and hook-like, serrate along their inner margins.

Description

Head: In dorsal view foreshortened due to the upper surface from the clypeus to the hind margin being slanted forward at an angle of ca 40° to the horizontal, resulting in the head without the mask being roughly triangular in profile (Fig. 1c);

from a dorsal perspective the head is approximately rectangular in outline (Fig. 1a), with heavy sculpturing on the upper margins of the postocular lobes and ventrally with two stout processes at each posterior corner, slightly hooked forward. When seen from a strictly orthogonal viewpoint from above, the head has a roughly

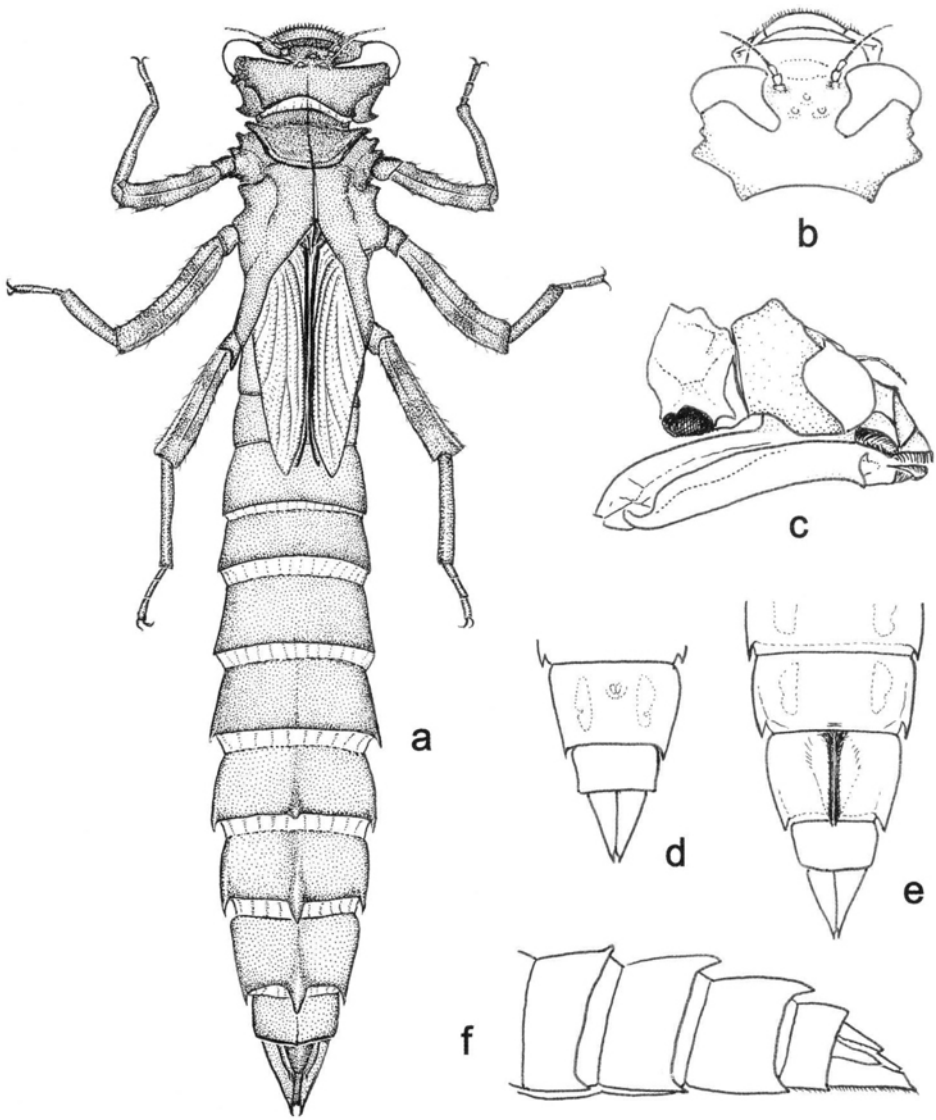

Figure 1: *Tetracanthagyna plagiata* exuvia — (a) ♂ habitus, dorsal view; (b) ♂ dorsum of head from orthogonal viewpoint; (c) ♂ prothorax and head in profile; (d) ♂ abdomen S9-10 and appendages, ventral view; (e) ♀ abdomen S8-10 and appendages, ventral view; (f) ♂ abdomen S7-10 and appendages, lateral view.

pentangular outline (Fig. 1b). Labrum with dense, moderately long fringing setae. Postclypeus and anteclypeus well defined and delineated by a distinct ridge, with the postclypeus slanted more abruptly downward at an obtuse angle to the anteclypeus. Frons and vertex marked by slight depressions and dimples respectively and forming an almost continuous surface with a broad, shallowly concave postocular region. Laterally the postocular area is produced to form broad flanges on either side, each with one small blunt marginal tubercle somewhat posterior to the eye, a large elevated, flattened, subacute, marginal process about halfway between the eye and the hind margin of the head and a similar, somewhat lower process at the hind margin (Figs 1b, c, 3b). Antennae 7-segmented; first two segments ca 2.5-3x as wide as remaining five, which taper slightly towards final segment. Eyes moderately large, primarily directed forward. Mask with prementum stout and strongly expanded distally (Figs 2a, 3f); terminal lobes slightly rounded with fringe of dense, short, brush-like setae; distally lateral margins of prementum with forward pointing recurved teeth, interspersed with a few conical setae. Labial palp short and stout at base, terminating in a strong, sharp terminal hook bearing subquadrate serrations along its inner margin (Fig. 2b). Movable hook strong and stout. Ventrally distal corners of prementum and outer surface of labial palp bear dense patches of short, mainly stout setae (Fig. 2b). In profile prementum distally curved sharply downwards (Fig. 3g). Mandibles robust, outer margin in dorsal

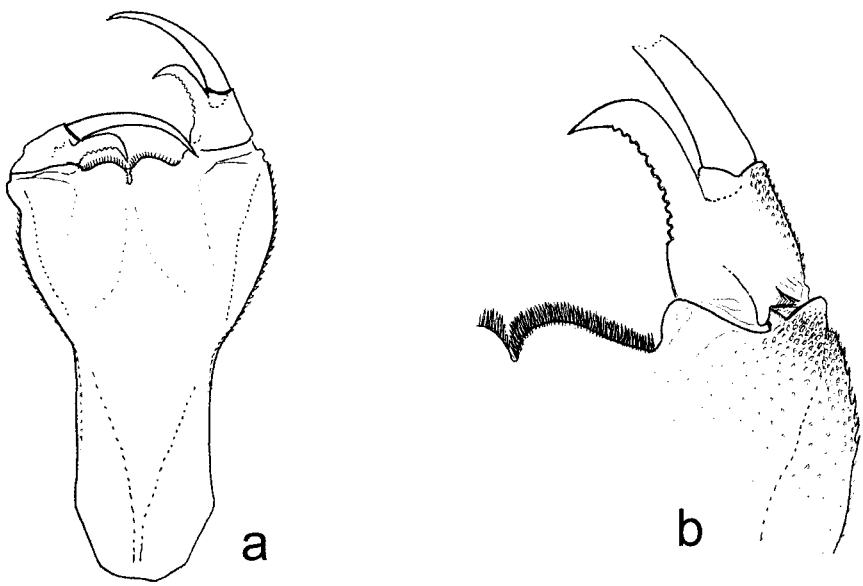

Figure 2: *Tetracanthagyna plagiata* ♂ exuvia — (a) prementum and labial palps, dorsal view; (b) detail of same, ventral view, showing concentration of short setae on outer angle of prementum and outer surface of labial palp.

view forming nearly a right angle, with a slight protuberance at the apex, covered with dense, short, stout setae similar to those on exposed outer surfaces of mask.
Thorax: Generally with heavy, angular sculpturing. Pronotum shield-shaped, shallowly rounded posteriorly with strong lateral processes; laterally prothorax with two well developed paired processes overlapping coxae. Mesothorax with broad paired flanges laterally, immediately anterior to point of insertion of coxae. Metathorax lightly sculptured. Legs short and robust; femora flattened; with indistinct spines on prothoracic femora and distinct keels on upper edge of meso- and metathoracic femora; all with sparse marginal setae.
Abdomen: Long and thin; S1-6 dorsally arch shaped in section tending to triangular in section in S7-10. Lateral spines present at hind margins of S6-9; strongly developed backward pointing mid-dorsal spines at hind margin of S8 and S9; weaker but distinct spine on S7, more prominent in female but present in both sexes (Figs 1f, 4b). S10 with strong dorsal carina but almost no rearward projection of hind margin to form a blunt spine. Anal pyramid comparatively long;

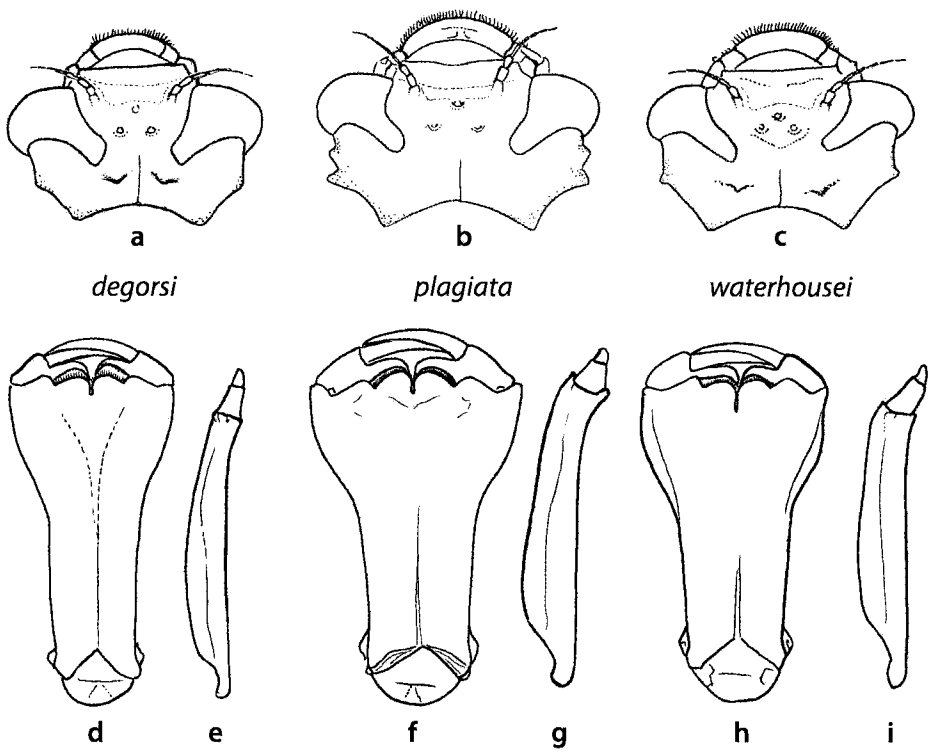

Figure 3: Female exuviae of three *Tetracanthagyna* species, head in dorsal orthogonal view (a-c) and mask in ventral and lateral view (d-i) — (a, d, e) *T. degorsi*; (b, f, g) *T. plagiata*; (c, h, i) *T. waterhousei*.

ca 1.6x length of S10 (Figs 1f, 4b). Paraprocts robust (Figs 1f, 4e), laterally flattened with lightly toothed edges, especially along upper margin, with thin finger-like process distally; lower margin with dense, moderately long setae. Epiproct distinctly serrate above; distinctly shorter than paraprocts. Cerci ca 1/2 length of paraprocts (male) to 1/3 length of paraprocts (female, Fig. 4b). Gonapophyses absent in male (Fig. 1d), which bears a small, paired, central genital scar towards the base of the sternum in S9; in female (Fig. 1e) gonapophyses extend for full length of sternum of S9 and slightly overlap S10.

Comparative notes

Head: The head of *T. plagiata* is generally more angular than that of *T. degorsi* or *T. waterhousei*. However the clearest distinction between the three species may be seen from an orthogonal view of the upper surface of the head. Lateral flanges of the postocular lobes are relatively broadest in *T. plagiata*, with processes more strongly developed (Fig. 3b). The small process on the lateral margin of the postocular lobe immediately behind the eye is present only in *T. plagiata*. *T. plagiata* lacks small paired tubercles on the upper surface of the postocular area. The postocular flanges are more strongly developed in *T. waterhousei* (Fig. 3c) than in *T. degorsi* (Fig. 3a), which has a relatively narrower, more rounded head seen from above from an orthogonal perspective. The prementum of *T. plagiata* appears distally very broad in ventral view (Fig. 3f), accommodating commensurately heavier labial palps, and is strongly down-turned apically seen in profile (Fig. 3g). The prementum of *T. waterhousei* in ventral view (Fig. 3h) is somewhat lighter and

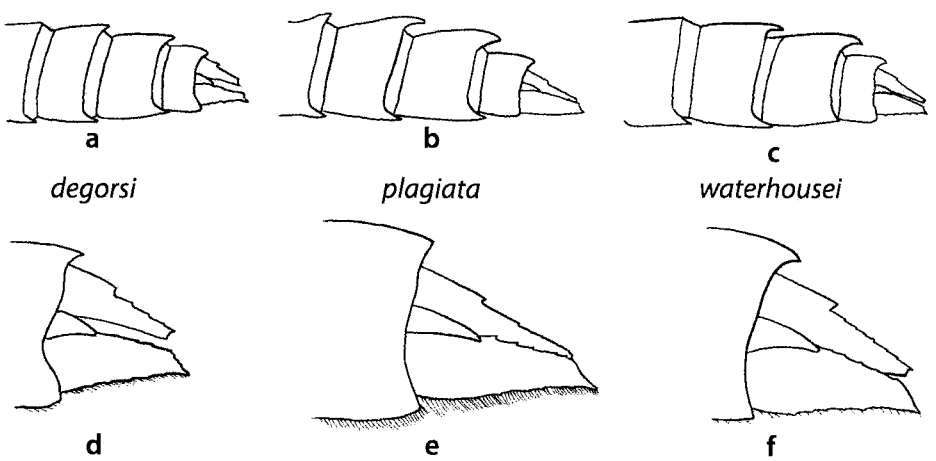

Figure 4: Female exuviae of three *Tetracanthagyna* species, S7-10 and anal pyramid in profile (a-c) and detail of ♀ anal pyramid (d-f) — (a, d) *T. degorsi*; (b, e) *T. plagiata*; (c, f) *T. waterhousei*.

less expanded distally, whereas that of *T. degorsi* (Fig. 3d) is only slightly expanded distally and is overall relatively gracile. In neither *T. degorsi* nor *T. waterhousei* is the prementum down-turned apically in profile (Figs 3e, i). The outer angle of the mandible is more acute in *T. plagiata* than in either *T. degorsi* or *T. waterhousei*, where it is more rounded, and the entire mandible is relatively longer than in the other species.

Abdomen: In *T. plagiata* there is a small middorsal spine at the hind margin of S7 (Figs 1f, 4b) that is lacking in *T. degorsi* (Fig. 4a) and *T. waterhousei* (Fig. 4c). The spines at the hind margin of S8-9 are very strongly developed in both *T. plagiata* (Figs 1f, 4b) and *T. waterhousei* (Fig. 4c). The dorsal carina of S10 is strongly produced mid-dorsally to form a spine at the hind margin in *T. waterhousei* (Fig. 4f), moderately so in *T. degorsi* (Fig. 4d) and virtually not at all in *T. plagiata* (Fig. 4e). The anal pyramid is proportionally longer and narrower in *T. plagiata* than in the other two species, being ca 1.65x the length of S10; in *T degorsi* and *T. waterhousei* this ratio is ca 1.5. In *T. plagiata* ventrolateral margins of the paraprocts are only slightly serrate and bear dense setae; In *T. degorsi* the ventrolateral margin of the paraprocts is distinctly serrate with a moderate density of setae, whereas in *T. waterhousei* these setae are sparse. In *T. degorsi* the cercus in the female is ca 0.33 the length of the paraproct, whereas in *T. plagiata* and *T. waterhousei* the cercus in the female is ca 0.4x the length of the paraproct. In males these ratios are ca 0.4 and 0.55 respectively.

Measurements [mm]: *T. plagiata* male exuvia, total length 57.5 (both specimens); female exuvia, total length 62 mm. *T. waterhousei* male exuvia, total length 54; female exuviae, total length 55-57. *T degorsi* female exuvia, total length 51.5. Although probably not completely reliable, size of exuviae is likely to provide a useful guide to separating these species.

Major diagnostic differences separating the three species are summarised in Table 1.

Biological notes on *Tetracanthagyna plagiata* larva

Habitat

The male larva was found in a slow flowing forest stream of ca 1 m width and 0.6 m depth with a mixed sandy mud substrate. The stream was filled with debris such as leaf litter and fallen branches. The surrounding vegetation was mature secondary forest. The female larva was found in a similar habitat. The stream was ca 1 m wide, 0.7 m deep with lush fringing vegetation, overgrown with ferns, grasses and sedges, partially shaded by mature trees growing along banks. The substrate was sandy with some detritus. At the site where the male larva was col-

Table 1. Diagnostic characters which separate F larvae and exuviae of *Tetracanthagyna degorsi*, *T. plagiata* and *T. waterhousei*.

Characters	*T. degorsi*	*T. plagiata*	*T. waterhousei*
Postocular lobes in orthogonal view	Lateral flanges narrow; two marginal processes poorly developed; dorsally two small tubercles in postocular area	Broad lateral flanges; three strong marginal processes; dorsally postocular area smooth	Lateral flanges moderately broad; two angular marginal processes; dorsally two small tubercles in postocular area
Prementum	Distally little expanded in ventral view; long and narrow; not down-turned in profile	Distally strongly expanded in ventral view and sharply down-turned in profile	Distally moderately expanded in ventral view; not down-turned in profile
Abdomen S7	No mid-dorsal spine	Small mid-dorsal spine at hind margin	No mid-dorsal spine
Abdomen S8-9	Moderately developed mid-dorsal spines at hind margin	Very strong mid-dorsal spines at hind margin	Very strong mid-dorsal spines at hind margin
Abdomen S10	Mid-dorsal carina moderately produced at hind margin to form a short spine	Mid-dorsal carina scarcely produced at hind margin	Mid-dorsal carina strongly produced at hind margin to form a spine
Anal pyramid	Shorter and broader at base; ca 1.5x length of S10	Long and narrow at base; ca 1.65x length of S10	Shorter and broader at base; ca 1.5x length of S10
Cercus	Ca 0.33x length of paraproct in female; ca 0.4x in male	Ca 0.4x length of paraproct in female; ca 0.55x in male	Ca 0.4x length of paraproct in female; ca 0.55x in male

lected, shrimps of the species *Macrobrachium trompii* and *Caridina temasek* were collected. We can assume that these two species form part of the larval diet.

Behaviour in captivity

As an F-1 stadium, the male larva spent much of the time grasping its wooden perch, head facing downwards with body held close to wood. It remained almost entirely submerged with only the tip of its abdomen just touching the water surface. It remained motionless in this ambush stance for long periods. Prey were

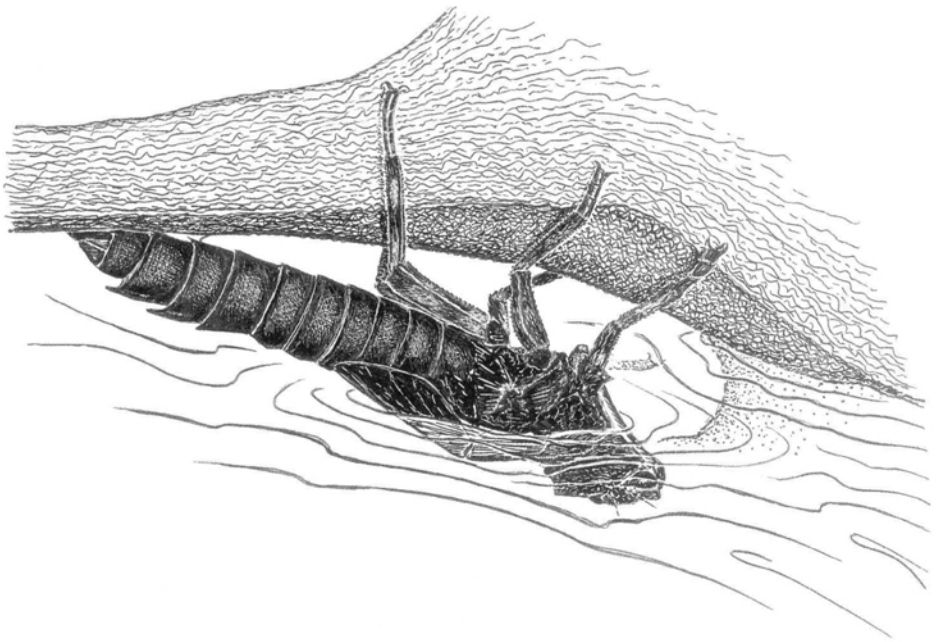

Figure 5: *Tetracanthagyna plagiata*, ♂ F stadium larva in ambush position, head just submerged.

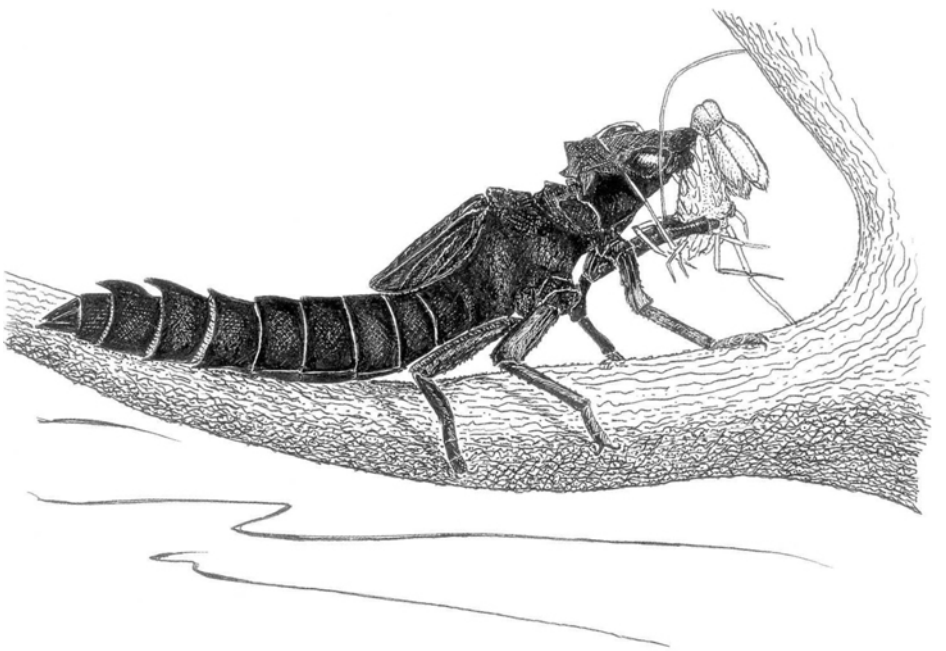

Figure 6: *Tetracanthagyna plagiata*, ♂ F stadium larva emerged from the water to handle and consume a shrimp.

only ever taken when they were offered or approached within striking range. Faeces were projected out of the water, adhering around the top of the glass tank. The larva moulted to the F stadium between 20 and 30 November 2009, two to three weeks after capture. As an F stadium larva, it still maintained the head down ambush tactic but was less sedentary with the body sometimes raised (Fig. 5). It was most successful in capturing prey when presented with shrimps. It would make deliberate slow movements towards a nearby shrimp before initiating a labial strike. The strikes were very forceful, so that the crushing sound of the shrimp's exoskeleton could sometimes be heard. Once the prey was captured, the larva would move rapidly and completely out of the water to consume it (Fig. 6). If the shrimp was of large size, the larva did not ingest it immediately but instead held it for five to ten minutes before consumption.

When not in ambush mode, the larva sometimes remained completely out of water, resting on a horizontal branch of the wood. When approached too close by an observer, it would rapidly swivel to the other side of the branch thus hiding itself from the observer. The last observed feeding was ca 15 days before emergence. After this time, it rested facing upwards, its body half to one-third submerged in water. Emergence took place in the early hours of 26 November 2010. When observed at 07:30 h, the adult was already fully emerged although the wings were yet to open. The total time spent in the F stadium was between 37 and 47 days.

When initially collected in the tray net, the female specimen exhibited thanatosis. Otherwise it behaved similarly to the male F stadium larva, predominantly facing head downwards, with the body either fully or partially submerged. Successful strikes underwater were quickly followed by turning around 180 degrees to climb out of water and consume the prey. Heads of fish were not consumed, but their vertebrae and associated bones were, as were the shells of freshwater shrimps. The following prey items were recorded: freshwater shrimp, *Macrobrachium* sp., halfbeak fish, *Dermogenys pusilla*, juvenile catfish, *Clarias* sp., frog, *Fejervarya cancrivora*. On 7 April 2010 it began to face upwards, with its abdomen partially submerged, but sometimes with its entire body out of water, and ceased feeding entirely. It emerged 13 days later in the morning.

Discussion

The specimens described here are the first confirmed exuviae of *Tetracanthagyna plagiata*. Although the F larva of *T. degorsi* was figured by Corbet (1999: 151) and more fully described by Orr (2001), both were slightly misleading regarding the shape of the head, and, in the latter case, in need of correction regarding the relative dimensions of the anal appendages: Figure 4d shows the correct proportions of the epiproct and paraprocts in *T. degorsi*, shown incorrectly by Orr (2001). The descriptions of the larva of *T. waterhousei* published by Matsuki (1988), are in

complete agreement with observations made in this study, but the head was not figured in detail.

It is thus now possible to readily identify all three *Tetracanthagyna* species for which larvae are known. In view of the clear differences exhibited, it seems probable that the as yet unknown larvae of *T. brunnea*, which is sympatric with *T. plagiata* in West Malaysia, and with *T. degorsi*, *T. plagiata* and *T. waterhousei* in Borneo, will also possess clear diagnostic characters. *T. bakeri* is found widely in the Philippines, except Palawan where *T. brunnea* occurs (Hämäläinen & Müller 1997), and does not overlap with any other species. Its larva is presently unknown but may also be expected to show distinguishing characters.

The habitat observed for *T. plagiata* is quite similar to that recorded for *T. degorsi* (Lieftinck 1954; Orr 2001). Near to the site where the male larva was found was a fallen rotting log across the stream. Presumably this was where a female would oviposit as recorded by other observers from similar habitats (Watanabe 2003; Leong & Tay 2009).

In the forest streams where *T. plagiata* larvae have been found, diverse potential prey items abound. A number of small, surface visiting fish occur naturally, including catfish, cyprinids and halfbeaks. Tadpoles of a number of frog species may also surface to gulp air occasionally. Freshwater shrimps regularly cling to the surfaces of submerged or semi-submerged plant material along these streams. Feeding behaviour of *T. plagiata* in captivity suggests that all these may provide food under natural conditions. The hooked structure of the labial palps probably indicates specialisation to feeding on larger prey captured near the water surface. *T. plagiata* appears to be adapted to larger prey than its congeners, having proportionally more robust and broader mouthparts, as well as greater overall body size. It is the only species so far recorded as feeding on shrimps. Evidence from captive larvae suggests prey are detected visually, but it seems likely that in nature, the larvae may feed mainly at night, as reported by Orr (2001) for *T. degorsi*. If this is the case prey may also be detected by sensors receptive to pressure changes or vibration in the water. This may be the function of the dense setae around the external extremities of the mask and outer surface of the mandibles. These structures are not present in larvae of other large aeshnids such as *Anax* or *Indaeschna*. As they are also absent in *Dendroaeschna*, a genus considered close to *Tetracanthagyna* by both von Ellenrieder (2002) and Peters & Theischinger (2007), they may be unique to *Tetracanthagyna* within the family.

Unlike many other aeshnids, *Tetracanthagyna* larvae do not actively pursue prey, being apparently fully committed to sit and wait predation. As is common among such strategists, they exhibit pronounced crypsis, with angular outlines, dark colours and an overall stick-like appearance which, when they are perched half submerged, may help conceal them from predators and prey alike. It is also of interest that they exhibit ballistic defaecation. Corbet (2004) discussed this behaviour in the context of ambush predation, suggesting it may be a strategy to avoid

contaminating the water surrounding the ambush site with faecal material which could be detected by potential prey. As the prey of *Tetracanthagyna* are generally highly mobile, species of this genus might provide good subjects for experimental testing of Corbet's (2004) hypothesis, either in nature or under laboratory conditions.

Acknowledgements

We thank Sharon Chan, Debbie Lim and all colleagues from Central Nature Reserve branch of the National Parks Board for supporting and leading the streams surveys. Tang Hung Bun and Graham Reels kindly loaned the male *Tetracanthagyna plagiata* exuvia and *T. waterhousei* exuviae respectively. Matti Hämäläinen, Graham Reels and Günther Theischinger made very helpful suggestions on the text. To all we express our gratitude.

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