

An annotated checklist of the Odonata of Brunei with ecological notes and descriptions of hitherto unknown males and larvae

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Abstract

This study records 175 species of odonates from Brunei, representing more than half the known Bornean fauna. Of these, 169 species were collected by the author and associates using a systematic sampling protocol at 35 sites throughout the country. Sites were located in diverse habitats: in primary forest, natural lakes and marshes and degraded areas. Species richness and faunistic composition are discussed for all sites and the levels of similarity between sites is assessed on the basis of species and higher taxonomic level comparisons. Patterns of habitat utilization are assessed for higher taxonomic groupings. Notes on behaviour and ecology are provided for all species for which adequate information was available. The previously unknown males of *Pericnemis triangularis* and *Drepanosticta versicolor* comb. nov. and the larvae of *Tetracanthagyna degorsi* and *Onychothemis coccinea* are described and figured.

Introduction

Even within Sundaland the Bornean odonate fauna is exceptionally rich and probably comprises to comprise at least 300 species. It is certain that a significant number of known species are as yet undescribed and very probably many new species remain uncollected. Of the 280 named species, approximately 40% are endemic, in sharp contrast with other well known insect groups, such as butterflies, for which the faunas of Borneo, Sumatra and Peninsular Malaysia are essentially similar in species richness and composition (Corbet & Pendlebury 1992; Otsuka 1988; Seki et al. 1991a, 1991b). In Borneo, Anisoptera and Zygoptera are almost equally represented but much higher endemism is exhibited by Zygoptera (66%) than Anisoptera (22%) (Lieftinck 1954). Within the island there are probably several distinct faunistic sub-regions but these are at present difficult to define given our very incomplete knowledge of the distribution of many species. In rough terms, about 63% of species are widespread in the lowlands,

15% are known only from the south or east and 22% are recorded only from the north or north-west including about 3% which are strictly montane or sub-montane. Until recently very little was known of the Odonata of Brunei, an area straddling the northern and western regions. One aim of this study is to provide as comprehensive a national checklist as possible.

Unlike terrestrial insects, in which species richness may be very high in small areas of primary forest (e.g. Orr & Häuser 1996a, 1996b), tropical odonates tend to form highly circumscribed communities. Typically, assemblages of 15-30 species are associated with several distinct aquatic ecosystems occurring within the tropical rain forest and in degraded and cleared areas. Reports of high local diversity (Thompson & van Tol 1993, this study, Site 1, see below) are invariably associated with small scale heterogeneity in vegetation, topography and soils and correspondingly in aquatic habitats. The lowlands of Brunei, which occupy most of the country, contain five edaphic climax forest types, broadly defined as mixed dipterocarp, kerangas (or tropical heath), freshwater swamp forest, peat swamp forest and mangrove (Whitmore 1984; Cranbrook & Edwards 1994). Using this classification Thompson & van Tol (1993) discussed the relation between habitat and odonate communities on a very local scale. This study documents species-habitat associations on a broader geographic scale, including a variety of sub-categories within the vegetation types listed above. Clearly associations with forest type are probably more directly determined by the physical and chemical properties of the water bodies occurring in these various situations, but it remains a fact that in wet tropical environments forest type is the simplest and most reliable way of characterizing habitats.

Many environmental factors may be expected to determine the distribution of odonates in tropical ecosystems. These include topography, soil type, stream velocity, substrate, water chemistry, turbidity, water temperature, surrounding vegetation (forest type), rheophytic vegetation and degree of shading. Highly localized or ephemeral conditions such as the presence of treeholes and puddles or fallen trees may also be important. Though at present we cannot state with certainty the significance of these various factors in the relationships of species to their environments, field experience gained from five years of systematic collection in diverse habitats throughout Brunei provides much baseline data suggesting possible lines of enquiry. In this paper I list species personally encountered, detailing their habitats, and discuss the ecology and behaviour of species for which sufficient information is available. I provide an analysis of patterns of odonate biodiversity in relation to habitat within Brunei. Several species recorded from Brunei by other collectors are also noted.

Area and methods

Material was identified mainly by direct comparison with the named collections of the National Museum of Natural History, Leiden, The Natural History Museum London, the Zoological Department Museum, Cambridge University and the private collection of Dr Allen Davies, Cambridge. A few species were determined from the literature, mostly with reference to original descriptions.

Collections were made throughout the more accessible parts of Brunei, with concentrated efforts at 35 sites (Fig. 1), which represented broadly all the lowland freshwater habitats found in the country. No site was above 150 m a.s.l. in altitude. At each of these sites, the characteristics of which are listed below, at least 10 man hours were spent in collecting. At most of the primary forest sites a much more intensive effort was made, with 50-150 man hours devoted specifically to collecting at each site, and in addition many chance discoveries were made in the course of other field activities. Although collecting efforts were concentrated in the middle part of the day from 09:00-15:00 h (local time which in practice was very close to solar time), in most localities at least some collections were made late in the afternoon until dusk. At localities known to be rich in crepuscular species, a major part of the sampling effort was made in the period 16:00-18:30 h (i.e. sunset). A significant number of species were collected nocturnally at light, either in dwellings, or at mercury vapour lights run in the forest for moth collection. The bulk of collections were made between 1990 and 1996, but most localities were revisited in 2000, by which time several key sites had been badly degraded due to development or fire.

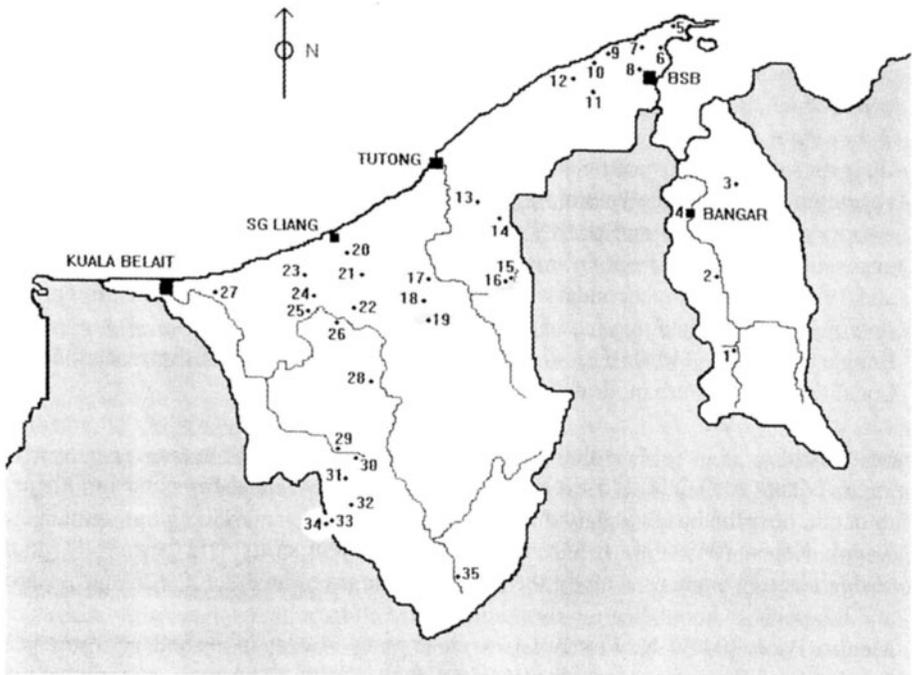


Figure 1. Location of main collecting sites in Brunei.

Main collecting localities

Localities (Fig. 1) listed according to the four administrative districts of Brunei – Temburong, Brunei-Muara, Tutong and Belait – were as follows:

Temburong

1. Kuala Belalong Field Studies Centre (04°32'N, 115°09'E), normally referred to as the KBFSC. Situated in primary lowland mixed dipterocarp forest on the banks of the Belalong River, a large stream flowing between steep ridges about 350 m in elevation. Three main habitat types with distinct faunas were present within a few hundred metres of the centre: 1. The main stream, about 20 m wide from bank to bank at the field station, sometimes expanding into broad pools – substrate mostly loose coarse stones and gravel but with numerous sand bars and silty areas behind log jams – a wide range of rheophytes present dominated by *Mymeconuclea*; 2. Smaller rocky tributaries including the Sg. Mata Ikan, no more than three to six metres wide and frequently narrower but with many open areas receiving full sunlight at some time in the day – these streams were mostly steep; 3. In the forest understorey, especially in the vicinity of phytotelmata and of marshy springs forming the sources of minor streams. For further information and habitat photographs see Cranbrook & Edwards (1994).
2. Batang Duri (04°34'N, 115°08'E). Secondary growth near a longhouse with drains and puddles beside the Temburong River and the broader lower reaches of the river itself, which at this point flowed over rounded boulders and was swift flowing.
3. Bukit Patoi (04°45'N, 115°11'E). Mixed dipterocarp forest with a small clear sluggish sandy/muddy bottomed stream flowing from the forest into open secondary vegetation, and eventually draining into a swamp. At the head of the stream was a short rocky section, and nearby were shallow, stagnant, leafy pools, and a small exposed pond scooped out by roadworks at the edge of the forest. Between 1996 and 1999 some of the secondary vegetation in the lower portion of the stream was severely thinned, changing the nature of the habitat.
4. Bangar (04°42'N, 115°04'E). A small town with nearby mixed dipterocarp forest. Localities were suburban, drains, ponds and houses (to light).

Brunei-Muara

5. Pantai Muara (05°02'N, 115°03'E). A series of old ornamental lily ponds, of about 1 m depth, near the beach at Muara.
6. Kapok Kanen (05°00'N, 115°02'E). A series of temporary and permanent pools beside a newly made road along the landward margin of an extensive mangrove area and the pools to about 50 m within the mangrove forest.
7. Mentiri Pools (04°57'N, 114°59'E). A clear rocky stream in secondary forest near Bandar Seri Begawan (hereafter referred to as BSB). The main rheophyte was *Pinanga*. On its lower reaches it became silty with some *Pandanus*. Much disturbed by damming since collections were made.
8. Sg. Tilong (04°57'N, 114°57'E). A mixed area of swampy forest and a sluggish stream in secondary forest near BSB.

9. Meragang (05°00'N, 114°59'E). Kerangas forest near Meragang Beach with a small shaded black-water stream.
10. University Brunei Darussalam (04°58'N, 114°52'E), normally referred to as UBD. Very degraded freshwater swamp and open cleared areas with drains and ponds.
11. Rimba Horticultural Centre (04°55'N, 114°52'E). A series of recently constructed large open ornamental dams near BSB with abundant waterlilies and sedges.
12. Tungku Swamp (04°56'N, 114°51'E). Freshwater swamp forest near the Tungku link road dominated by *Campnosperma*. The area was severely disturbed in 1998.

Tutong

13. Lamunin pipeline road (04°46'N, 114°42'E). An extensive area of freshwater swamp forest grading into black-water peat swamp forest accessible from the Lamunin pipeline road
14. Sg. Burong, Lamunin (04°45'N, 114°44'E). A disused logging road along a steep ridge through degraded forest with some Lalang (*Imperata*) and Bracken. Feeding ground for many crepuscular aeshnid species. In 1997 fires destroyed much of the forest and very few aeshnids were observed in 2000.
15. Benutan Stream (04°43'N, 114°48'E). A small, largely shaded stream with mixed rocky, sandy and silty substrates, which emptied via a waterfall into the Benutan reservoir. The stream was notable for its variety of rheophytes, which included in various sections, *Myrmeconauclea*, *Pinanga* and *Pandanus*.
16. Benutan Reservoir (04°43'N, 114°47'E). A large artificial impoundment with open areas near the dam wall and primary dipterocarp forest surrounding its catchment.
17. Long Mayo (04°39'N, 114°40'E). A small shaded stream on the sandy floodplain of the Tutong river running through riverine forest.
18. Long Mayo (04°38'N, 114°40'E). A freshwater swamp near Long Mayo, lying in a depressed area at the boundary of extensive areas of secondary and primary dipterocarp forest. Mostly shaded, with small sunny patches, the swamp consisted of numerous clear pools and small rivulets.
19. Tasek Merimbun (04°35'N, 114°40'E). A natural, large, shallow, clear-water lake with an extensive growth of reeds and sedges around its margins.

Belait

20. Andalau forest reserve (04°39'N, 114°32'E). A shallow ridge in an extensive area of primary mixed dipterocarp forest floristically distinct from the KBFSC. Temporary puddles and phytotelmata were the only nearby breeding habitats.
21. Sg. Lumut (04°37'N, 114°31'E). A sluggish shaded stream with substrate sandy to muddy with a dense growth of *Pandanus* around its banks, often obscuring the stream. Surround by alluvial forest with numerous streamlets, and shallow leafy pools often some several metres wide.
22. Sungei Badas (04°35'N, 114°31'E). A small black-water stream on the Labi Road adjoining a marshy area, similar in vegetation to site 28. Severely degraded in 2000, when none of its stenotopic species were observed.
23. Badas pipeline road (04°37'N, 114°26'E). An extensive open black-water drain along the Badas pipeline road adjoining peat swamp forest. In places there were

shallow marshy areas surrounded by long grass. Burning of the adjacent forest in 1997 severely degraded this habitat.

24. Badas pipeline road (04°36'N, 114°26'E). A small stream emerging from freshwater swamp forest with small permanent pools nearby, flowing into the drain. By 2000 the forest had been burned along the length of the stream, and the water completely choked with secondary growth. None of the stenotopic species recorded previously survived.
25. Badas forest reserve (04°35'N, 114°25'E). An area of Kerangas forest traversed by a narrow vehicular track. In 1995 several semi-permanent pools were produced by a bulldozer making a second track. This area was reduced to a small remnant following forest fires in 1997.
26. Sungei Belait (04°33'N, 114°27'E). A section of the Belait river where it crossed the Labi road, near Sg. Mau. At this stage the river was broad, sluggish and silty. The collecting locality included the exposed banks of the river itself, and the numerous pools and streamlets which drained into it from the muddy alluvial floodplain.
27. Kuala Belai (04°35'N, 114°18'E). A road running through mixed peat swamp forest with a black-water drain alongside. Most collecting was done in a marshy area inside the forest with small pools partly exposed to sunlight. Owing to burning I was unable to relocate the site in 2000. Although large areas of undisturbed peat-swamp forest remained nearby, these represented different floristic associations from the study site and host a significantly different fauna.
28. Luagan Lalak (04°31'N, 114°28'E). An extensive black-water marshy area with a deep channel running through a broad growth of sedges, especially *Hydrolitha*. In 2000 the area remained intact but inaccessible owing to the collapse of a walkway.
29. Sg. Rampayoh (04°21'N, 114°27'E). The lower sections of the Sg. Rampayoh near its crossing with the Labi Rd. The stream here was clear, shallow and fairly slow flowing. The substrate was coarse sand. It was 5-20 m in width and presented a mixture of exposed sunny areas and shaded parts. Surrounding vegetation was primary mixed dipterocarp forest, with narrow alluvial floodplain dominated by bamboos.
30. Sg. Rampayoh (04°19'N, 114°28'E). The upper sections of the Sg. Rampayoh, more than 4 km from the Labi Rd. The stream was narrower and swifter flowing than lower down, with a rocky substrate and predominant growth of *Pinanga* on its banks.
31. Sg. Mendaram (04°20'N, 114°26'E). Close to the Labi Rd, similar in characteristics to last.
32. Sg. Langsat (04°16'N, 114°29'E). A small, mostly shaded, rocky stream rising steeply from the Labi Road in primary dipterocarp forest.
33. Bukit Terajah (04°13'N, 114°28'E). A sluggish steep sided stream running between high sandy banks, mostly shaded. Surrounding vegetation largely bamboo and secondary growth.
34. Marudi Trail (04°10'N, 114°27'E). A log trail through peat swamp forest beyond the Bukit Terajah longhouse.
35. Sg. Ingei (04°06'N, 114°42'E). A moderate sized clear stream with rocky and pebbly substrates flowing in a narrow valley between low ridges vegetated with primary dipterocarp forest. The stream was little shaded and rheophytes included *Pinanga*

and *Pandanus*. Nearby were hot springs with shaded marshy areas draining into the stream. An area about 5 km distant below this site which included areas of swamp forest and kerangas as well as the stream was sampled extensively by Thompson in 1992 (Thompson & van Tol 1993).

Annotated checklist of species recorded from Brunei

ZYGOPTERA

AMPHIPTERYGIDAE

Devadatta sp.

Sites 1, 7, 32, 35. Found in small rapid streams in dipterocarp forest, and around boggy areas inside the forest. Males commonly perched on twigs just above small cascades, or around small pools. A male was observed guarding a female ovipositing in a leaf-pack wedged between stones at the head of a cascade. Male territorial behaviour was similar to that described for *D. argyoides* (Selys) by Furtado (1970). This species is almost certainly distinct from *D. podolestoides* Laidlaw, from which it differs in size, coloration and venation (M. Hämäläinen in litt.). It was previously treated as *D. podolestoides* (Thompson & van Tol 1993).

CALOPTERYGIDAE

Most species occurred on streams and in swampy areas in primary forest. Where present they were often abundant and easily observed but sexual behaviour was infrequently seen. The species of *Vestalis* usually cannot be separated without close examination of the male appendages (Lieftinck 1965).

Neurobasis longipes Hagen

Site 1. Usually present and sometimes abundant on the main stream at the KBFSC and on some larger tributaries. The males flew across and up and down the stream and frequently perched on emergent branches near fast flowing water. Females were also commonly seen in these situations. Mating was rarely observed but was preceded by a distinct courtship display. The slender, long legged larvae (figured in Lieftinck 1965), were found at night clinging to vegetation in fast water. The taxon, long treated as a subspecies of *N. chinensis* (Linnaeus), was reinstated to specific rank by Hämäläinen (1993).

Vestalis amabilis Lieftinck

Sites 7, 8, 9, 15, 17, 18, 21, 29, 30, 31, 32, 33, 35. Exceedingly common in forest in flat terrain near small sluggish streams and swampy areas in low lying dipterocarp and

kerangas forest; also occurring on clear *Pinanga*-bordered streams in dipterocarp forest. Both sexes were very frequently encountered along forest paths in bamboo groves in alluvial forest at densities of one every two or three metres. Apparently they maintained small feeding territories in these situations. Males were often spaced at similar densities along the streams where they perched on twigs and in the rheophytic vegetation, from where they pursued passing females. Sexual behaviour beyond abortive chases was infrequently observed but ovipositing females were sometimes courted by males which fluttered around them in a broad semicircle, about 1 m in radius, displaying the brilliant violet iridescence of their wings. This behaviour was most intense from 11:30-12:30 h. Unguarded females oviposited in loose leaf-packs around the margins of streams and runnels, often plunging the tip of the abdomen deep into mud. At Sg. Ingei a male was collected with a *Forcipomyia* midge riding on his thorax. It is believed this midge species differs from *F. debehamae* found on *Libellago hyalina*. The biology of *V. amabilis* is further discussed by Thompson (2000).

***Vestalis amaryllis* Lieftinck**

Site 1. Abundant on small tributaries at the KBFSC, and in surrounding forest where both sexes frequently perched in sunny patches, apparently for feeding purposes. Females oviposited in vegetation along the streams, including small pieces of rotting wood and leaf-packs. Rapid sexual chases over the stream were frequent.

***Vestalis amnicola* Lieftinck**

Site 3. Very abundant everywhere along the stream at Bukit Patoi but observed nowhere else. Females oviposited in leaf-packs, usually commencing about 11:00 h. Males guarded perches along the stream near favoured oviposition sites and mated with females after they commenced laying. There was little courtship, the male landing beside the female, seizing her and carrying her to his perch. Mating lasted 5-15 minutes after which the female resumed oviposition in the original site guarded closely by the male. Feeding behaviour was similar to that of *V. amabilis*. Larvae, probably of this species, were found in leaf-packs near riffles.

***Vestalis amoena* (Hagen in Selys)**

Site 1. Found only sporadically on the main stream at the KBFSC. A female was once observed ovipositing unguarded in loose dead leaves, in a quiet rocky backwater among small stones. The larvae, presumably of this species, were collected from the undersides of small stones at the edge of the river in fast flowing water.

***Vestalis atropha* Lieftinck**

Site 1. Found only on small tributaries at the KBFSC. Not uncommon but distinctly scarcer and more sporadic than *V. amaryllis*. Habitat and behaviour very similar to that species.

***Vestalis beryllae* Laidlaw**

Site 1. Only found in deep forest at the KBFSC, well removed from water sources except boggy springs and phytotelmata. Males, distinguishable by their very long abdomen,

defended sunny patches on low vegetation and were quite common. Females, in which the abdomen is of almost normal length, were seldom encountered. The breeding habitat is unknown.

CHLOROCYPHIDAE

Most species were found in fast running water in forest habitats. Males defended small territories over fallen logs in the water which served as the oviposition substrate. Usually courtship was fairly elaborate. Females were guarded closely immediately following mating but continued to oviposit unguarded as they wandered out of the male's territory. Both sexes spent long periods resting on logs near the water level and were particularly vulnerable to predation by aquatic spiders. Agonistic and courtship behaviour was discussed for many species by Orr (1996). Larvae were found for only two species.

Heliocypha biseriata (Selys)

Site 1. Sporadic but sometimes abundant on the main stream of the Sg. Belalong around log jams. Males maintained territories over the entire sunlit part of the jam, ranging from the fast water on the streamward side to more sheltered water towards the river bank. Territorial contests were frequent and vigorous, with considerable turnover in the males occupying particular perches. Courtship involved the display of white tibiae and was also vigorous. Males tended to guard females more closely than did *Rhinocypha* species, following them beyond the boundaries of their territories. Females sometimes submerged completely while ovipositing.

Libellago aurantiaca (Selys)

Sites 7, 17, 21, 29, 30, 31, 35. Most common over slow flowing sandy bottomed forest streams with abundant dead wood, but also found around large pools in swifter streams, and in sluggish muddy bottomed streams in swampy areas. Males perched on logs or floating leaves where they defended small territories and courted females vigorously when they attempted to oviposit. Most courtship and mating occurred from 09:00-12:00 h with most oviposition from 11:00-1500 h. Marked males and females remained around the oviposition sites for up to 10 days, females characteristically returning to lay every other day. Displaced and immature males frequently perched in low vegetation nearby. Females often oviposited in groups in dead wood just under the water.

Libellago hyalina (Selys)

Sites 3, 9, 12, 17, 23, 24, 25, 26, 27, 34. Very common in runnels in forested swampy areas, particularly in black-water, but sometimes also in small slow forest streams in dipterocarp forest. Males guarded small territories of a few square metres and perched in sunny patches. Marked individuals were recaptured regularly within 20 m of the initial place of capture up to nine days after marking. Unlike most members of the family, females were seized by the males while ovipositing without apparent courtship. Eggs were laid in root masses and floating vegetation, especially fragments of wood.

Predation of ovipositing females by Nepidae and, once by a mature larva of *Rhodothemis rufa*, was observed. At Badas, both sexes frequently carried the ceratopogonid midge, *Forcipomyia debehamae* Cranston (Orr & Cranston 1997). Infected individuals were shown to have lower residency times at the site. Larvae were dredged from among decaying vegetable matter.

***Libellago lineata* (Burmeister)**

Recorded by Thompson & van Tol (1993) in a stream in freshwater swamp forest, Sg. Ingei.

***Libellago semiopaca* (Selys)**

Sites 1, 26, Tutong River. Very abundant at the KBFSC around log jams on the main stream. Also found around fallen timber and artificial landings on the lower Belait and Tutong rivers, where the water was sluggish, deep and muddy. KBFSC specimens resembled those from the Danum Valley, Sabah, where the species occurred in similar situations on small pristine streams entering the Segama river, and males from both localities had a more extensive black terminal patch on the forewing and more extensive green markings on the abdomen than did those from the Tutong and Belait rivers. The former specimens resembled *L. mima* Lieftinck – since synonymised with *semiopaca* (Lieftinck 1954) – except that the pterostigma was lacking on the forewing of the male. In view of the similarity of specimens from KBFSC and Danum, locations on opposite sides of the island of Borneo, and the obvious habitat differences with no known intermediate distributions, it is possible that the Tutong and Belait specimens represent a different species from those from KBFSC, and possibly *mima* should be resurrected. Males of *semiopaca* at KBFSC established small territories on fallen logs which also served as the oviposition substrate. Preferred sites were at the outer edge of the log jams near fast water, but suitable sites in more protected areas were also defended. Males spent much of their time airborne in territorial contests. Females oviposited in the logs along the waterline, mostly near faster water, often in large groups. Most courtship and mating occurred from 09:00-11:00 h with most oviposition from 11:00-15:00 h. Marked males and females remained around the oviposition sites for up to 10 days, females characteristically returning to lay every other day. Several males were recorded repeatedly on the same log for more than seven consecutive days, apparently never moving more than a few tens of metres throughout their lives. Only about 15% of individuals were ever recorded shifting to other log jams 50-100 m from the initial point of marking.

***Libellago stictica* (Selys)**

Site 1. Sporadic and vagrant, found only at the KBFSC on the main stream where males appeared in the early afternoon from 13:00-15:00 h and established small territories on large fallen logs toward the centre of the stream, always near fast flowing water.

***Rhinocypha aurofulgens* Laidlaw**

Site 1. Found only on the main stream at Kuala Belalong and on the Sg. Temburong but not beyond the boundaries of the primary rainforest. Syntopic with *L. semiopaca*, this

species tended to prefer faster water, where it perched on dead logs. Territorial contests between males were very frequent and conspicuous but courtship and mating were less often observed. Courtship was unusual in that the male remained perched for most of the time while displaying his wings and abdomen to the female. Ovipositing females were seldom courted. Females were frequently observed from 12:00-15:30 h ovipositing in groups together with *L. semiopaca*.

***Rhinocypha cognata* Kimmins**

Site 1. Uncommon and inconspicuous along the Sungei Mata Ikan at the KBFSC. Males perched 2-4 m above the stream on leaves and contested sunspots. Contests were normally brief. In life the dorsum of the male abdomen was deep blue. When erecting this species, Kimmins (1936) suggested that *R. stygia* Förster may be conspecific, in which case the name *stygia* takes precedence. *R. stygia*, type locality Mt Kinabalu, was described as completely black, possibly on the basis of a discoloured specimen. As the male type of *R. stygia* is now lost and the female of *R. cognata* is unknown, fresh material is required to resolve the status of these species.

***Rhinocypha cucullata* (Selys)**

Sites 1, 15. Sporadic on the main stream at the KBFSC, where it tended to occupy fallen logs in slower water behind the larger log jams, and also found in a silty section of Benutan Stream. Territorial behaviour was very similar to that of *R. aurofulgens*. Courtship involved a vivid aerial display of wings and pale blue, expanded tibiae.

***Rhinocypha humeralis* (Selys)**

Sites 1, 3. Abundant at the KBFSC around riffles on smaller tributaries and in similar situations at Bukit Patoi. Absent from the main stream at the KBFSC. Males perched on stones and fallen logs defending territories in sunny patches. Courtship was vigorous and ovipositing females were frequently molested. Oviposition was in dead wood near the water surface or sometimes in logs lying over the stream. Males guarded females only briefly after copulation. A single larva was found in a leaf-pack in the stream at Bukit Patoi.

***Sundacypha petiolata* (Selys)**

Site 32. Found only at Sg. Langsat, where it was common. Males perched on stones and logs in pools in a clear, rocky forest stream, in heavily shaded and more open areas. No sexual behaviour was observed.

***Sundacypha striata* Orr**

Sites 21, 35. Common at Sg. Lumut on a sluggish, *Pandanus* bordered stream, and in faster water at Sg. Ingei but also in the vicinity of *Pandanus*. Males perched on overhanging vegetation and on twigs or logs near the water surface. Agonistic interactions between territorial males involved slow ascending flights, in which two individuals faced each other closely. They exhibited a stationary wing display in which the hindwing, which bears a broad apical dark area, was held stationary and canted so as to turn the face of the wing towards the opponent. This is the reverse of the

typical display in most *Libellago* species in which the forewing, which bears a dark apical mark, is held stationary (Orr 1996). A female was once observed laying in a rotting log, and a male courted her with a typical semicircular dance vividly displaying the white tibiae.

EUPHAEIDAE

Mostly occurring in similar situations to the Chlorocyphidae, euphaeids were much more rapid in flight. Mating probably involved some courtship in many species, but usually the actions took place too rapidly to be easily observed. Larvae of *Euphaea*, distinguished by the presence of abdominal gills, were normally easily discovered under stones in riffles. The adults typically emerged on stones or vegetation close to the water surface.

Dysphaea dimidiata (Selys)

Sites 1, 2, 30, 31. Exceedingly common at the KBFSC, and present elsewhere in fast flowing rocky streams in dipterocarp forest. Males perched with wings spread in sunny patches on stones, logs and emergent branches in very fast and medium water. Territorial contests were frequent and vigorous, with rapid chases of up to 100 m. Females, which were seldom seen, were ambushed by males and captured following rapid pursuit, probably without courtship. Oviposition occurred in tandem, the female inserting her eggs into large fallen logs just below the water level at the edge of the main current. The tandem pair covered at least several hundred m in search of suitable substrates, not spending more than a minute or so at each site. Larvae were not found.

Dysphaea lugens (Selys)

Sites 15, 29, 30, 31, 35. Absent at the KBFSC, but common on rapid and sometimes more sluggish forest streams. Occurred together with *D. dimidiata* on the upper Sg. Rampayoh and at Sg. Mendaram. The females differed substantially in appearance from *D. dimidiata* and were more readily distinguished in flight than the males. Behaviour was similar to *D. dimidiata*. Oviposition was observed in logs in slow and fast water. In one instance a tandem pair decoupled on a large log at the head of a deep rapid. The male perched above while the female crawled under the log for about three minutes. When she re-emerged they joined in tandem again and flew some 100 m to another oviposition site. Larvae were sought but not found.

Euphaea ameeke van Tol & Norma-Rashid

Sites 7, 17, 18, 21, 30, 31, 32, 35. Especially abundant on most *Pinanga* streams in Brunei, generally in faster water than *E. impar* which was present at the same localities. *E. ameeke* also occurred less commonly in runnels in swampy areas and sluggish streams. Males defended small territories on perches overhanging the stream. Females were ambushed and seized immediately on landing following a rapid chase. There was little evidence of further courtship display. The male guarded the female for

at most a few minutes following mating, after which she continued to oviposit beyond his territory and he returned to his perch. Further behavioral observations are provided by Thompson (1998). Larvae were common under stones in fast running riffles.

***Euphaea impar* (Selys)**

Sites 1, 3, 29, 30, 35. Abundant on certain small streams in dipterocarp forest, most frequently in the slower flowing reaches of *Pinanga*-bordered streams where the males perched low on vegetation maintaining small territories. The dark apical patch on the forewing may be used in brief agonistic displays. Courtship was rudimentary but more developed than in *E. ameeka*. Females were ambushed and following a rapid chase, the female landed on a stone or in vegetation. The male hovered above her for no more than a few seconds before seizing her and mating. At the KBFSC it was observed only once, on the Sg. Mata Ikan.

***Euphaea subcostalis* (Selys)**

Site 1. Found only on small sunlit tributaries at the KBFSC, where the males perched conspicuously on leaves, twigs and stones. Preferred perches appeared to be those closest to the water surface. Agonistic behaviour was infrequent, limited mainly to a few rapid chases in the morning from 08:30-10:00 h while territorial occupancy was established. Females were pursued rapidly until they escaped or landed, typically on a leaf. Courtship was brief, probably serving to display the iridescent blue-green patches on the male hindwing. Ovipositing females were mostly unguarded. Eggs were inserted into small pieces of rotting wood. Larvae were common under stones in shallow riffles.

***Euphaea tricolor* (Selys)**

Sites 1, 2. Very common on the main stream at the KBFSC, and along the Temburong river, sometimes as far down as Batang Duri. Males perched on logs near fast water towards the centre of the stream. Sexual behaviour was similar to that of *E. subcostalis*. Larvae were most common under stones in slightly sheltered water near log jams. Teneral adults were frequently found in the morning from 07:00-08:00 h clinging to logs a few cm above the water surface.

LESTIDAE

The family is poorly represented in Borneo, and only two species were encountered, both breeding in swampy areas.

***Lestes praemorsus* Hagen in Selys**

Sites 4, 6, 10, 23 (shallow swampy areas). Common in swampy areas and drains adjacent to forest, or in cleared areas throughout Brunei, usually in company with *Neurothemis fluctuans*. Males perched in small territories with tip of abdomen uptilted and wings partially spread. Mating occurred near the perch, and the female oviposited extensively within the territory, closely guarded by the male. Among lestids, non-contact

guarding is probably unusual and was not recorded in a survey of this behaviour by Corbet (1999).

Orolestes wallacei (Kirby)

Sites 25, 26. In Badas forest near a damp patch on the road, males perched on damp earth and when disturbed flew up into the trees where they rested with their abdomen held vertically and wings outspread. Nearby a teneral female was seen to have emerged from a large shallow pool. Quite common also in alluvial swamp beside the Belait river.

MEGAPODAGRIONIDAE

Robust zygopterans commonly resting with the wings held outspread. Most were found in forest habitats or in swamps and streams in primary forest. Four species in all three Bornean genera have been recorded from Brunei.

Bornargiolestes sp.

Site 1. A single male was recorded from the KBFSC, perching on leaves in the forest understorey ca 1 m above the ground. In life it superficially resembled *Devadatta podolestoides*. A concerted effort to obtain further material met with failure. The specimen is very immature, overall pale brown with lighter abdominal markings, but the anal appendages are indistinguishable from those of *B. nigra* Kimmins, the only member of the genus and known only from the holotype male. It is however considerably smaller and with a proportionally shorter abdomen than *B. nigra*, hence until further material becomes available it is prudent to treat it as of uncertain status. As far as I am aware this is only the second specimen of this genus ever collected. The holotype of *B. nigra* was taken at 1,000 m on Mt Dulit. The mature colouring is black and pruinulent pale blue. The legs are absent. In the present specimen the legs are exceptionally short for the family. If it should prove to be *B. nigra*, it will be one of several species previously recorded from Mt Dulit which have been subsequently found at the KBFSC, and it may also be expected to occur on Gunung Mulu.

Podolestes chrysopus Selys

Thompson & van Tol (1993) recorded this species from peat swamp forest near Sg. Ingei.

Podolestes orientalis Selys

Sites 8, 18, 20, 21, 32, 33, 34. Often abundant in freshwater swamp, alluvial and peat swamp forest. In some localities both sexes were common in mixed dipterocarp forest in gently undulating terrain, adjacent to swampy areas interlaced with rivulets and pools. Males established territories over small pools in the swamp. At Sg. Lumut, a mating pair were observed in the vicinity of a small boggy pool about 13:00 h. In the forest near long Mayo swamp both sexes were found well removed from the breeding ground perching on leaves in sunspots 2-4 m above the ground.

***Rhinagrion borneense* (Selys)**

Sites 1, 3, 15, 17, 29, 30, 31, 35. Most commonly found on the banks of forest streams, especially where *Pinanga* is present. Males rested on vegetation with their wings outspread 1-3 m above the stream and defended small territories, usually in sunny patches. Males engaged in vigorous ascending flights during which they faced each other and flexed the tip of the flattened abdomen upward displaying the terminal pale green flash. Contests were terminated by a brief chase. The tibiae and femora bear pale green markings which presumably have some signaling function. These are only superficially like the markings of chlorocyphids and it is uncertain whether they play any role in courtship, which was never observed. Females were seldom seen and neither sexual behavior nor oviposition were observed. Larvae, probably belonging to this species, were found among coarse sand at the bottom of a small pool in the stream at Bukit Patoi. Ceratopogonid midges, presumably *Forcipomyia* sp., were found attached to the wing veins of some individuals. At the KBFSC it was observed only once, on the Sg. Mata Ikan.

COENAGRIONIDAE

Tiny to large, slender species occurring in all types of habitats with standing or gently flowing water, with many species in ponds and drains in disturbed open areas. Oviposition was commonly in tandem in submerged vegetation but many variations occurred, especially in forest species.

Agriocnemidinae

***Agriocnemis femina* (Brauer)**

Sites 3, 5, 6, 10, 23. Probably common in many localities in shallow exposed drains and ponds, this species, and possibly other members of the genus were certainly under-collected, since it was taken at only five localities, but almost certainly seen at many others, including sites not counted in this survey. The adults were rather sedentary and inconspicuous, but were active for almost the entire day.

***Agriocnemis pygmaea* (Rambur)**

Site 6. One female only was taken in late afternoon at a roadside drain near mangrove. Also present were numerous *Aciagrion borneense*. Possibly present at other localities and overlooked.

***Argiocnemis rubescens* Selys**

Sites 3, 13, 30. Occurring infrequently in open swampy areas near forest. No other observations were made on this widespread species.

***Mortonagrion alcyone* (Laidlaw)**

Site 30. A single female was taken in a silty backwater of the upper Sg. Rampayoh. Thompson & van Tol (1993) record it from alluvial forest, which is probably a more usual habitat.

Mortonagrion falcatum Liefstinck

Site 23. Along with its congeners which were not recorded, this species was probably under-collected on account of its small size. It was collected only at Badas drain, where it was common, and it appeared to be absent from severely disturbed and secondary habitats. Liefstinck (1954) gave the distribution of this insect as east Borneo hence this record represents a considerable range extension. Presumably this reflects under-collecting of a small and inconspicuous species.

Argiinae*Onychargia atrocyana* (Selys)

Sites 13, 14, 20, 32. Local but common in several localities with differing habitats, including freshwater swamp forest, clear rocky streams in primary dipterocarp forest, and in degraded dipterocarp well removed from water. Both sexes rested on foliage, usually from 1.5-4 m above the ground.

Ischnurinae*Aciagrion borneense* Ris

Sites 2, 4, 6, 11, 23. Common in well vegetated drains, ponds and swampy areas. Oviposited in tandem throughout the day.

Ischnura senegalensis (Rambur)

Sites 3, 4, 5, 6, 8, 10, 13. Common in drains and ponds in exposed secondary habitats throughout Brunei and one of the first species to colonize newly made drains. Most females were androchromatic, with several specimens of the golden yellow form recorded.

Xiphiagrion cyanomelas (Selys)

Sites 3, 6, 7. Quite common and probably frequently overlooked in well vegetated drains and ponds, especially at forest margins. Oviposition in tandem occurred throughout the afternoon until sunset.

Pseudagrioninae*Amphicnemis*

Mostly found in primary and secondary forest close to swampy areas. Although often very numerous, sexual activity was never observed. As the genus is extremely speciose in Borneo (Liefstinck 1940, 1953a, b), every effort was made to collect large series from diverse localities, but only four species were found.

Amphicnemis erminea Liefstinck

Sites 18, 25, 27, 34. Common in certain forested swampy areas, including kerangas forest where the males were found in shaded situations. This species was first recorded in Brunei by Thompson & van Tol (1993), being previously known only from south-east Borneo.

Amphicnemis martini Ris

Site 27. Common only at Kuala Belai in peat swamp forest. Males guarded small pools in shaded areas.

Amphicnemis remiger Laidlaw

Sites 3, 8, 10, 13, 18, 21, 34. Widespread and common in swampy areas in primary and secondary forest, frequently entering buildings. Both sexes were frequently found resting on leaves in the understorey some distance from water.

Amphicnemis wallacii Selys (?)

Sites 18, 20, 21, 32, 35. Common in various forested swampy areas. Habits similar to *A. remiger*. The median spine arising from the posterior margin of the prothorax is more recurved than is usual in *A. wallacii* but in other respects it agrees closely with this species (Lieftinck 1940).

Archibasis

Members of the genus were confined to relatively undisturbed, shaded habitats in swampy areas. Oviposition occurred in tandem. The genus was probably under-collected in my samples, and because of the difficulty of field recognition, behavioral notes are based entirely on voucher specimens.

Archibasis incisura Lieftinck

Sites 21, 26, 30. Common around small pools in alluvial freshwater swamp at Sg. Lumut where males monopolized patches of sunlight. Territorial contests were frequent; males faced each other closely and slowly ascended 1-2 m until one broke off and was chased away. Tandem pairs were observed around the pools in the afternoon.

Archibasis melanocyana (Selys)

Sites 13, 24, 27. Moderately abundant in some localities in freshwater swamp and peat swamp forest. Males rested in sunny patches on the vegetation 1-3 m above small runnels in the swamp.

Archibasis tenella Lieftinck

Sites 21, 35. Occurred in similar localities to *A. incisura* and apparently with similar habits.

Archibasis viola Lieftinck

Sites 18, 24. Not rare in some localities in freshwater swamp, around small pools and slow flowing streams, sometimes in company with *A. melanocyana*.

Ceriagrion cerinorubellum (Brauer)

Sites 2, 3, 4, 5, 6, 8, 10, 11, 12, 16, 19, 23, 27, 28. Very common in roadside drains and other disturbed habitats in open areas. Less frequently seen around the margins of dams and natural lakes. Aggressive insects, they were twice observed feeding on teneral *Archibasis* and *Pseudagrion* species.

Pericnemis triangularis Laidlaw

Sites 1, 20. Apparently confined to primary mixed dipterocarp forest where it bred exclusively in phytotelmata. Males rested at the tips of leaves from 3-10 m in the forest understorey, especially in small open gaps with sunlight penetrating to the forest floor. Females oviposited alone, laying their eggs in the bark and moss immediately above the water surface in treeholes of all sizes. During this process they appeared particularly reluctant to place the tip of their abdomen in the water, perhaps because of the prevalence of large predators, such as the larvae of *Indaeschna grubaueri* and *Lyrithemis cleis*. Larvae, which have enlarged lateral lamellae with distinctive terminal markings (Orr 1994), were extremely common in phytotelmata (Orr 1997; Kitching & Orr 1996). The male was hitherto unknown.

Description of the male (Fig. 2)

Head: Dorsal side anterior to frontal ridge pale yellowish brown except for the labrum, which has very fine black marking on the lateral margins, and the postclypeus, which has a broad black margins anteriorly and laterally, with a broad dark intrusion centrally. Posterior to frontal ridge, including vertex and occiput, bronzy black with two small obscure yellowish spots on either side of the anterior ocellus. Ventrally, labium and maxillae yellowish brown except at the extremities which are tipped with black.

Thorax: Prothorax: anterior and median lobes pale yellowish brown with small black saddle in the posterior half of the anterior lobe, and a mid-dorsal streak flanked by two lateral marks in the form of inverted T's in the median lobe. Posterior lobe entirely purplish black dorsally, at its posterior margin produced into a backward pointing, slightly upturned triangular spine. Synthorax: mesepisternum with broad median band of dark metallic purple, almost reaching the humeral suture. Remainder of synthorax pale yellowish brown except for a small purplish spot at the anterior angle of the mesepimeron adjacent to the humeral suture, but not extending into mesinfraepisternum. Legs pale yellowish brown. Wings hyaline with open reticulation. R_{3+4} and IR_3 arising jointly at the subnodus. Pterostigma short, basally acute, dark brown encircled by a broad pale margin.

Abdomen: Dorsally purplish black, ventrally dark brown. Appendages (Fig. 2): superiors bifid, upper branch black, slightly shorter than S9, thin, tapering and strongly recurved downward and inward distally, with a slight subapical expansion. Lower branch pale with dark extremity, curving upwards, almost meeting the tip of the upper branch with which it forms a pincer. Inferiors pale in colour, very short and squat, tapering upwards.

Measurements (mm): Hw 31.5-32.3, abdomen incl. appendages 48.0-48.6.

Differs from *P. stictica* (Selys) in the markings and coloration of the head and thorax, in overall size, and in the structure of the superior anal appendages. Although these are of similar general form, the dorsal branch in *triangularis* is more strongly recurved and the ventral branch is paler and curved more abruptly towards the tip than in *stictica*.

Pseudagrion lalakense Orr & van Tol

Sites 22, 28. Very locally distributed. Found only in black-water of low pH in and around the central channel at Luagan Lalak and in similar situations at Sg. Badas.

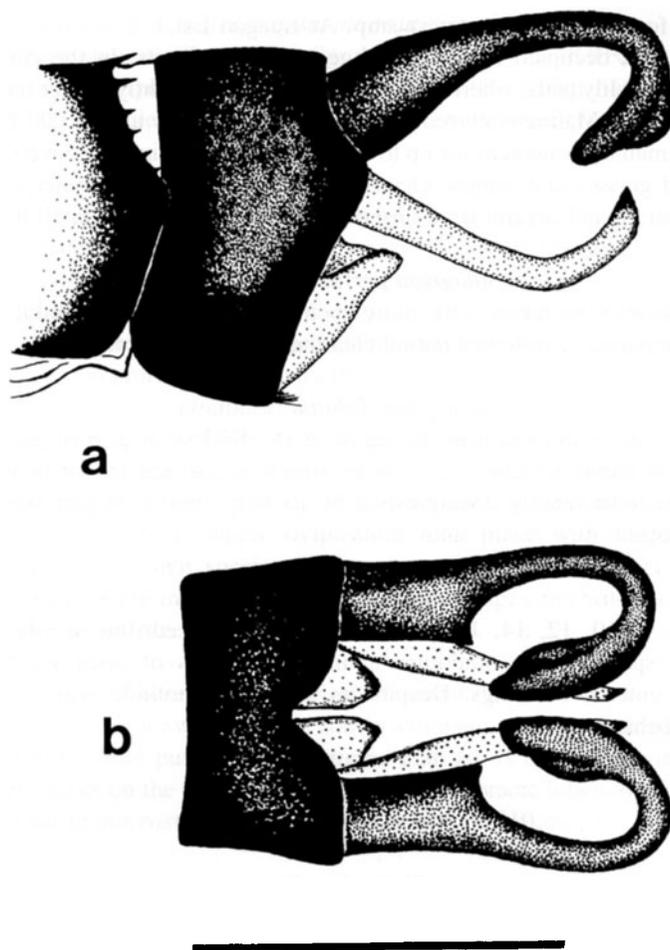


Figure 2. *Pericnemis triangularis* – (a) lateral view of male appendages and S9-10; (b) dorsal view of S10 and male appendages. Scale bar = 1 mm.

Mating and oviposition occurred at the same time of day as *P. microcephalum*, but eggs were laid under lily pads near the bank, and possibly in the stems of *Hydrolitha*, whereas *P. microcephalum* in this situation appeared to oviposit under lily pads towards the centre of the channel. The bionomics of this species were discussed by Orr & van Tol (2001).

***Pseudagrion microcephalum* (Rambur)**

Sites 4, 5, 6, 8, 10, 11, 12, 16, 19, 22, 23, 28, 34. Very common in secondary habitats, especially ponds and drains, and in larger natural lakes; infrequent in open areas in

peat swamp forest and freshwater swamp. At Luagan Lalak it occurred together with *P. lalakense*, but occupied a broader range of microhabitats. In the central channel, males perched on lily pads, whereas *P. lalakense* perched slightly higher on the leaves of the fringing sedge. Mating occurred in the afternoon, usually after 13:00 h and the pair sometimes remained in tandem for up to three hours, eggs being laid under lily pads and in submerged grasses and sedges. Occasionally females nearly submerged themselves during oviposition and several were observed taken by nepids and small fish.

***Pseudagrion perfuscatum* Lieftinck**

Site 3. Two males were taken in the more open part of the stream at Bukit Patoi in May 2000. Their appearance followed partial clearing between 1996 and 1999.

***Stenagrion dubium* (Laidlaw)**

Site 1. Two males were taken in the forest at the KBFSC near a boggy area. It was very similar in habits to *Coeliccia* species which it also resembled in markings and venation. It is most readily distinguished by its very short legs and very large, blue postocular spots.

***Teinobasis rajah* Laidlaw**

Sites 2, 4, 3, 8, 10, 12, 14, 17, 20, 21, 25, 28, 34. Occurring mostly in disturbed habitats, this species was sometimes abundant in areas of open secondary forest. It frequently entered buildings. Despite its abundance nothing was observed of its reproductive behaviour.

PLATYCNEMIDIDAE

Two genera occur in Borneo, the Philippine *Risiocnemis* recorded earlier (Kimmins 1936; Lieftinck 1954) now believed to have been erroneously labeled (Lieftinck 1981). The genus *Coeliccia* is in need of revision, and determinations of several species are only tentative. Most species occur in primary forest, typically in swampy areas but also on small streams.

Calicnemidinae

***Coeliccia campioni* Laidlaw (?)**

Site 1. Occurring rarely in the forest at the KBFSC, mostly during wet seasons. Three males were taken, one from a canopy fogging exercise by Roger Kitching. The prothoracic structure and anal appendages exactly fit Laidlaw's (1918) description of *campioni*, but the specimens differ in that abdominal S9-10 are almost entirely blue dorsally, and 'cuneiform marks' opposite the lateral ocelli, described for *C. flavostriata* Laidlaw, are present and blue in colour. The colours are very unstable and it is possible Laidlaw erred in his original description owing to poorly preserved material. It is also very probable that *campioni* is a junior synonym of *C. borneensis* (Selys) (K.D. Dijkstra in litt.).

***Coelliccia cyaneothorax* Kimmins**

Site 1. Occurring sporadically on the Sg. Mata Ikan at the KBFSC. Mating pairs were sometimes seen flying in tandem up and down the stream but oviposition was not observed. The species has otherwise only been recorded from Mt Dulit at an altitude of 750 m.

***Coelliccia macrostigma* Laidlaw (?)**

Site 24. Two males were taken guarding pools in swamp forest. This may be true *macrostigma* based on the anal appendages as figured by Laidlaw (1918). Otherwise it can be distinguished from similar forms (below) by the presence of a small semicircular incision on the inner margins of the blue antehumeral bands on the mesepisternum, and a broad black area on prothorax with only thin pale markings.

***Coelliccia* sp. A aff. *macrostigma* Laidlaw**

Sites 8, 9, 18, 20, 29, 31, 32, 33. Common in many localities in dipterocarp forest, especially around low swampy areas, and sometimes in secondary forest. Males defended small forest pools where oviposition took place with the male standing guard nearby. Possibly a new species, these specimens are quite distinct from putative *macrostigma* above, differing from it in the anal appendages and with the inner margin of the antehumeral bands lacking any incision.

***Coelliccia* sp. B aff. *macrostigma* Laidlaw**

Site 35. Uncommon in a swampy area and in company with *nigrohamata* (?) at Sg. Ingei. Less distinct from putative *macrostigma* than sp. A but with broad pale saddle between black marks on the anterior and posterior prothoracic lobes. Anal appendages a little shorter than in *macrostigma* (?), about the length of S10.

***Coelliccia nigrohamata* Laidlaw (?)**

Sites 1, 35. Specimens which seem to belong to this species were common in the forest at Kuala Belalong, and Sg. Ingei where they rested on the leaves of low vegetation near marshy areas giving rise to small streams. In one female the antehumeral bands were completely divided into anterior and posterior spots. Specimens occurred with many features attributed by Lieftinck (1953a) to *C. resecta* Lieftinck, but there did not appear to be any clear discontinuity over the range of variation even though many specimens combined 'definitive' characters of the two species. An unusual amount of variation occurred in the small yellow markings on the head and prothorax, but the genae were always yellow, not black as described in *resecta*. It is probable that *resecta* is a junior synonym of *nigrohamata* (K.D. Dijkstra in litt.).

Platycnemidinae***Copera vittata* (Selys)**

Sites 17, 26, 29. Stagnant streams and swampy areas, mostly in disturbed forest. Local but very abundant where it occurred. Subadult "ghost" forms were frequently observed in forest near swampy areas.

***Copera* sp.**

Sites 3, 8, 34, 35. Common at Bukit Patoi and Sg. Ingei in swampy areas and slow moving streams. This form is close to *C. vittata* but the legs are black, rather than red and there are also slight differences in the male appendages and the structure of the female prothorax. It is most probably a new species.

PLATYSTICTIDAE

Small to medium size finely-built species with clear, falcate wings. Usually found in primary forest on very small streams or boggy seepages in steep terrain. Many species were highly inconspicuous as they flitted about in deep shadow, and to judge from their appearance in canopy fogging samples, some may fly higher than has previously been supposed. Several are known from only a very restricted range but this may reflect under-collecting. There almost certainly remain undiscovered species in Borneo and at least four of a probable eight species recorded in this study appear new to science. The present separation of *Protosticta* and *Drepanosticta* on the basis of minor venational details is untenable and requires review. Larval characters have been discussed by Lieftinck (1934a).

***Drepanosticta attala* Lieftinck**

Site 1. A single male was collected by Roger Kitching in a canopy fogging exercise conducted at dawn in the forest at the KBFSC. This species was previously only known from West Kalimantan.

***Drepanosticta* sp. A aff. *crenitis* Lieftinck**

Site 1. Two males answering the original description of *D. crenitis* fairly closely, with the exception of the prothorax which is yellowish, rather than black, were taken in the forest at the KBFSC, in deep shade, near a marshy area at the head of a small stream. In the same locality females belonging to two species were found, neither belonging to *D. crenitis* and neither definitely associated with this species. The superficially very similar *D. versicolor* (Laidlaw) was also present.

***Drepanosticta* sp. B aff. *crenitis* Lieftinck**

Site 1. Three females were taken at the same locality as the last. The hind margin of the prothorax bears a small, partly erect, median spine. It might be the female of the last species, the unknown female of *D. dentifera* Laidlaw, or an entirely new species. Given the co-occurrence of at least two very closely related species it will probably not be possible to associate males with females until we find copulating pairs.

***Drepanosticta* sp. C aff. *crenitis* Lieftinck**

Site 1. Two females were taken at the same locality as the last two species. The posterior margin of the prothorax bears two short submedial spines. Abdominal markings also differ slightly from the female of *Drepanosticta* sp. B. As with the last species this might be the female of *Drepanosticta* sp. A, *D. dentifera* or an entirely different species.

As noted above, its status should be treated as uncertain until it can be associated with a male and adequate material is obtained.

Drepanosticta forficula Kimmins (?)

Sites 1, 35. One male was recorded in the forest near Sg. Mata Ikan at the KBFSC and one female from Sg. Ingei. Clearly distinguished from *rufostigma* by the appendages and markings on the head, it is smaller (male Hw 21 mm, abdomen + appendages 34 mm) than Kimmins' type specimens from Mt Dulit with slightly different abdominal marking. It is the same size as *D. rufostigma* from the KBFSC, to which it is very similar in general appearance.

Drepanosticta rufostigma (Selys)

Sites 1, 32, 35. Common on small tributaries in primary mixed dipterocarp forest. Males rested on foliage above the water. Females were observed ovipositing unguarded in living leaves overhanging the water above a cascade. A larva, probably of this species, was taken from a leaf-pack at the edge of a riffle.

Drepanosticta versicolor (Laidlaw) comb. nov.

Sites 1, 35. This species frequented boggy areas in primary mixed dipterocarp forest, particularly soaks at the heads of small streams in hilly areas. They flew mostly in the shade and were very inconspicuous on the wing and when resting, being overall fuscous to black with inconspicuous blue abdominal markings. Formerly placed in *Protosticta* on the basis of venation, the discovery of the male indicates that this species undoubtedly belongs in *Drepanosticta*, close to *D. crenitis*.

Description of the male (Fig. 3)

Head: Dorsally bronze-black, except for labrum and anteclypeus which are yellowish cream in colour, and the second antennal segment and distal part of the first antennal segment which are pale dirty yellow. Ventrally, labrum and maxillae dark brown.

Thorax: Dorsum of prothorax with posterior margin produced into a very long, thin, slightly recurved median spine, about 1.6 mm in length, somewhat longer than the remainder of the segment. Prothorax and synthorax uniform dark brown on dorsum and sides, ventrally black as far as coxae. Coxae dark basally, especially on prothorax, becoming paler distally. Remainder of legs uniform pale dirty yellow in colour. Wings hyaline; venation dark reddish brown with major veins darker. Crossvein Cu-A (ac) forked near wing margin to form a 'Y'. Pterostigma almost square with rounded margins, chocolate brown in colour with a very fine pale line around the inner margins.

Abdomen: Dark brown grading to nearly bronze-black dorsally in the middle of each segment. S1-6 each with a very small bluish white dorsal spot at the anterior margin. Dorsum of S9-10 almost entirely bluish white. Appendages brown (Fig. 3). Superiors long, somewhat longer than S9, thin and gradually tapering, slightly down curved distally, with a long broad interior ventral flange from their midpoint to a point just basal to the apex. Inferiors slightly shorter, thin and slightly incurved, with a short terminal hook and a broadly triangular, inward-directed subapical spine of similar length.

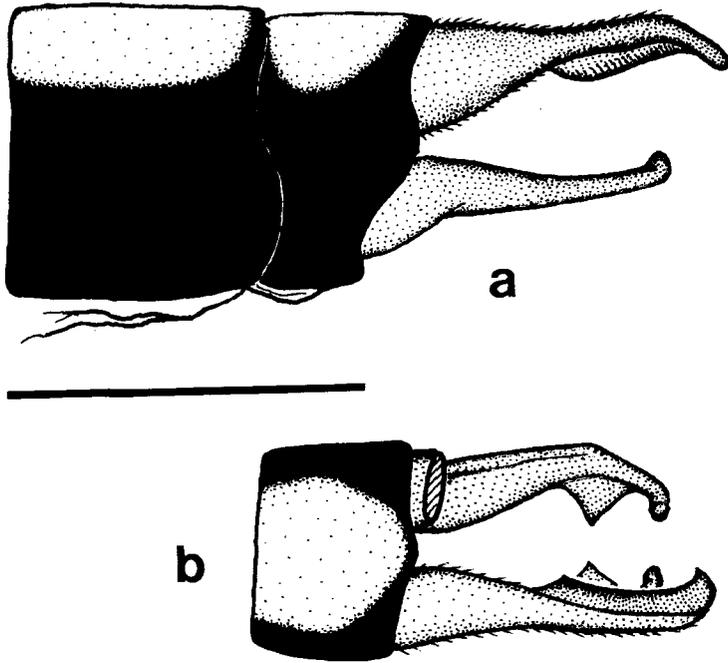


Figure 3. *Drepanosticta versicolor* comb. nov. – (a) lateral view of male appendages and S9-10; (b) dorsal view of S10 and male appendages, right superior removed to show inferior. Scale bar = 1 mm.

Measurements (mm): Hw 16.8-17.2, abdomen + appendages 25.1-26.2.

Apart from the differences in venation and sexual characters the male is very similar to the female, colour differences from Laidlaw's (1913) description probably owing to the superior state of preservation of my material and the availability of colour photographs of living specimens. It should be noted that this description also corresponds closely to *D. monoceros* Lieftinck. I have not examined the type of *D. monoceros* but should it prove conspecific with *D. versicolor* the latter name takes precedence.

Protosticta feronia Lieftinck

Recorded from kerangas and mixed dipterocarp forest at Sungei Ingei by Thompson & van Tol (1993).

Protosticta sp. A aff. *feronia* Lieftinck

Site 1. A single male was taken in forest at the KBFSC near the source of the Sg. Mata Ikan. It was flying at a height of about 3 m. In size and general appearance this species is very similar to *P. feronia* but differs significantly in markings, venation and the structure of the male terminalia.

***Protosticta* sp. B**

Site 1. One male was collected by Roger Kitching in a canopy fogging exercise conducted at dawn in the forest at the KBFSC. A female was taken nearby, perched on vegetation, 4 m above a boggy spring. The male terminalia are almost indistinguishable from those of *Drepanosticta dulitensis* Kimmins but the specimen differs in venation and in the extraordinary length of the abdomen.

PROTONEURIDAE

Medium sized zygoptera of fine build. A large number of very similar *Prodasineura* species occurred in primary forest and were among the commonest odonates in shaded forest streams and freshwater and peat swamp forests in Brunei. Oviposition was frequently observed and was either in tandem or alone, usually about water level in root masses of rheophytes. A number of specimens taken in this study do not match any described species and probably more species await discovery.

***Elatoneura analis* (Selys)**

Sites 15, 17, 30, 35. Very local but common in certain localities, particularly at Sg. Ingei on the main stream. Males rested on the leaf-tips of *Pandanus*. Oviposition was among *Pandanus* roots. At Benutan creek mature males and females were observed in which the normal orange coloration was replaced everywhere by pale blue, a characteristic sometimes associated with sub-adults. The one specimen captured, a male, was very similar in its markings to normal *analis* and the anal appendages appear identical. In the absence of contrary evidence this is considered a local colour variant.

***Prodasineura collaris* (Selys)**

Sites 13, 18, 24. Sporadic but sometimes abundant in small streams in freshwater swamp forest. Oviposited in tandem in root masses of *Pandanus*, the male adopting the sentinel position. This was the only blue species of *Prodasineura* recorded.

***Prodasineura dorsalis* (Selys)**

Site 24. Locally abundant in freshwater swamp forest. Males perched in sunny patches on leaves about 1-2 m above the water surface and such sites were frequently contested. Oviposited in tandem in root masses of *Pandanus* with the male in the sentinel position.

***Prodasineura* sp. aff. *dorsalis* (Selys) (?)**

Sites 9, 12, 13, 18. Recorded from freshwater swamp forest, with habits similar to those of *P. dorsalis*. Although not rare, the species occurred at low densities and was easily overlooked. It resembles *P. dorsalis* and *P. auricolor* Fraser but is probably distinct from both, being distinguished by well defined pale blue posthumeral bands. At present I have not been able to examine sufficient relevant material to proceed with description.

Prodasineura haematosoma Lieftinck

Site 3. Found only in sluggish semi-shaded parts of the stream at Bukit Patoi, where it was very abundant. Both sexes perched on low vegetation over the stream. Oviposition was in tandem in root masses in the stream banks.

Prodasineura hosei (Laidlaw)

Site 30. A single specimen only was found sitting in *Pinanga* beside clear swift running water on the upper Sg. Rampayaoh. The specimen agrees well with the original description of *P. hosei* except that the lateral orange stripe on the synthorax is greatly reduced.

Prodasineura sp. aff. *hosei* (Laidlaw)

Sites 7, 9, 15, 18, 21, 29, 31, 32, 33, 35. Extremely abundant in certain streams in mixed dipterocarp forest, especially where *Pinanga* was present. A few specimens were taken in swamp forest with *Pandanus*. On *Pinanga* streams both sexes rested on vegetation over the water. Oviposition was in the afternoon in root masses around the stream banks, normally in tandem. The male of this species differs from typical *hosei* in the length of the antehumeral stripes and the female is also distinctively marked. Insufficient material was collected for a rigorous analysis of their status. These specimens may be conspecific with specimens from Mt Dulit and Marudi (Claudetown) placed with reservations in *P. peramoena* (Laidlaw) by Kimmins (1936).

Prodasineura hyperythra (Selys)

Site 3. Found only in sluggish parts of the stream at Bukit Patoi. Habits were similar to *P. haematosoma*. The distinction between the two species is slight but appears consistent.

Prodasineura verticalis (Selys)

Sites 1, 15, 26, 30, 33. Common on the main stream at the KBFSC and elsewhere on streams in mixed dipterocarp forest. Occasionally in streams in freshwater swamp forest. At the KBFSC, males frequently hovered very low over swiftly flowing water, flying along the edges of the shadows cast by the surrounding foliage. Although tandem pairs were frequently seen in the afternoon near the river banks, females generally oviposited alone, typically in root masses in the banks in sluggish backwaters behind log jams.

ANISOPTERA

AESHNIDAE

The majority of aeshnid species were crepuscular feeders, and could be found hawking late in the afternoon to well after sunset, particularly around exposed ridges in forested country. Even species which were active in full sunlight were also observed flying late

in the afternoon until dark. Anecdotes of activity late in the evening are also provided by Lieftinck (1934b). Sexual behaviour and oviposition however frequently took place in deep shade even in the middle of the day. At Sg. Burong, numerous species regularly hawked along a disused roadway running through selectively logged forest. It was usually easy to recognize the various genera on the wing as they flew high around the treetops following swarms of small Diptera, although specific determination usually required capture. As the evening progressed the Diptera swarms descended followed by the dragonflies which flew 1-2 m above the ground. There was a distinct generic succession of activity, with *Oligaeschna* flying first, from about 16:15 h onward, followed by *Gynacantha*, then *Heliaeschna* and *Tetracanthagyna* which appeared at or just before sunset (Table 1). Large aeshnids were also seen fleetingly in many forest localities and flying along slow flowing streams, especially at Bukit Patoi, but were never captured. Driving into mixed peat-swamp forest at Kuala Belai around sunset substantial numbers of large aeshnids were regularly seen hawking above the road and could be clearly observed as they approached the car windscreen. The majority were probably *Heliaeschna* and *Gynacantha* species but some individuals bore the strong brown costal streak characteristic of certain male *Tetracanthagyna* and *Linaaeschna polli*. As *Tetracanthagyna* seem to be associated most commonly with clear running water I would suggest these black-water localities as being the best places to seek *L. polli*. Aeshnid larvae are known to develop mostly in shallow forest pools or slow flowing water (Lieftinck 1954). No aeshnid other than *Indaeschna grubaueri* was ever taken or seen at the KBFSC, probably because of an acute shortage of forest pools given the steep topography. *I. grubaueri* was the only species recorded from phytotelmata (Orr 1994; Kitching & Orr 1996).

Table 1. Flight period of crepuscular aeshnid genera hawking at Sungei Burong.

minutes before sunset	120	105	90	75	60	45	30	15	0	-15	-30
<i>Oligaeschna</i>			████████████████████								
<i>Gynacantha</i>					████████████████████						
<i>Tetracanthagyna</i>								████████████████████			
<i>Heliaeschna</i>									???	████████████████████	

Aeshninae

Anax guttatus (Burmeister)

Sites 4, 5, 8, 10, 11, 23. Common around drains and ponds in disturbed habitat throughout Brunei. Although principally diurnal, being active from mid-morning onwards, it was often seen late in the afternoon until sunset. Most reproductive

behaviour probably took place later in the afternoon (after 15:00 h) and at Pantai Muara unattended females were observed ovipositing under lily pads after dusk. Larvae were frequently encountered and were highly aggressive towards one another. When offered small fish or tadpoles as prey the latter were invariably preferred.

***Anax panybeus* Hagen**

Site 5. A single male was taken late in the afternoon at Pantai Muara. The species may have been more common and widespread than this record suggests but it was certainly everywhere outnumbered by *A. guttatus*.

***Gynacantha basiguttata* Selys**

Sites 4, 8, 9, 10, 13, 14, 18, 21, 29. Common in primary and secondary forest in flat terrain, especially in alluvial forest. Frequently coming to light. At Sg. Lumut males were often present from the early afternoon to dusk, guarding a large (4x7 m) shallow, leaf-bottomed pool. Mating was observed once about 15:00 h, and following separation the female proceeded to oviposit in the leaf litter with the male perching nearby. Larvae were found in this situation under leaves.

***Gynacantha bayadera* Selys**

Site 14. One male was taken at Sg. Burong, hawking low along a ridge about one hour before sunset.

***Gynacantha dohrni* Krüger**

Sites 8, 13, 14, 20, 21, 29. Common in the same situations as *basiguttata* and with similar habits. Both sexes were often seen in large numbers hawking for small Diptera at Sg. Burong. A large proportion of females had intact appendages and were clearly teneral. Three such females dissected were judged to be virgin by the absence of sperm in the spermathecae. Males in particular were often seen in deep forest in the middle of the day, mostly resting on the stems of small saplings but sometimes hawking along forest paths. Males shared the pool at Sg. Lumut with *basiguttata*, and three matings were witnessed from 13:00-16:00 h. Typically the female arrived at the pool and began probing the leaf litter. While thus occupied she was seized by a male who carried her high into the nearby vegetation. Within a few minutes she returned to oviposit unmolested. In Brunei *G. dohrni* was the most common member of the genus in primary forest, but *basiguttata* was more frequently found in secondary forest as well, hence was more widespread.

***Gynacantha maclachlani* Krüger**

Site 25. One specimen only, taken during the day along a narrow path, deep in kerangas forest at Badas.

***Heliaeschna crassa* Krüger**

Sites 4, 8, 14, 27. Flying very late, specimens were mostly taken at light near primary or secondary dipterocarp forest. One male took up residence on my verandah at Sg. Tilong, where he rested on vegetation all day, then left to start hawking for insects

just before sunset, returning ca 2.5 h later. In mixed peat swamp forest at Kuala Belai a mating pair in the wheel position fell to the ground near a light sheet nearly two hours after sunset. The male was eating a chironomid and it was surmised that the two were hawking around the light when they encountered each other and mated. Several specimens appeared in student collections, apparently taken inside houses near secondary forest.

***Heliaeschna idea* (Brauer)**

Sites 8, 14. Found in similar situations to *H. crassa* but less common.

***Heliaeschna simplicia* (Karsch)**

Sites 4, 10. A female was taken at light in the government rest house, Bangar, and a male at the UBD.

***Indaeschna grubaueri* (Foerster)**

Sites 1, 3, 31, 35. Common in primary dipterocarp forest where it generally flew quite low in the understorey. It was basically diurnal in habits although it was sometimes seen hawking late in the afternoon, often in the canopy, and sometimes came to light. Males were most frequently encountered guarding breeding sites, which included small forest pools, rocky pools beside forest streams and large phytotelmata, especially buttress pans (Orr 1994). The larvae were often extremely abundant in these situations, and appeared to interfere little with one another. Males mated with females as they approached these sites to oviposit. Eggs were inserted into leaf litter, frequently with the male guarding from a nearby perch. In captivity larger larvae thrived on a diet of tadpoles but were never known to capture small fish when these were offered.

***Tetracanthagyna degorsi* Martin**

Sites 4, 3. One male was taken at light in Bangar. Larvae were discovered at night in the creek at Bukit Patoi in slow flowing water. They perched on dead branches entirely or almost entirely out of the water with the head directed toward the water surface. This may be a specialization for catching fish, which appear to be their main prey. Captive individuals, which remained underwater by day, emerged at night and took small fish swimming near the surface and consumed most of the flesh. They were distinctly better at capturing fish and showed more willingness to eat them than other large aeshnids such as *Indaeschna grubaueri* or *Anax guttatus* which appeared to prefer tadpoles. Any such feeding specialization is surely related to a preference for streams, rather than small ponds in which fish would be rarely encountered. Wilson (1995) describes similar habits for the larvae of *T. waterhousi* McLachlan.

The larva of this species was known to Lieftinck (1954), and his drawing of the larva was recently published (Corbet 1999) while this paper was undergoing review. A detailed description of the larva follows.

Description of the final instar larva (Fig. 4)

General form elongate and slender (Fig. 4a), two mature larvae were 51-52 mm in length.

Head: slightly broader than long, with an angular outline, especially in the region of the occiput. Three pairs of tubercles present, the first flattened and rounded at the upper margins of the frons, the second lying just behind and between the antennal sockets, and the third on the occiput. Antennae 7 segmented. Eyes small and well separated. Prementum (Fig. 4b) very long (ca 10 mm), narrow at base and expanding abruptly in its distal third; distal margin with paired rounded lobes fringed with short setae. Labial palp with thin, internally serrate, hooked process arising from its inner angle. Setae absent. Movable hooks very long and curved distally; broadly overlapping when at rest.

Thorax: with pronotum, meso- and metanotum angulate and bearing blunt spines; metanotum with rounded crenulated flanges posteriorly. Legs short and robust. Femora flattened with indistinct spines along the anterior margin of the prothoracic femora.

Abdomen: long and thin with broad lateral flanges on S1-9. Angulated along mid-dorsal line, especially in posterior segments. S5-9 bearing distinct lateral spines, largest on the posterior segments; S1-4 with slight projection arising from near the middle of the lateral flange. S8-10 with prominent dorsal spine at the posterior margin and S6-7 with smaller rounded processes. Anal pyramid short and narrow, only slightly longer than S10. Paraprocts robust, laterally flattened with lightly toothed edges, terminally obliquely truncated, slightly shorter than epiproct (Fig. 4c). Epiproct thin and slightly forked distally. Cerci slightly more than half length of epiproct (male) or about one third length of epiproct (female). Dorsal process in male about same length as cerci. Overall ground colour dark brown with distinct darker mottling on the head. Legs distinctly banded.

The tuberculate head and thorax, small eyes, lack of setae on the labial palp and thin elongate abdomen should distinguish this species from other aeshnid genera likely to be encountered in the region. At present the larvae of *Linaeschna*, *Heliaeschna* and *Oligaeschna* are unknown. I know of no other aeshnid larva with the inner process on the labial palp so thin and hooked, perhaps an adaptation to a piscivorous diet.

Tetracanthagyna plagiata (Waterhouse)

Site 14. Females of this species were observed frequently at Sg. Burong just on sunset, where they could be seen hawking at a height of at least 15 m near the crowns of trees. One male was taken at light and others, probably of this species, were seen flying very rapidly over the shoulder of a ridge at the same locality.

Brachytroninae

Oligoeschna buehri (Foerster)

Sites 8, 14, 29, 30. Uncommon in alluvial forest beside the Sg. Rampayoh and taken occasionally at Sg. Burong hawking for insects in late afternoon with other aeshnid species. To judge from an absence of females, which were distinctive even in flight, this was not a common insect at the latter locality. A female was taken in day time ovipositing in very small (1.5 m diameter) shallow pools lined with a thick layer of rotting leaves and humus in deep shade in secondary dipterocarp forest. Some pools were almost dry with only a few wet leaves on the surface. A search of the top 10 cm of leaves failed to reveal larvae.

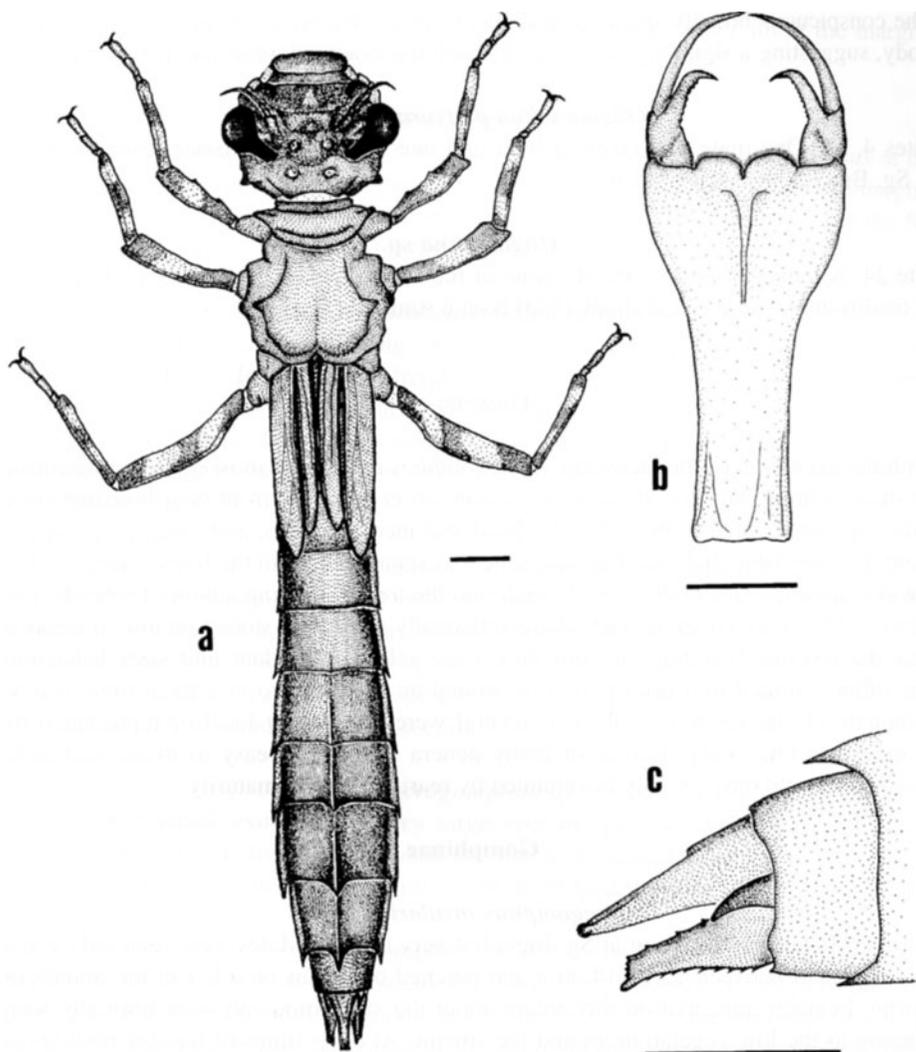


Figure 4. *Tetracanthagyna degorsi* – (a) dorsal view of final instar larva (female); (b) dorsal view of prementum and labial palps with mask extended; (c) lateral view of terminalia (female). Scale bars = 3 mm.

Oligoaeschna foliacea Lieftinck

Sites 8, 14. Very numerous at Sg. Burong where both sexes hawked for insects along a disused logging road from between 16:00 h and sunset, at about 18:00 h. Typically they flew about 5 m above the ground for the first hour of activity, descending to 1-2 m near dusk. A majority of females were teneral, with appendages intact, and probably mostly virgin, as dissections of three such individuals showed a lack of sperm in the spermatheca.

The conspicuous broadly spatulate appendages of the female are held well out from the body, suggesting a signaling function, although the exact nature of this is uncertain.

Oligoaeschna platyura Lieftinck

Sites 4, 14. One male was taken at light and one hawking with other aeshnid species at Sg. Burong at about 17:15 h.

Oligoaeschna sp.

Site 24. A female, almost certainly none of the above species, was taken in deep shade in freshwater swamp forest about 11:00 h on a sunny day.

GOMPHIDAE

With the exception of the lacustrine *Ictinogomphus decoratus*, most gomphids occurred on streams in primary forest and were seldom observed away from their breeding sites. Forest species tended to be extremely local and inconspicuous, and often very swift in flight. It is probable that much of their time was spent feeding in the forest canopy, since it was common to see both sexes fly high into the trees following a bout of reproductive activity. Males of larger species characteristically rested on stones or low vegetation near the riverine breeding site but they were seldom abundant and such behaviour was often confined to a brief period of around an hour or two at a fixed time of day. Although 11 species were collected, several were either very local or represented by a single specimen only. Larvae of many genera were fairly easy to locate and adult specimens could only reliably be obtained by rearing these to maturity.

Gomphinae

Burmagomphus insularis Laidlaw

Site 35. Moderately common at Sg. Ingei but very cryptic. Males were seen only when they appeared between 12:00-14:00 h and perched on stones on a bar in the middle of a riffle. Females appeared on the stream about the same time and were normally seen clinging to the low vegetation around the stream. At other times of the day both sexes appeared to retreat to the subcanopy of the surrounding forest.

Heliogomphus sp. (?)

Site 1. A single female specimen, was captured on the Sg. Mata Ikan at the KBFSC. It appeared about 10:00 h and flew several times up and down the stream. Several sightings of fugitive gomphids at this locality probably belonged to this species.

Leptogomphus coomansi Laidlaw

Sites 7, 21, 31. Both sexes were common along Sg. Lumut where they sat on the *Pandanus* overhanging the water or in nearby vegetation. When disturbed they were sluggish in flight and prone to settle again. A very fresh teneral female was taken in vegetation at the edge of a large (20x30 m) deep pool below a small waterfall at

Menteri. Larvae, probably of this species, were dredged from leafy silt at the margins of the stream at Sg. Lumut.

Leptogomphus mariae Lieftinck (?)

Sites 31, 35. A female, probably of this species, was taken clinging to *Pandanus* at the edge of a large pool in the main stream at Sg. Ingei and another was observed emerging from underwater onto a stone in the centre of a small sandy bottomed pool on the Sg. Mendaram. The exuvia was carried away by the current.

Macrogomphus parallelogrammus albardae (Selys)

Sites 29, 35. Quite common flying over the stream in the slower reaches at Sg. Rampayoh and Sg. Ingei. Males frequently hovered in midstream. Females were captured by males as they flew up or down the stream and mating took place in the nearby vegetation. Females oviposited over shallow water with a fine sandy or silty substrate, laying eggs in a few brief passes then flying along the stream to the next suitable area.

Macrogomphus quadratus (Selys)

Sites 8, 17. Common along a small sluggish stream about 1-1.5 m in depth and 2-3 m wide in alluvial forest near Kg Long Mayo. Males were relatively slow in flight and frequently perched on small twigs up to 1 m above the water surface, sometimes quivering their wings. Females were observed ovipositing alone in slow running water in a shallow (0.5 m) sandy bottomed section.

Macrogomphus sp.

Site 15. The larval exuvia of a very large species, possibly *M. parallelogrammus albardae* (Selys), was found on a *Pandanus* leaf at Benutan Creek. As is usual in the genus the rectal basket is equipped with a well developed snorkel.

Microgomphus chelifera (Selys)

Site 1. A teneral male, still unable to fly, was taken clinging to a rattan above a sheltered backwater on the Sg. Belalong, near the KBFSC. Larvae probably belonging to this species were frequently found in the deep silt and finely macerated leaf litter nearby.

Onychogomphinae

Megalogomphus sumatranus (Krüger) (?)

Sites 1, 29, 35. Fairly common on larger forest streams, including the main stream at the KBFSC. Near the middle of the day males rested on stones and twigs near the side of the river, normally in the region of accumulated logs and silty backwaters. Larvae were commonly found in fine gravel at the edge of fast running water. Females were seldom seen and both sexes were extremely rapid in flight. Mating and oviposition were observed once at Sg. Ingei. The female hovered at the head of a narrow, swiftly-flowing runnel. A patrolling male seized her in flight and carried her 15 m up into

the surrounding vegetation where the wheel was achieved immediately. The female returned within 5 minutes and commenced ovipositing over a small submerged gravel bank, a few metres downstream from the site of encounter, with a series of rapid back and forth flights, each time dipping her abdomen into the water surface. The form of *sumatranus* occurring in North Borneo is distinctly smaller than specimens from Sumatra and should probably be treated as a distinct subspecies.

Hageniinae

Sieboldius japonicus (Selys)

Site 1. A single male was recorded in January 1995 on the Sg. Belalong at the KBFSC, sitting on a low stone in a gravel bar located midstream in the region of a major riffle. When disturbed it flew back and forth along the stream several times over a distance of about 150 m returning to inspect its perch but not landing. Eventually it flew off and was not seen again over the next five days. The flattened foliform larva was found by P. Cranston in leaf-packs in riffles near the place of the adult sighting.

Lindeniinae

Ictinogomphus acutus (Laidlaw)

Sites 14, 23. Sporadically quite common in the black-water drain at Badas. One female was taken at Sg. Burong in secondary vegetation far from water.

Ictinogomphus decoratus melaenops (Selys)

Sites 7, 11, 16, 19, 28. Very common on lakes and large ponds, including artificial ponds at the Rimba Horticultural Centre, and natural lakes such as Tasek Merimbun, and Luagan Lalak. Sometimes found on sluggish open streams. Males rested on emergent vegetation 0.5-1 m above the water, and were neither particularly wary nor rapid in flight. Matings were observed infrequently throughout the day and oviposition was unaccompanied by the male. The rounded, flattened larvae were occasionally dredged from vegetation near the water surface in various localities. Cast exuviae were sometimes found on top of lily pads.

CORDULIIDAE

The majority of the Corduliidae were fugitive forest dwellers. Their presence was often highly unpredictable and ephemeral. Species inhabiting open areas of standing or slowly flowing water tended to be more abundant and regular in occurrence. Larvae of several *Macromia* species and of *Macromidia fulva* were frequently encountered in a variety of microhabitats in the streams at the KBFSC although seldom in large numbers. Large corduliids, probably *Macromia* species, were sometimes seen flying very swiftly along the smaller streams in patchy sunlight and shadow at the KBFSC and other primary mixed dipterocarp forest sites.

Corduliinae

Hemicordulia tenera Lieftinck

Sites 24, 31. Common in 1992 for several months on a small stream in freshwater swamp forest, then not seen again in several years. Males hovered in shafts of sunlight over small pools on the stream. A single female, almost certainly this species, was found dead on foliage at Mendaram, apparently sucked dry by an arthropod predator.

Metaphya micans Laidlaw

Recorded by Thompson & van Tol (1993) in peat swamp forest, Sg. Ingei.

Idionychinae

Idionyx yolanda Selys

Site 35. A single female was taken feeding on a swarm of small Diptera beside the stream at Sg. Ingei. Thompson & van Tol (1993) record this species from freshwater swamp forest nearby.

Macromidia fulva Laidlaw

Site 1. One afternoon in 1995 a large flight of at least 100 teneral appeared over the main stream at the KBFSC from 16:00-16:30 h. Mature specimens were never captured nor seen with certainty, although fugitive specimens flying rapidly over the shaded margin of the river may have belonged to this species. Larvae were quite common in deep leaf litter in protected backwaters.

Macromiinae

Epopthalmia vittigera (Rambur)

Sites 3, 11, 16, 19, 22, 28. Common on large open bodies of standing water, both natural and man-made. Males patrolled back and forth over a large area often ranging more than 250 m. A female was taken ovipositing in a small pond at the edge of the forest at Bukit Patoi.

Macromia cincta Rambur

Sites 23, 29. Moderately common in a few localities including a deep, open, black-water drain at Badas and an open area of the stream on the lower reaches of the Sg. Rampayoh. Very rapid in flight and almost never perching. A female was observed ovipositing at the edge of the stream at the latter locality.

Macromia corycia Laidlaw

Sites 30, 35. Two females were taken at the edge of streams in dipterocarp forest, ovipositing in shadow in slow flowing shallow water near the bank. Differences between the (previously unknown) female and known male coloration parallel exactly those observed between the sexes in *M. gaesteckeri* Krüger from Java (Lieftinck 1950).

***Macromia westwoodii* Selys**

Site 1. Bred from late instar larvae found at night in a sheltered rock pool adjoining the Sg. Mata Ikan at the KBFSC. The long legged spider-like larvae were clinging to the rock near the water surface. Large anisopterans which may be the adults of this species sometimes flitted very rapidly along the tributary and sometimes on the main stream of the Sg. Belalong, but were not common.

LIBELLULIDAE

Being conspicuous insects libellulids were well sampled. Males frequently perched for much of the day beside breeding sites where they were easily captured. Most species bred in standing water or gently flowing water in either open areas, including disturbed areas and natural lakes and marshes, or forested swamps. A few species bred in rivers and flew over fast flowing water (*Zygonyx*, *Onychothemis*) and species of *Lyriothemis* could be found inside mixed dipterocarp forest where they bred in phytotelmata or shallow forest pools. A few genera, e.g. *Rhyothemis*, *Neurothemis*, *Orthetrum* and *Pantala* were far ranging and were often encountered feeding on sunny hilltops far from their breeding habitat.

Tetrathemistinae

***Hylaeothemis clementia* Ris**

Recorded in early literature from alluvial forest in Brunei (Laidlaw 1912).

***Risiophlebia dohrni* (Krüger)**

Sites 8, 21, 26, 27. Males perched in low vegetation or hovered over tiny sun dappled pools in freshwater swamp forest and peat swamp forest. Females were observed ovipositing in these situations, guarded by the male.

***Tetrathemis irregularis* Brauer**

Sites 2, 3. Extremely localized but common where present. Males were always present at a small exposed pool of clear water created by road works, about 1 m deep, into which the forest stream at Bukit Patoi drained prior to its diffusion into a swampy area. They perched on exposed twigs, sometimes flying over the pool, and mated with females which arrived irregularly throughout the day.

Brachydiplactinae

***Brachydiplax chalybea* Brauer**

Sites 2, 4, 5, 6, 8, 10, 11, 12, 13, 16, 19, 22, 23, 27, 28, 34. Very common in drains, dams, lakes and swamps in open areas exposed to direct sunlight, frequently in company with *Orthetrum testaceum*. At an artificial reservoir at Rimba Horticulture Centre (BSB) males established territories from 08:00-17:00 h with a peak in agonistic interactions from 10:00-12:00 h. Most territorial males moved two or three times a day. Females started

to arrive about 12:00 h with maximal mating and oviposition from 14:00-15:00 h. During oviposition the male hovered closely over the female, frequently entering into disputes with other males. Exuviae were often present in large numbers in the grass around the dam.

***Brachydiplax farinosa* Krüger**

Recorded by Thompson & van Tol (1993) in freshwater swamp near Sg. Ingei.

***Brachygonia oculata* (Brauer)**

Sites 8, 9, 12, 13, 14, 17, 21, 24, 25, 26, 27, 34. Very common in almost all freshwater swamp forest and often in peat swamp forest. Males guarded small puddles and mated with arriving females, which they then guarded from a nearby perch as they oviposited in shallow pools. They overlapped frequently with *Orchithemis* and *Tyriobapta* species but tended to be further removed from running water. Both sexes perched in a regularly spaced fashion along forest paths in the Kerangas forest at Badas and in similar localities, well removed from their breeding grounds, maintaining territories which may be related to feeding.

***Brachygonia ophelia* Ris**

Site 27. A rare species, one male was taken guarding a very small puddle in disturbed peat swamp forest at Kuala Belai.

***Chalybeothemis fluviatilis* Lieftinck**

Sites 22, 28. A very local species, it was common at the edge of a deep channel at Luagan Lalak and sometimes occurred at Sg. Badas, precisely the locations to which *Pseudagrion lalakense* was restricted. Reproductive activity commenced around 11:00 h and continued until about 15:00 h.

***Nannophya pygmaea* Rambur**

Sites 10, 12, 22, 23, 25, 26, 27, 34. Locally very common in drains adjoining freshwater swamp forest and peat swamp forest. It was found in partly exposed areas, typically with lush growth of grass around the edges, but not usually in large bodies of water. Males maintained tiny territories a metre or so in diameter much as described for the species in Japan (Tsubaki & Ono 1986). Sexual competition was intense and ovipositing females were frequently stolen and remated while their mates were engaged in territorial defense. They were frequently found in company with *Libellago hyalina*, *Orthetrum sabina* and *O. chrysis*. The two latter species were sometimes observed preying on the tiny adults.

***Raphismia bispina* (Hagen)**

Site 6. Uncommon. Males perched close to the water in sun patches well inside the mangrove forest at Kapok Kanen. Pools guarded were distinctly saline, as previously noted by Lieftinck (1954).

Tyriobapta kukenthali (Karsch)

Site 18. This species was only taken at Long Mayo swamp where it was moderately common. The males guarded pools in little rivulets. *T. torrida* occurred infrequently at the same locality.

Tyriobapta laidlawi Ris

Sites 18, 24, 27. Widely distributed in freshwater swamp forest and sometimes peat swamp forest. Males rested on the trunks of trees in the manner of *T. torrida*. The species was also almost always present at a small, leafy stagnant pool beside a small stream inside steep dipterocarp forest on the Labi Rd.

Tyriobapta torrida Kirby

Sites 3, 18, 21, 30. Very abundant in several localities near swamps or marshy backwaters on larger streams. Both sexes rested on the trunks of trees, often several hundred metres from the breeding habitat, where they appeared to establish feeding territories. Mating and oviposition were frequently observed in stagnant water throughout the day, the males guarding the females from a nearby perch.

Libellulinae*Agrionoptera insignis* (Rambur)

Site 8. Uncommon and local. Found only around a small pond in an open area in secondary forest near Sg. Tilong.

Agrionoptera sexlineata Selys

Sites 21, 25. Common in kerangas in Badas Forest Reserve where both sexes haunted forest paths, perching briefly in sunny patches. At this locality and in alluvial freshwater swamp at Sg. Lumut it bred in larger shallow leaf-bottomed pools. Males perched on twigs over the water defending territories no larger than 3-4 m².

Cratilla lineata (Brauer)

Sites 1, 13, 24, 25, 35. Very common in peat swamp forest and marginal open areas, where it bred in shallow pools; also found in freshwater swamp, kerangas and occasionally in mixed dipterocarp forest where it flew together with *C. metallica*.

Cratilla metallica (Brauer)

Sites 1, 3, 13, 20, 25, 35. Especially common in primary mixed dipterocarp forest where it bred in shallow pools along with *Indaeschna grubaueri*. It also occurred less frequently in kerangas and peat swamp forest. Larvae were aggressive and appeared to exclude many other species from smaller puddles. It sometimes also bred in degraded large phytotelmata, from which much of the leaf litter had been removed, where it may have excluded *Lyriothemis cleis*. Males perched near suitable breeding sites and mated with incoming females.

Lyriothemis biappendiculata (Selys)

Site 35. A small series of males was taken at Sg. Ingei in an open boggy area from which water seeped into the stream. Elsewhere in Borneo I have always seen it in similar situations.

Lyriothemis cleis Brauer

Sites 1, 3, 25, 29, 31. Common in primary mixed dipterocarp forest, especially the KBFSC and in the Labi area; less frequently in Kerangas and advanced secondary forest. At the KBFSC, Mendaram and Bukit Patoi it was commonly found breeding in phytotelmata, and did not appear to utilize larger bodies of standing water which were frequented by *Cratilla metallica*, which often replaced it in larger treeholes once these had been significantly disturbed. The larvae, along with those of *Pericnemis triangularis* were the most important predator in phytotelm systems and closely resembled those described from Sulawesi (Kitching 1986). Males stood guard over treeholes and mated with females as they arrived. The ecology of the larvae and its role in the treehole environment have been discussed elsewhere (Orr 1994, 1996; Kitching & Orr 1996). Specimens were also taken in numbers at Sg. Rampayoh in secondary forest by the stream margin and in kerangas at Badas, both localities with no known larger phytotelmata and only a little standing water. It is possible that they may occasionally breed forest pools in these situations.

Nesoxenia lineata (Selys)

Sites 8, 21, 26, 33. In Brunei this was an uncommon species, recorded from a variety of swampy areas in different forest types, but most commonly in alluvial freshwater swamp. Males perched for long periods on twigs beside small pools.

Orchithemis pruinans (Selys)

Site 24. Encountered regularly in a patch of freshwater swamp forest at Badas where males guarded small pools about a metre in diameter, mating with females as they arrived, which then commenced ovipositing, while the males returned to a nearby perch. The indisputable female was so widely at variance with Ris' (1909) description that I believe this to be incorrect, applying perhaps to a female *pulcherrima*, which is a highly variable species in both sexes. Present specimens, if not associated with a male, would probably have been placed in *O. xanthosoma* Laidlaw, although they do not fit exactly descriptions of this species either (Laidlaw 1911; Ris 1919). In female *pruinans* from this collection there was only a single row of cells proximally in the forewing discoidal field to at least beyond the level of the nodus, frequently extending to the wing margin.

Orchithemis pulcherrima Brauer

Sites 12, 13, 17, 18, 20, 21, 24, 25, 26, 27, 33, 34. Taken in numerous localities in freshwater swamp and peat swamp forest, usually with some slowly running water. Two distinct but variable forms of the males occurred; the black or pruinulent blue *exsudans* Selys and the red or yellow *pulcherrima* Brauer. Similar dimorphism occurred in females but the red form was rare, and a brown form which may simply represent a

juvenile state was sometimes prevalent. In the males there appeared to be no structural difference between the two forms, and both could be seen interacting with each other agonistically. In form *pulcherrima* this took the form of a rather slow head to head ascending flight, with the abdomens cocked upward at about 90°. There seems to be some spatial separation of the two forms, especially at Bukit Terajah longhouse, where the darker form was confined to the stream and its margins, whereas the red form was more common in the forest and swamp beyond. At a sluggish stream near Long Mayo only the red form has been observed. Careful study of sexual behaviour and ecology is required to clarify the status of these forms.

***Orchithemis xanthosoma* Laidlaw**

A male was recorded by Thompson & van Tol (1993) in heath forest, Sg. Ingei.

Orthetrum

Species of this genus exhibited a wide range of habitat preferences ranging from very disturbed temporary pools to primary forest (Table 2). As a rule they preferred slow flowing water although sometimes *chrysis*, *testaceum* and especially *sabina* also occurred, sometimes abundantly, around man-made dams and natural lakes such as Tasek Merimbun. They were mostly absent from stagnant swampy areas and normally preferred open areas with full or partial sunlight.

Table 2. Habitat preferences of *Orthetrum* species. Lighter shading indicates areas of less frequent occurrence.

	Shallow drains, seepages in open degraded areas	Deeper drains ponds and sluggish streams in open degraded areas	Drains and ponds in open areas adjoining primary forest, especially mixed dipterocarp and kerangas	Natural slow streams in within primary forest or old regrowth	Backwaters in fast flowing open rivers in primary forest
<i>O. glaucum</i>	██████████				
<i>O. sabina</i>	████████████████████				
<i>O. testaceum</i>		██████████	██████████		
<i>O. chrysis</i>		██████████	████████████████████	██████████	██████████
<i>O. pruinatum</i>					██████████

***Orthetrum chrysis* (Selys)**

Sites 1, 2, 3, 8, 13, 15, 16, 17, 19, 22, 23, 24, 25, 28, 29, 30, 31, 32, 33, 34, 35. Very common in a variety of situations. Most frequently *chrysis* occurred in moderately degraded areas in mature secondary forest or bordering primary forest and sometimes could be found around small sluggish streams within primary forest. It occurred occasionally in artificial dams and natural lakes though *testaceum* was more common in these situations. In areas of high density males hovered over ovipositing females guarding them closely and often become engaged with rivals. Oviposition occurred from about 09:00-16:00 h with the male hovering in attendance.

***Orthetrum glaucum* (Brauer)**

Sites 7, 8, 10, 14, 22 and various unrecorded localities in Bandar Seri Begawan. Characteristic of highly degraded, completely open areas, vegetated with *Imperata* and *Acacia*.

***Orthetrum pruinosum schneideri* (Foerster)**

Sites 1, 30, 35. The species was recorded at only three localities, all on relatively strong flowing streams in primary mixed dipterocarp forest, where it was generally very common. Males perched in conspicuous positions in the vicinity of backwaters with a sandy or muddy bottom. Oviposition occurred throughout the day, females remaining only very briefly at any site.

***Orthetrum sabina* (Drury)**

Sites 1, 2, 4, 5, 6, 7, 8, 10, 11, 13, 14, 16, 19, 22, 23, 28, 33. A very common species occurring in similar situations to *glaucum* but also in open swampy areas, lakes and dams and even temporary muddy pools. It was frequently observed in gardens, and in areas of lalang (*Imperata* sp.) around forest margins. It was a fierce predator and was recorded taking butterflies of the genera *Curetis* (Lycaenidae), and *Junonia* (Nymphalidae), as well as *Pseudagrion microcephalum* and a teneral female of *Orthetrum chrysis*. It flew quite late and sometimes could be seen foraging at the same time as crepuscular aeshnids at Sg. Burong but it flew much lower and took larger prey. In May 2000 it was recorded at the KBFSC for the first time in the vicinity of the field station; nine years after the site was originally cleared.

***Orthetrum testaceum* (Burmeister)**

Sites 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 14, 19, 31, 33. Very common in open degraded habitats, breeding in drains, lakes and dams and roadside puddles. This species overlapped with *chrysis* in less disturbed habitats. In addition to the recorded localities it was present in most roadside swamps and drains, even adjoining natural forest. First recorded at the KBFSC in 1995, by 2000 it had become well established in the vicinity of the station. This species and *sabina* were omitted from the analysis of the KBFSC fauna in the discussion below, as they were clearly both recent invaders.

Pornothemis serrata Krüger

Sites 13, 21. A single female was taken in freshwater swamp forest near Lamunin., and a male in similar habitat at Sg. Lumut.

Pornothemis starrei Lieftinck

The unknown female of this species was taken in a small shop in Bandar Seri Begawan, Yaohan complex. The specimen resembled the male in principal features of size, body shape and venation (Lieftinck 1948), but is not sufficiently well preserved to provide a basis of a definitive description. Lieftinck (1954) gives the distribution of this species as southern Borneo.

Sympetrinae

Diplacodes trivialis (Rambur)

Sites 5, 8, 10, 13, 23. Common in shallow drains, ponds and swampy areas in open disturbed areas. Frequently found in gardens and open grassy areas, often together with *Orthetrum glaucum*. In less degraded situations it sometimes occurred in open marshy areas bordering forest.

Neurothemis fluctuans (Fabricius)

Sites 2, 3, 4, 5, 6, 8, 10, 11, 14, 16, 19, 22, 23, 27, 28, 32, 33. Extremely common and ubiquitous in exposed shallow marshy areas in the vicinity of ponds, drains and swamps. It preferred to breed among thick grassy vegetation, often in water no more than a few cm deep which became very hot (over 40°C) in the direct sunlight in the middle of the day. In forested areas it occurred only around the exposed margins. Both sexes were frequently found foraging far from water, especially among low vegetation such as bracken and lalang (*Imperata*). *N. fluctuans* in North Borneo differs from Javanese specimens in size and behaviour, and probably deserves at least subspecific rank. Several synonyms are available.

Neurothemis ramburii (Brauer)

Sites 6, 7. Somewhat uncommon around deeper drains and ponds in disturbed habitats, and possibly in natural lakes.

Neurothemis terminata Ris

Sites 2, 3, 5, 7, 8, 11, 12, 13, 16, 19, 22, 23, 25, 27, 31, 33. Common everywhere around deeper drains and ponds in disturbed habitats, and in open natural swamps and lakes. In forested areas it was sometimes present in clearings and in marshy backwaters of larger rivers.

Rhodothemis rufa (Rambur)

Sites 16, 23. Not common. A male was taken on Benutan Reservoir at the edge of primary forest and a female bred from a larva found in Badas drain. The larva was clinging to vegetation just below the surface from where it ambushed and ate an ovipositing *Libellago hyalina*.

Trithemistinae

Pseudagrionoptera diotima Ris

Site 23. A single female was taken ovipositing in an open swampy area close to peat swamp forest at Badas.

Pseudothemis jorina Foerster

Site 16. Found at one locality only, at the base of a broad waterfall leading from a small stream which cascaded into the Benutan Reservoir impoundment. Males were seen skimming very low and fast over the water, resting frequently on pieces of flotsam which were carried out into the reservoir, whereupon they flew back to the foot of the falls and alighted on a new floating perch. A male was eventually secured by tethering a piece of floating branch and casting it into the water. When a male landed on it, it was drawn sufficiently close to the bank to allow capture. The genus has not been previously recorded in Borneo.

Trithemis aurora (Burmeister)

Site 3. Only one male of this normally common species was ever seen. It was holding a territory over an open stretch of stream at Bukit Patoi. Its appearance followed partial clearing between 1996 and 1999.

Onychothemistinae

Onychothemis coccinea Lieftinck

Sites 1, 29, 35. Common on larger streams, especially on swift flowing reaches where it bred in sheltered water behind sandbars and log jams. Males perched on logs at the periphery of such sites intercepting females which flew in rapidly and seldom remained more than a minute. Following a brief mating lasting ca 20 seconds, they quickly dropped their eggs and departed. Larvae common in fine gravel and silt, sometimes under stones in fast flowing water. As the larvae have hitherto been virtually unknown (see Wilson 1995) a description is provided.

Description of the final instar larva (Fig. 5)

Overall appearance smooth with rounded margins, moderately elongate (Fig. 5a).

Head: broader than wide, distinctly rounded in outline. Eyes very small and scarcely protruding. Labrum broadly rounded, clearly visible from above. Antennae moderately long and seven segmented. Prementum basally narrow, distally expanded. Distal margin produced to form an obtuse angle, sparsely fringed with short setae. Inner surface of prementum with row of 10 long, robust setae on either side. Labial palp subtriangular; six long internally directed fine setae arising from near the dorsal margin; movable hook at apex relatively long; distal margin with five rounded, subquadrate serrations, each bearing at its proximal corner a short stout seta surrounded by three shorter, finer setae. Proximal margin of palp with sparse fringing of short setae (Fig. 5b).

Thorax: Prothorax with short lateral processes at anterior angles, and blunt processes posteriorly. Legs moderately long, bearing sparse setae on tibiae, especially metatibiae.

Abdomen: smooth and rounded in profile. Short blunt lateral projections arising from posterior margins of S8-9. Distal segments finely setiose laterally. Anal pyramid very short. All appendages robust and broadly triangular. Cerci in female slightly shorter than epiproct and about half length of paraprocts. Kuala Belalong specimens were uniform ochreous in colour owing to a fine layer of silt adhering to body and external setae. The true ground colour is probably uniform dark brown. Early instar larvae had several processes on the occipital region of the head and were slightly elongate, resembling the general form of a young aeshnid larva, but the form of the mask was exactly as for mature specimens. Several features serve to distinguish this larva from various libellulid genera, including the distinctive globular head, the tiny eyes, the form of the crenulations on the inner edge of the labial palp, and the general lack of armature on the abdomen.

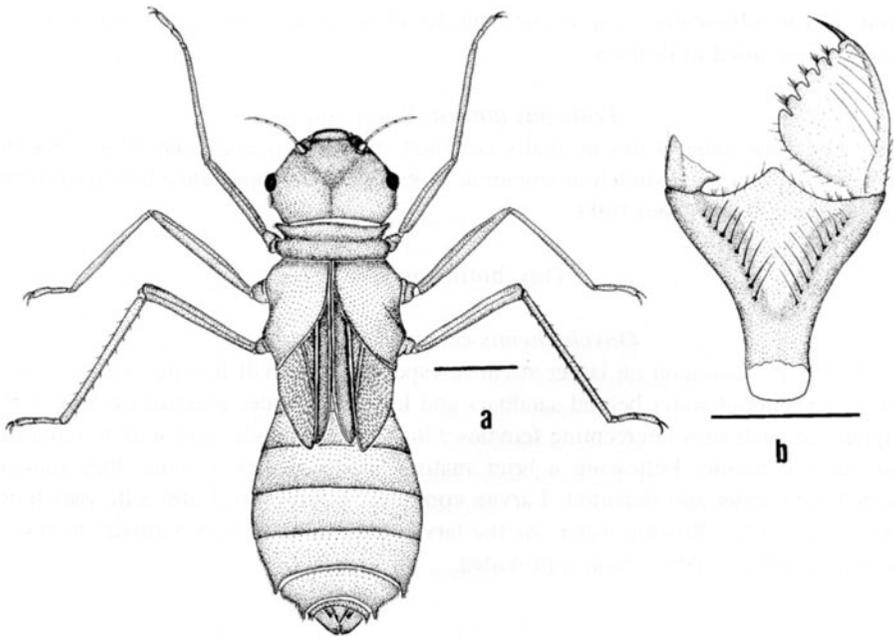


Figure 5. *Onychothemis coccinea* – (a) dorsal view of final instar larva (female); (b) dorsal view of prementum and labial palps with mask extended. Scale bars = 3 mm.

***Onychothemis culminicola* Foerster**

Sites 29, 30, 35. Common on streams in dipterocarp forest, preferring slower flowing reaches with more silty substrates than *O. coccinea*, with which it overlapped broadly.

Trameinae

Camacinia harterti Karsch

Site 19. One female only was taken at Tasek Merimbun by J.K. Charles. Evidently this species and *C. gigantea* (Brauer) which may also have been sighted at this locality are scarce in Brunei.

Hydrobasileus croceus (Brauer)

Sites 1, 4, 5, 11, 13, 16, 19, 22, 23, 28. Common in some localities, especially around open black-water ponds near peat swamp forest, and over larger expanses of water such as Tasek Merimbun and Luagan Lalak. At artificial impoundments such as the Benutan Reservoir and smaller dams it occurred sporadically. One female was taken in the understorey of the forest at the KBFSC at night. Oviposition occurred in tandem, from 12:00-14:00 h.

Pantala flavescens (Fabricius)

Sites 4, 5, 6, 8, 10, 16, Bukit Retak. Found everywhere in disturbed habitats, it was frequently numerous at tops of hills where they hawked in large numbers from early morning until sunset. It was common at cleared hilltops even in primary forest, many kilometers from its breeding habitat. It was the only odonate present on the summit of Bukit Retak, a peak of 1,618 m in the midst of an extensive tract of primary forest. Sometimes it was extremely abundant after rain wherever water was lying on the ground. Breeding seemed to be mainly in temporary pools in open areas.

Rhyothemis aterrima Selys

Sites 16, 19, 22, 23, 27, 28, 30, 35. Very common in certain situations, especially deep black-water swamps and drains, but present on most larger undegraded bodies of deep standing water. Also present in some numbers on very large pools and backwaters on the upper Sg. Rampayoh and Sg. Ingei. Massed flights of hundreds were sometimes seen flying at canopy level beside forest at Benutan reservoir. Males are extremely aggressive and constantly engaged in high speed chases and audible clashes. In many specimens the edges of the dark wings were extremely ragged.

Rhyothemis obsolescens Kirby

Sites 3, 12, 17, 19, 22, 23, 27, 32, 33, 34. A very common species occurring in exposed marshy areas, permanent deep backwater drains in forested areas, exposed sluggish streams and certain lakes. It sometimes occurred in large numbers among low vegetation on exposed hilltops such as Bukit Terajah and Bukit Patoi. It was not common in highly disturbed areas lacking nearby forest.

Rhyothemis phyllis (Sulzer)

Sites 2, 4, 5, 11, 16, 19, 28. A very common species around lakes and larger ponds, it occurred less frequently in permanent drains and around shallow marshy areas. Feeding swarms were observed regularly along the path in Badas forest reserve late in the afternoon, but it apparently bred only in open areas.

Rhythemis pygmaea (Brauer)

Sites 32. An uncommon and local species, recorded only from Sg. Langsat, Labi Road, where it was apparently breeding in a sunlit pool on a small stream where it left the forest. Swarms of teneral were observed at this location.

Rhythemis triangularis Kirby

Sites 19, 23. An uncommon species recorded only from Tasek Merimbun, where it was usually present in fair numbers in isolated pockets around the lake margins, and rarely at Badas, in a black-water drain near swamp forest.

Tholymis tillarga (Fabricius)

Sites 2, 3, 4, 5, 6, 8, 10, 11, 16, 19, 23, 27. Very common around drains, ponds and lakes and found throughout Brunei in disturbed areas. Activity commenced about three hours before sunset when males established territories. Most mating and oviposition occurred in the half hour before sunset. Activity ceased abruptly soon after sunset and the species was only occasionally attracted to light.

Tramea

The following two species could not be separated on the wing, hence it is possible they may have occurred together at any of the localities mentioned.

Tramea phaeoneura Lieftinck

Sites 13, 23, 27. Taken regularly in localized swampy areas and drains adjoining peat swamp forest where males perched for long periods on elevated posts, mostly in full sunlight.

Tramea transmarina euryale Selys

Sites 16, 19, 22, 28. Quite common on natural large bodies of standing water, Merimbun, Sg. Badas, Luagan Lalak, and sometimes on large man made dams, especially Benutan Reservoir.

Zyxomma obtusum Albarda

Sites 2, 4, 5, 6, 8, 10, 11, 16, 23, 25. Common in drains and ponds in open disturbed areas and along roadsides. Activity began just after sunset or a little earlier in shaded situations, and continued for at least an hour. At Pantai Muara the pruinescent white males flew rapidly around the ornamental ponds 10-20 m in diameter, intercepting ovipositing females. There was little evidence of individual territories and male agonistic interactions were rare. As with other crepuscular species it was frequently attracted to light.

Zyxomma petiolatum Rambur

Sites 4, 6, 12, 13, 23, 27, 33. Like *obtusum*, very common in drains, but also occurring deep in swamp forest where it was often active in the early afternoon. Normally in open areas activity began about two hours before sunset and continued until about half an hour after. Frequently attracted to light.

Urothemistinae

Aethriamanta gracilis (Brauer)

Apparently a rather scarce insect in Brunei, a single male was taken at an artificial pond at Bukit Sharbandar, near UBD.

Urothemis signata insignata (Selys)

Sites 16, 19, 22, 23, 28. Abundant on larger bodies of standing water in relatively disturbed habitats. Also in deep black-water drains near peat swamp forest. Males commonly perched in full sunlight in the 'obelisk' position.

Zygonychinae

Zygonyx iris errans Lieftinck

Sites 1, 30. Fairly common in sections of swift flowing water on the upper Sg. Rampayoh. Males characteristically hovered low over small rapids and cascades where they were very inconspicuous against the reflected background of moving light. Females, which oviposited in pools and riffles at the head of such rapids were captured and mated while laying.

Discussion

This study records approximately 170 odonate species from Brunei. It is likely that between five and ten of these are new to science. It may thus be assumed that the total number of named species recorded is at least 160 and to this could be added a further seven species listed by Thompson & van Tol (1993), Lieftinck (1954) and Laidlaw (1912) as occurring in Brunei. The resulting total of 167 species represent nearly 60% of the known Bornean fauna of about 280. Among named species, endemics constitute 60% of the Zygoptera and 16% of the Anisoptera, slightly lower than the percentages for the island as a whole, as might be expected from a sample of a regional fauna where widespread species contribute a relatively greater proportion. Several species recorded previously only from west or south Kalimantan have been found in Brunei, suggesting they have been greatly under-collected. Even more surprising, is the first Bornean record of the highly conspicuous libellulid *Pseudothemis jorina*. Overall, most families are well represented, with the Calopterygoidea (68%) and Libellulidae (75%) particularly prominent (Table 3). Strong faunistic affinities with lowland north Borneo and Mt Dulit in Sarawak are evident, especially at Site 1. The number of new forms discovered, including those noted above as well as the recently described *Euphaea ameeka* (van Tol & Norma Rashid 1995), *Sundacypha striata* (Orr 1999) and *Pseudagrion lalakense* (Orr & van Tol 2001), suggest that Brunei may represent part of a significant centre of endemism within Borneo, a conclusion also drawn by Thompson & van Tol (1993).

Although the collection is overall highly representative of the north Bornean fauna, there is much variation in species and higher taxonomic level profiles between sites.

Table 3. Family breakdown of numbers of species collected compared with totals for the known Bornean fauna.

Superfamily group	No. of species in Borneo	No. of species collected	Percentage of Bornean total
Calopterygoidea	38	26	68
Amphipterygidae	1	1	100
Calopterygidae	9	7	78
Chlorocyphidae	20	12	60
Euphaeidae	8	6	75
Lestidae	5	2	40
Megapodagrionidae	8	4	50
Coenagrionidae	39	23	58
Platycnemididae	13	8	62
Platystictidae	14	8	57
Protoneuridae	20	9	45
Aeshnidae	29	16	55
Gomphidae	23	11	47
Corduliidae	13	8	62
Libellulidae	71	53	75

The average number of species per site is 18 (Fig. 6), with a maximum of 49 species from Site 1 and a minimum of seven species from Site 9. The numbers of species per site has been influenced by both natural and artificial habitat heterogeneity, and to some extent by collecting effort, which varied by up to a factor of 10 between some sites. However, collecting effort has probably been a less important source of variation than might have been expected since open and secondary habitats could be sampled far more rapidly and effectively than primary forest, and low collecting effort usually reflects the fact that no new discoveries were made at a site after several days collecting, even when it was revisited months or years later.

Many common species were found at only one or two sites. In general, primary forest, especially mixed dipterocarp, freshwater swamp and kerangas, tend to support shade loving stenotopic species with a high number of endemics, whereas open and disturbed habitats as well as peat swamp forest and mangrove are characterized by wide ranging, sun loving, eurytopic species. Only a few species are specialized to the harsher environments of highly acidic water in peat swamps, or oligohaline pools on the landward margins of mangrove. Similarity analysis of sites basing on species present invariably separates site 1 from the remaining sites. Using complete linkage (Fig. 7), there is a recognizable pattern of associations which fit with the more visible features of the sites. For example the first major cluster includes most open areas, either natural or disturbed, with mainly standing or slowly flowing water. The second major cluster includes mainly primary forested sites with either streams or marshy areas with small

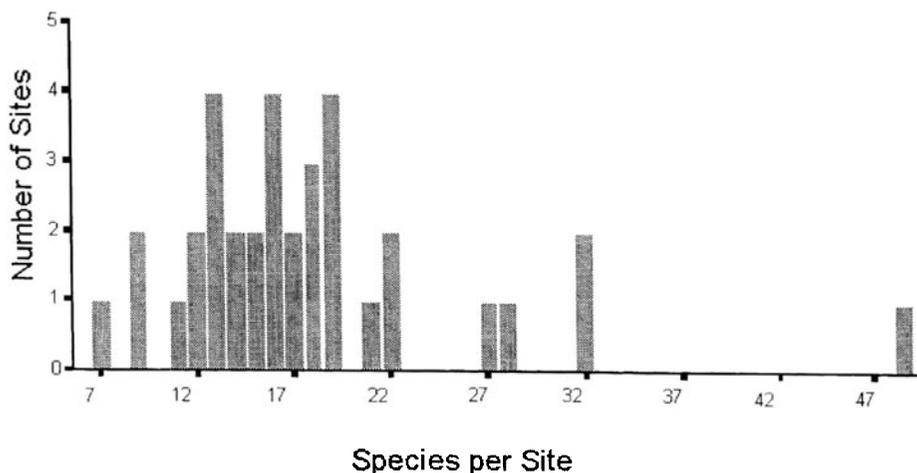


Figure 6. Frequency distribution of sites, versus number of species per site.

streams. Very similar sites such as 22 and 28 with deep slow flowing black-water in open marsh, 19 and 16 with natural and artificial lakes, 5 and 11 with exposed drains and ponds, 34 and 12 with forested shallow black-water swamp, all cluster close to one another. Mixed dipterocarp forest sites with stream banks dominated by the rheophytic palm *Pinanga*, form another cluster (31, 7, 32, 15, 30, 29) along with the heterogeneous site 33. It is of interest that the mixed dipterocarp forest sites with streams, including the group above plus sites 1, 3 and 35 are rather dissimilar in terms of species present. By contrast, swampy and open sites show greater degrees of similarity regardless of proximity, hence much of the beta diversity in odonates throughout the area sampled is probably owing to faunistic differences between various microhabitats, especially streams, within primary mixed dipterocarp forest.

A somewhat different and more generalized pattern is provided by family and family-group profiles for different sites, where the relative proportions of the Calopterygoidea, Coenagrionidae, 'Other Zygoptera' (Lestidae, Megapodagrionidae, Platycnemididae, Platystictidae, Protoneuridae), Libellulidae and 'Other Anisoptera' (Aeshnidae, Gomphidae, Corduliidae) have been considered (Fig. 8). All mixed dipterocarp forest sites (1, 3, 29, 30, 35) show a relatively high proportion of calopterygoids, with very few coenagrionids and libellulids, except at site 3 where the stream flowed into an open drain. Minor families of both suborders are also well represented at these localities. Conversely calopterygoids and minor zygopteran families are almost lacking from open drains and lakes (5, 11, 16, 19, and 28), but there is a high proportion of coenagrionids and libellulids. Swampy forests (13, 21, 24, 27) and heterogeneous disturbed habitats tend to have intermediate family profiles, with calopterygoids occurring only rarely in highly disturbed areas (4, 8, 10, 23).

A high degree of habitat specialization within the forest environment is illustrated by the species distributions of three sub-sites at site 1, the KBFSC, all within 10-200 m of

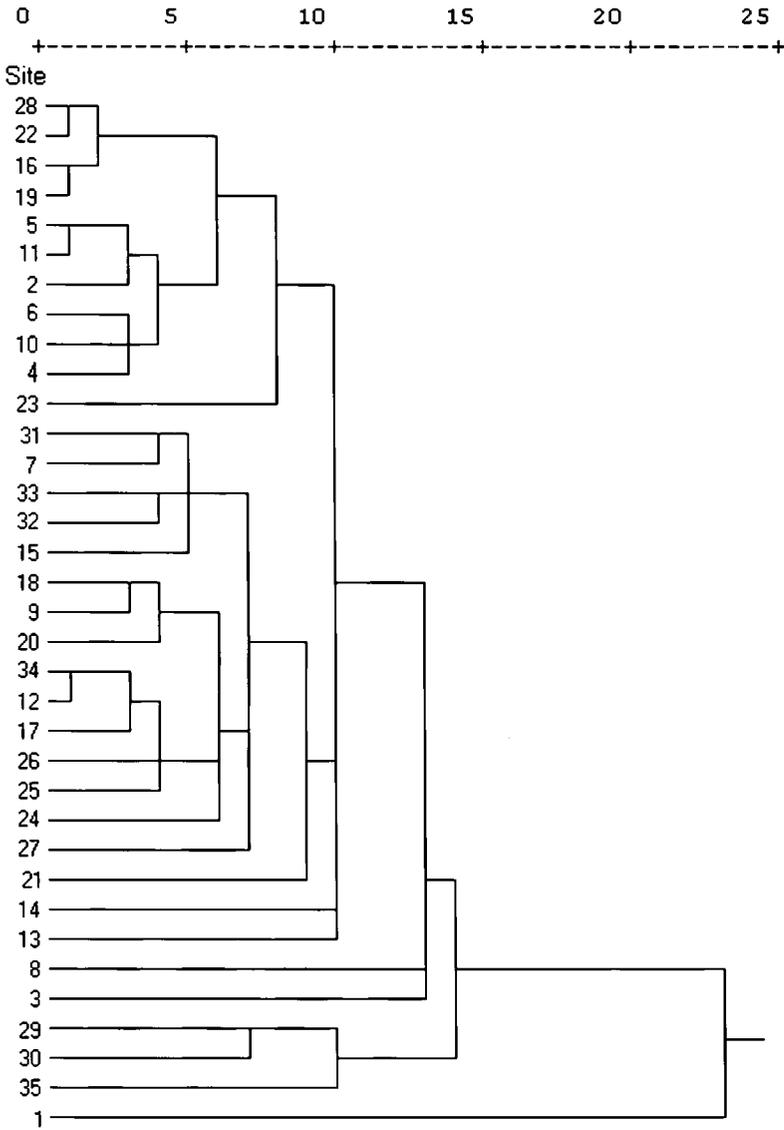


Figure 7. Dendrogram illustrating degree of similarity between sites in terms of species present, based on complete linkage analysis of squared euclidean distance.

each other. These are the main stream, the small tributary colloquially known as the Sg. Mata Ikan, and the forest understorey above the streams, which includes some marshy areas and phytotelmata. The three sub-sites host, respectively 20, 15 and 20 species.

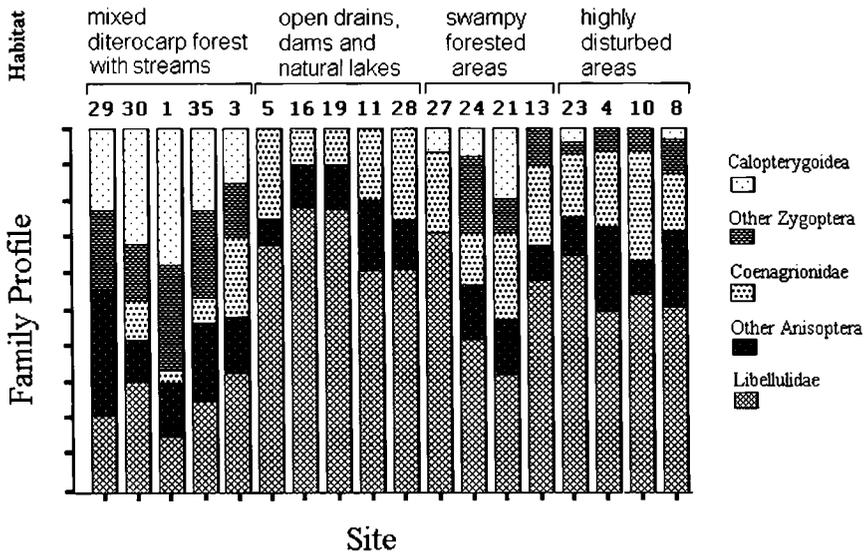


Figure 8. Family and family-group profiles for selected sites illustrating a range of habitats.

Of these, only three species were shared between forest and tributary, two between the main stream and the tributary and one between the main stream and the forest (Fig. 9a). The family profiles (Fig. 9b) are not markedly different for the three sub-sites, although the main stream has a preponderance of calopterygoids and Coenagrionidae are present only in the forest.

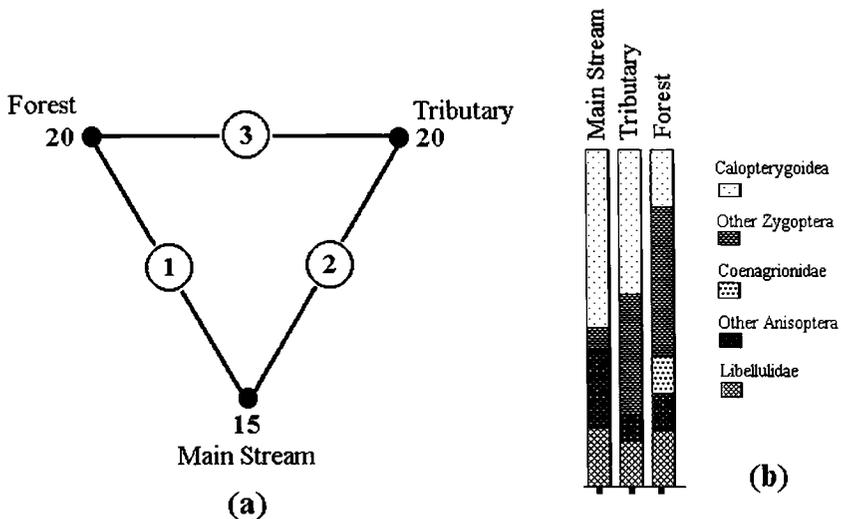


Figure 9. Microdistribution at KBFSC – (a) numbers of species in the forest, tributary and main stream respectively with species shared between habitats enclosed in circles on connecting lines; (b) family and family-group profiles for the three habitats.

One curious feature revealed by this survey is the complete absence of certain widespread eurytopic species which are common elsewhere in North Borneo and throughout the region. These include *Trithemis festiva* (Rambur) and *Crocothemis servilia* (Drury). These species, if present in Brunei, are certainly very rare since every effort was made to discover them. It is a matter of disappointment that I failed to relocate *Linaeschna polli* Martin, perhaps the most primitive extant aeshnid (G. Peters in litt.), known only from the unique male holotype taken in the Brunei Bay area and housed in the National Museum of Natural History, Leiden.

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