

Chapter 5

Zoogeographical patterns among mayflies (Ephemeroptera) in the Malay Archipelago, with special reference to Celebes

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ABSTRACT

Twenty genera of mayflies occur on Celebes, with perhaps 1 to 4 undescribed species per genus. One genus of Heptageniidae is known only from larvae. The fauna of the Greater Sunda Islands contains 48 genera; 33 of these do not reach Celebes. Of the 20 genera on Celebes, 7 are found east of Celebes, 6 apparently reach New Guinea, and 2 occur in the Cape York region of Australia. In essence, the mayfly fauna occupying Celebes, the Moluccas and New Guinea is an attenuated Oriental fauna. There are 3 new endemic genera on Celebes, 2 in the Baetidae and one in the Leptophlebiidae. One of these, Genus Sw in the Leptophlebiidae, represents the only mayfly in the Celebes fauna having transantarctic relationships, its nearest relative being in Australia, with other members of the lineage in New Caledonia, New Zealand, southern South America, Madagascar, Sri Lanka, and south India.

INTRODUCTION

The island archipelagos lying between Southeast Asia and Australia are a geographically complex region, where elements of various freshwater biotas have intermingled. No good review of mayfly distributions in this part of the world has been published since that of Ulmer (1939 - 1940), who did a monumental study of the mayflies of the Greater Sunda Islands, describing 11 new genera, two of which have since proved to be junior synonyms (*Pseudoligoneuria* = *Chromarcys*, *Thraululus* = *Thraulus*). Subsequently several new genera which occur in the region have been described: *Ecdyonuroides* from Vietnam (Dang, 1967), *Dipterophlebiodes* from Borneo (Demoulin,

1954), *Uracanthella* from the U.S.S.R. (Belov, 1979), *Hyrtanella* from Borneo (Allen and Edmunds, 1976), and *Chopralla* from Ceylon, Borneo and Vietnam (Waltz and McCafferty, 1987). In some cases there are differences of opinion regarding the recognition or synonymy of genera, such as *Ecdyonuroides* and *Compsoneriella*.

We review here those genera known to occur on one or more of the islands lying between the Southeast Asian mainland and Australia. Previous modern sources of mayfly distribution data in these islands and surrounding regions were the collections of G. F. and C. H. Edmunds in the Malay Peninsula and Borneo (Sabah), collections by W. L. and J. G. Peters in northern Thailand, collections by J. Bishop in peninsular Malaysia, and collections by T. Soldán in Vietnam. We have had access to data on the Celebes mayfly fauna from three recent collections: the collections of J. van Tol which are being studied by A. W. M. Mol (Netherlands), collections by D. Dudgeon that are being studied by the Peters group (Florida), and the collections of D. A. and J. T. Polhemus, which are at the University of Utah. The Polhemus collections have also provided much new data on mayfly distribution over the entire area from Thailand to New Guinea and northern Australia.

THE MAYFLY FAUNA OF CELEBES

There are no previously published records of Ephemeroptera from Celebes; knowledge of the fauna began with Project Wallace. The fauna is essentially an extension of the Oriental fauna,

Table 1. Distribution of Ephemeroptera genera in the Malay Archipelago and surrounding regions

Taxon	ASIA	IND	FOR	MAL	BOR	SUM	JAV	LSN	CEL	PHI	NML	CML	NGU	SOL	AUS
OLIGONEURIIDAE															
<i>Chromarcys</i>	X	X		X		X									
<i>Isonychia</i>	X		X	X	X	X	X								
BAETIDAE															
<i>Acentrella</i>	X		X			X									
<i>Baetis</i>	X	X	X	X	X	X	X	X	X	X			X		
<i>Baetis</i> - ally									X			X	X		
<i>Centropitulum</i>					X										
<i>Chopralla</i>	X	X			X										
<i>Cloeon</i>	X	X	X		X	X	X	X	X	X		X	X		X
<i>Jubabaetis</i>										X					
<i>Liebebiella</i>	X	X	X	X	X	X	X	X	X	X	X		X		
<i>Plarybaetis</i>	X	X		X	X				X	X					
<i>Procloeon</i>	X	X	X			X	X			X					
<i>Pseudocloeon</i>							X								
Genus A													X		
Genus E									X						
Genus G									X						
HEPTAGENIIDAE															
<i>Afronurus</i>	X						X			X					
<i>Afronurus</i> - ally									X						
<i>Atopopus</i>		X			X					X					
<i>Componeuria</i>				X	X	X	X		X						
<i>Ecdyonuroides</i>	X					X									
<i>Epeorella</i>					X										
<i>Epeorus</i>	X	X	X	X	X										
<i>Heptagenia</i>	X				X	X	X								
<i>Heptagenia</i> - ally						X			X						
<i>Rhithrogena</i>	X	X	X			X	X	X							
<i>Rhithrogeniella</i>		X				X	X								
<i>Thalerosphyrius</i>	X	X		X		X	X								
LEPTOPHLEBIIDAE															
<i>Choroterpes</i>	X	X	X	X	X	X	X								
<i>Choroterpides</i>	X	X	X	X		X	X	X		X					
<i>Dipterophlebiodes</i>				X	X										
<i>Habrophlebiodes</i>	X					X	X		X	X					
<i>Isca</i>	X	X		X		X			X						
<i>Simothraulius</i>					X										

Explanation of geographical abbreviations: ASIA = Sri Lanka, India, or China, IND = Indochina, FOR = Formosa, MAL = Malay Peninsula (below Isthmus of Kra), BOR = Borneo, SUM = Sumatra, JAV = Java and Bali, LSN = Lesser Sunda Islands (Lombok to Timor), CEL = Celebes, PHI = Philippines, NML = North Moluccas (Halmahera, Bacan, Obi), CML = Central Moluccas (Ambon, Ceram, Buru), NGU = New Guinea, Bismarcks, Waigeo, Misool, SOL = Solomons, AUS = Australia

Table 1. (cont.)

Taxon	ASIA	IND	FOR	MAL	BOR	SUM	JAV	LSN	CEL	PHI	NML	CML	NGU	SOL	AUS
LEPTOPHLEBIIDAE															
<i>Thraulus</i>	X	X		X	X		X			X		X X			X
Genus B															
Genera M & N													X		
Genus Su					X					X					
Genus Sw									X						
POTAMANTHIDAE															
<i>Potamanthodes</i>	X	X	X	X	X										
<i>Rhoenanthus</i>	X	X		X	X	X	X								
EUTHYPLOCIIDAE															
<i>Polyptocia</i>		X			X										
EPHEMERIDAE															
<i>Eatonigenia</i>	X	X			X		X			X					
<i>Ephemera</i>	X	X	X	X		X	X								
PALINGENIIDAE															
<i>Anagenesia</i>	X	X			X	X	X		X		X				
<i>Plethogenesia</i>													X		
POLYMITARCYIDAE															
<i>Ephoron</i>	X	X			X	X	X								
<i>Povilla</i>	X	X			X	X	X								
EPHEMERELLIDAE															
<i>Hyrtanella</i>	X	X		X	X										
<i>Teloganodes</i>	X			X	X	X	X	X	X	X					
<i>Teloganopsis</i>						X	X								
<i>Uracanthella</i>	X		X	X	X										
TRICORYTHIDAE															
<i>Neurocaenis</i>	X	X		X	X	X	X	X	X	X					
<i>Teloganella</i>	X			X	X	X			X						
NEOEPHEMERIDAE															
<i>Neoephemeropsis</i>	X	X		X	X	X	X	X		X					
<i>Potamanthellus</i>	X	X			X										
CAENIDAE															
<i>Caenodes</i>	X				X	X	X		X	X					
<i>Caenomedeia</i>									X		X		X	X	
<i>Tasmanocaenis</i>													X		X
PROSOPISTOMATIDAE															
<i>Prosopistoma</i>	X	X		X		X	X		X	X	X		X	X	X

Explanation of geographical abbreviations: ASIA = Sri Lanka, India, or China, IND = Indochina, FOR = Formosa, MAL = Malay Peninsula (below Isthmus of Kra), BOR = Borneo, SUM = Sumatra, JAV = Java and Bali, LSN = Lesser Sunda Islands (Lombok to Timor), CEL = Celebes, PHI = Philippines, NML = North Moluccas (Halmahera, Bacan, Obi), CML = Central Moluccas (Ambon, Ceram, Buru), NGU = New Guinea, Bismarcks, Waigeo, Misool, SOL = Solomons, AUS = Australia

composed largely of previously described Oriental genera plus three new endemic genera in various stages of description. The genera of mayflies occurring in Celebes are discussed by family and genus below with special attention to geographic patterns. The three principle groups are: (1) genera endemic to Celebes, (2) Oriental genera whose most easterly occurrence is in Celebes, (3) Oriental genera extending through Celebes and eastward to the Moluccas and New Guinea, or beyond.

Baetidae: Six genera of Baetidae are present on Celebes. Two are new genera that are endemic. Genus E (A. W. M. Mol, in press) is known only from the larvae, although we have females and some males that seem assignable to this genus. It is most closely related to the genus *Jubabaetis* Müller-Liebenau of Luzon. A single male baetid representing Genus G (Waltz and Edmunds, in ms.) collected by D. A. Polhemus in the Lore Lindu region is so distinctive in its wing venation that its relationships cannot be determined with certainty.

The genus *Baetis* is an unnatural assemblage as presently known, but recent advances have been made in separating out natural lineages. *Baetis* formerly was used for all Baetidae with paired marginal intercalaries in the forewing and with the hind wing present. Some mayflies in Celebes are assignable to *Baetis* in the old sense, but more study is needed to determine the real affinities of these mayflies and to determine if they are *Baetis* in the more restricted sense. One of the two species of *Baetis* reported from New Britain (Demoulin, 1969) has characters that place it in the group of New Guinea mayflies that we discuss under *Liebebiella*, while the other is placed by Müller-Liebenau and Hubbard (1985) in the *Baetis molawinensis* group.

The genus *Cloeon* is widely distributed, being present in Celebes and east to the Moluccas, New Guinea and Australia. We have seen true *Cloeon* in New Guinea only from the southern part of Papua New Guinea; it may have reached New Guinea from the Moluccas, but more probably via the Lesser Sunda Islands to Australia and then to New Guinea. More detailed data is needed.

The genus *Platybaetis* is represented on Celebes by several species as determined by larvae (A.W.M. Mol, pers. comm.). The adults of *Platybaetis* are undescribed, but we have adults from North Celebes that also seem tentatively assignable to this genus.

In the Oriental realm the generic name *Pseudocloeon* has been applied to all adult

Baetidae with paired intercalary veins in the interspaces of the forewing and with the hind wing lacking. The name would thus apply to mayflies with diverse larval types. The association of larvae and adults is essential for taxonomy in the Baetidae, and since the larvae of the type-species of *Pseudocloeon* are unknown the application of the genus name is uncertain. Waltz and McCafferty (1987b) limited the use of *Pseudocloeon* to *P. kraepelini* Klapalek from Java. The Oriental species previously believed to represent *Pseudocloeon* were instead placed in a new genus, *Liebebiella*.

Adults from Celebes which appear to be *Liebebiella* have two distinct types of metanota. One of these has a relatively inconspicuous metanotal hump, and the other has a finger-like hump. The first form is probably true *Liebebiella*, and the second may represent what we have called "*Baetis* - ally". In addition, the adults of Genus E and *Platybaetis* also have double marginal intercalaries and lack hind wings.

Larval specimens which conform to the old concept of *Pseudocloeon* are widespread in the Malay Peninsula and Greater Sunda Islands. These larvae have a median caudal filament with only a few segments (less than 1/10 as long as the cerci), no hind wings, cerci with only a light row of median setae, the head relatively depressed, the body depressed, and the legs relatively long. Larvae of this type are distributed in the Malay Peninsula, Java, Luzon, Leyte, Mindanao, Palawan, Celebes and Flores. Edmunds reared adults from such larvae in the Malay Peninsula. Reliable generic assignment of these mayflies will require more study, and our listing of them as *Liebebiella* in Table 1 is provisional.

Two unnamed larval specimens from the Toraut River, north Celebes, again generally correspond to this type but the abdomen is very short, and the thorax and abdomen are broader. Of great interest is the fact that all of the "*Liebebiella*" - type larvae from Celebes have gills on abdominal segments 1 - 7, while larvae from Bacan, Ambon and New Guinea corresponding to the same general shape lack gills on abdominal segment 1.

Except for *Cloeon*, the baetid mayflies of New Guinea and nearby islands share three characters: (1) intercalary marginal veinlets between the veins of the forewing are in pairs, (2) the hind wings are absent, (3) there are no gills on abdominal segment 1 in the larvae. The larvae of these mayflies are fairly diverse, including some with flattened bodies, long legs, and a short median caudal filament, and others with a relatively rounded body cross section, normal leg lengths, and three caudal filaments of

subequal length. The body forms suggest that two or more lineages dispersed to the New Guinea area, but the uniform loss of the hind wings and gills on segment 1 argues for a single dispersal that has undergone subsequent adaptive radiation. A major study of the Baetidae of this region is necessary to clarify the major lineages and their distributions.

Heptageniidae – Three genera of Heptageniidae are found on Celebes. Members of the genus *Compsoeunia* are abundant and widespread. *Afronurus* is apparently represented by seven larvae from the Marana River in south Celebes that are very similar to *A. ollifi* Schoonbee from South Africa, with long pointed maxillary palpi, a relatively narrow pronotum, and no filaments on gill 7. We are referring to these larvae as *Afronurus* - ally in table 1, since they and *A. ollifi* differ from the type-species, *A. peringueyi* (Petersen), in the characters noted above. The similarity between these Celebes larvae and South African specimens is convincing evidence that the *ollifi* - lineage has spread between Southeast Asia and South Africa independently of the *peringueyi* - lineage of *Afronurus*.

A third genus in Celebes is almost certainly congeneric with the larvae which Ulmer (1940) described from Sumatra as *Compsoeunia*. Our examples from a swift clear stream near the south end of Lake Mooat at 1000 m. and from the upper Sungai Metalanga near Doloduo have the distinctive maxillae of Ulmer's larvae, the extremely reduced gill lamellae on segment 1, and narrow lance-like gill lamellae on segments 2 - 3. By teasing the wings from the wing pad of a mature larva, it is seen that the adult will have abundant crossveins in the forewing and therefore cannot be *Compsoeunia*. Ulmer (1939) described two species of *Heptagenia* from the Greater Sunda Islands, both with unknown larvae. The Celebes larvae are allied to *Heptagenia*, and probably congeneric with Ulmer's *Heptagenia lieftincki*. Pending resolution of this problem we have listed the Celebes larvae and related material as "*Heptagenia* - ally" in Table 1.

The maxillae of the *Ecdyonurus* - *Afronurus* - *Cinygmina* - *Compsoeunia* - *Thalerosphyrus* group in Asia have been used as a trait to cluster these genera with the Holarctic *Electrogenia* - *Nixe* - *Leucrocota* group. *Compsoeunia* and *Thalerosphyrus* are also allied by the acute elongate processes of the supracoxal sclerites. Interestingly, the Celebes larvae of *Heptagenia* - ally also have elongate supracoxal processes. Our present knowledge suggests that these structures have evolved independently in the two lineages, perhaps as anti-predator devices. Flowers and Pescador

(1984) have noted that the eggs of *Afronurus* and *Cinygmina* are morphologically unique, and our examination of larvae from Asia indicates that the characters separating these two nominal genera to be vague, despite the reared material described by Jensen (1972) and Braasch and Soldán (1984).

Leptophlebiidae – Three genera of this family are known from Celebes. *Habrophlebiodes* occurs in Asia and eastern North America; it is represented by at least one new species in collections from Celebes, but does not occur farther east. *Isca* occurs on mainland Asia (Hong Kong, India) and the Malay Peninsula, and once again reaches its eastern limits on Celebes; the Celebes forms are larger and more primitive than typical *Isca*. Genus Sw (Peters and Edmunds, in press), a member of the *Atalophlebiodes* - complex, is abundant in Celebes and is biogeographically of great interest. It is the only mayfly genus in the entire region that appears to be derived from an Australian group with southern affinities, its relatives being in Australia, New Caledonia, New Zealand, and southern South America. As is the case with all mayfly lineages exhibiting southern distributions, neither genus Sw nor its relatives are in New Guinea or nearby islands.

Palingeniidae – The only representative of the burrowing mayflies on Celebes is the widespread genus *Anagenesia*. We have adults only, collected by D. Dudgeon. The genus is also reported from Halmahera in the north Moluccas (Demoulin, 1965).

Ephemerellidae – *Teloganodes* is the only genus in this family to reach Celebes, and it attains its eastern limits there. Another genus of teloganodine Ephemerellidae is also found in Queensland, but it belongs to a more primitive lineage than does *Teloganodes*.

Tricorythidae – two genera occur in Celebes. *Neurocaenis* is a common African-Oriental genus that extends from Sri Lanka to the Philippines. *Teloganella* is a genus heretofore placed in the Ephemerellidae and previously known only from females collected in Sumatra. We now have males and immatures and are herein transferring the genus to Tricorythidae. A single male was taken in dawn light trap collections in north Celebes by the junior author, and we have additional specimens from South India (Kerala), the Malay Peninsula, and Borneo. The larvae are relatively rare in collections; the only specimen whose microhabitat is known was found by the senior author on silt-covered wood in very slow water along the banks of a large river in peninsular Malaysia.

Caenidae – this family is present on Celebes, but the application of correct names is difficult. The genera *Caenodes* and *Caenomedea* are both known to occur from Africa to the Oriental region, with *Caenomedea* extending eastward as far as the north Moluccas and New Guinea, and *Caenodes* to the Solomons. The genus *Tasmanocaenis* was described from Australia and reported from New Guinea; we have two distinct caenid larval forms from the latter island. Adult Caenidae from Celebes are referable to *Caenomedea* and some larvae key to *Caenodes*. The taxonomy of the group is based primarily on adult male characters, while most of our Celebes specimens are either larvae or females.

Prosopistomatidae – the genus *Prosopistoma* is known from one species in Europe, several in Africa, and several species in Madagascar (one named). In the Oriental region the genus is known from named species in India, Sri Lanka, Vietnam, Leyte, Mindanao, and in the Australasian region from New Guinea, Queensland, and the Solomon Islands. Several apparently undescribed species are present in our collections from Celebes, and we have additional species from the Malay Peninsula, Luzon, Palawan, Celebes, and Bacan in the north Moluccas. A new species is also being described from Queensland (W. L. Peters, pers. comm.).

REGIONAL ZOOGEOGRAPHY

Most mayflies are conservative in their dispersal. This is illustrated by the 33 genera of Oriental mayflies that are known from one or more of the Greater Sunda Islands but apparently do not reach Celebes. They are as follows: Oligoneuriidae (*Isonychia*, *Chromarcys*), Bactidae (*Acentrella*, *Centropitulum*, *Chopralla*, *Procloeon*, *Pseudocloeon*), Heptageniidae (*Atopopus*, *Compsoneria*, *Ecdyonuroides*, *Epeorella*, *Epeorus*, *Heptagenia*, *Rhithrogena*, *Rhithrogeniella*), Leptophlebiidae (*Choroerpes*, *Choroerterpides*, *Dipterophlebiodes*, *Simothraulius*, *Thraulius*, Genus Su), Potamanthidae (*Potamanthodes*, *Rhoenanthus*), Euthyplociidae (*Polyplocia*), Ephemeridae (*Ephemer*, *Eatonigenia*), Polymitarciidae (*Ephoron*, *Povilla*), Ephemerellidae (*Hyrtanella*, *Teloganopsis*, *Uracanthella*) and Neoephemeridae (*Neoephemeropsis*, *Potamanthellus*).

Apparently 20 genera of mayflies occur on Celebes. Because mayflies may be seasonal in occurrence and some are very patchy in distribution, there are probably more genera in Celebes, and also in the Greater Sundas, awaiting discovery. Of the 17 non-endemic genera on Celebes, 13 are shared with Sumatra, 10 with Java,

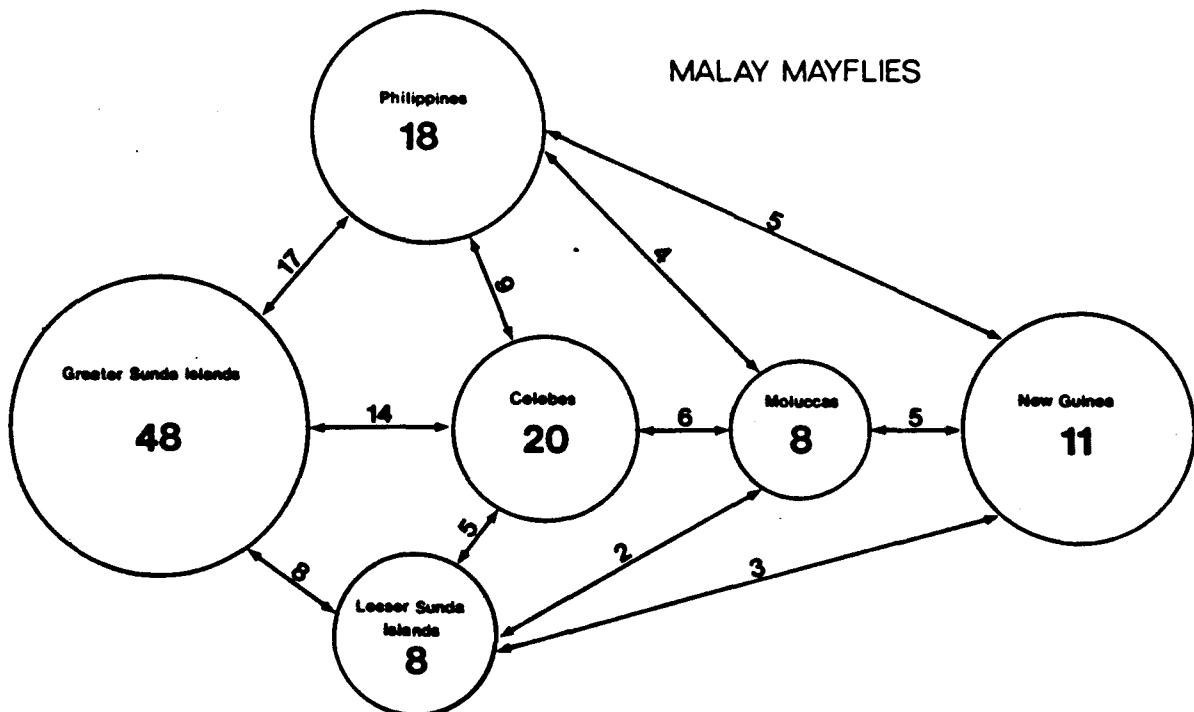


Fig. 1. Numerical relationships between mayfly genera in various regions of the Malay Archipelago. Larger numbers within circles represent the number of genera occupying a given island or group. Smaller numbers on arrows represent the number of genera shared between regions.

only 10 with nearby Borneo, and only 7 with the Malay Peninsula. Part of this pattern undoubtedly results from inadequate exploration of the fauna. A summary of generic level similarities between the mayfly faunas of various subregions is presented in Figure 1.

The distributions of mayfly genera in the Malay Archipelago and surrounding areas are summarized in Table 1. A few mayfly genera are known only from the Greater Sunda Islands, but some of these may occur in continental Asia; several genera previously known only from the Greater Sundas have been recently reported from the Asian mainland or are reported from Asia herein.

Of the 20 mayfly genera on Celebes only 7 reach the Moluccas, New Guinea, or both. New Guinea has several undescribed endemic genera and many undescribed species, but all can apparently be traced to radiation from 7 stocks, 6 of them Oriental and occurring in the Moluccas.

Tasmanocaenis seems to be the only uniquely shared genus between New Guinea and Australia, and it is interesting, in light of the land connection known to have existed between New Guinea and northern Australia across the Torres Strait in the Pleistocene, that no genus of the diverse and endemic Australian leptophlebiid and siphonurid fauna is shared between the two land masses. The ecological barrier between mesic rain forest New Guinea and arid desert and savannah Australia has apparently been insurmountable to south temperate mayflies. New Guinea has instead received its mayflies via a few dispersals of Oriental genera through Celebes and the Moluccas, and has a very poor mayfly fauna for an island of its size and topographic complexity; in this regard it resembles an oceanic more than a continental island.

Our survey of the regional distribution of mayflies in the Malay Archipelago has revealed many significant range extensions, which are summarized below and in Table 1.

Oligoneuriidae – the genus *Chromarcys* has been known from China, Sri Lanka, and Sumatra. We now have specimens from north Thailand.

Heptageniidae – *Atopopus* was formerly known from Borneo (Sabah) and the Philippines; we have seen specimens from Vietnam (Bishop Museum). *Epeonus* is widespread in the Holarctic region and has been reported from peninsular Malaysia; we have a striking new species from Mt. Kinabalu, Borneo. *Rhithrogeniella* is known from Java, Sumatra and Vietnam; we also have adult specimens from northern Thailand.

Ephemerellidae – the genus *Hyrtanella* was known only from Borneo (Sabah), but the genus is now known to occur in the Malay Peninsula, northern Thailand, and south India (Kerala). *Uracanthella* was known east of the Urals and in the Amur region of Siberia; we have specimens from south Korea, the Malay Peninsula, and Borneo (Sabah).

Neoephemeridae – *Neoephemeropsis* was known from the original collection in Sumatra and from peninsular Malaysia. We can now add its occurrence in Bali, Lombok, Flores, Borneo (Sabah), Mindanao, and India (Kaukuhl River, a tributary of the Ganges). The genus *Potamanthellus* was known only from China, Burma and Tonkin. We now report it from northern Thailand, the Malay Peninsula (Selangor, Perak), and Borneo (Sarawak, Sabah).

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