

First larval descriptions, new species, and evaluation, of the Southeast Asian genus *Atopopus* (Ephemeroptera, Heptageniidae)

by T.-Q. Wang and W.P. McCafferty

Department of Entomology, Purdue University, West Lafayette, IN (USA) 47907

SUMMARY

Systematics of the previously enigmatic heptageniid mayfly genus *Atopopus* is presented, and the larval stage of the taxon is described for the first time. *Atopopus edmundsi*, n. sp. is described from larvae, male adult, and female subimago from Malaysia (Sabah). Larvae of *A. tibialis* are described for the first time and are distinct from those of *A. edmundsi*. The male adults of *A. tibialis* and *A. tarsalis* are also reviewed and compared. *Atopopus spadix*, from Australia, is placed in genus *inquirenda* and transferred to the family Leptophlebiidae.

Mouthparts and basal leg characters are important for species diagnosis of the larvae of *Atopopus*, and wing and leg characters are important for species diagnosis of adults. *Atopopus* belongs to the *Ecdyonurus* group of heptageniid genera. A cladogram of the three valid species of *Atopopus* is deduced from apomorphies present in the adult stage. *Atopopus edmundsi* and *A. tarsalis* appear to be sister species in north Borneo, whereas the more basally derived *A. tibialis* is found in the Philippines.

Keywords : Ephemeroptera, Heptageniidae, *Atopopus*, larva, new species.

RÉSUMÉ

Le genre Sud Asiatique *Atopopus* : premières descriptions des larves, découverte d'une espèce nouvelle, et évaluation (Ephemeroptera, Heptageniidae)

Il est traité de la systématique du genre d'Ephémère Heptageniidae *Atopopus* — jusqu'ici énigmatique. La phase larvaire de ce taxon est décrite pour la première fois. *Atopopus edmundsi* n. sp. de Malaisie (Sabah) est décrite sur la base de larves, de l'adulte mâle et de la subimago femelle. Les larves d'*A. tibialis* sont décrites pour la première fois et sont distinctes de celles d'*A. edmundsi*. Les adultes mâles d'*A. tibialis* et d'*A. tarsalis* sont aussi revus et comparés. *Atopopus spadix*, d'Australie, est placée en genre *inquirenda* et transférée dans la famille des Leptophlebiidae. Les caractères distinctifs importants pour la diagnose spécifique d'*Atopopus* sont observés sur les pièces buccales et la région proximale des pattes pour les larves, sur l'aile et les pattes pour les adultes. Parmi les genres d'Heptageniidae, *Atopopus* appartient au groupe *Ecdyonurus*. Un cladogramme des trois espèces valides d'*Atopopus* est déduit des apomorphies présentes au stade adulte. *Atopopus edmundsi* et *A. tarsalis* paraissent être des espèces sœurs du Nord de Bornéo, tandis qu'*A. tibialis*, dérivée en position la plus basale sur le cladogramme, est trouvée dans les Philippines.

Mots clés : Ephemeroptera, Heptageniidae, *Atopopus*, larve, espèce nouvelle.

INTRODUCTION

The heptageniid genus *Atopopus* EATON (1881) was erected on the basis of adults of *A. tarsalis* Eaton from Malaysia (Sabah). A second species, *Atopopus tibialis* ULMER (1920), from the Philippines, has also been known from adults only. HARKER (1950) described adults from Australia as *A. spadix* Harker. It was the opinion of RIEK (1970) that this species was incorrectly placed to family, and it does not appear in the Australian catalogue of Ephemeroptera by CAMPBELL (1988). The family Heptageniidae has not been included in

general treatments of the Australian fauna (CAMPBELL 1988, PETERS and CAMPBELL 1991), nor is it expected to occur in the Australian biogeographic realm (McCAFFERTY and EDMUNDS 1979). The type specimens of this species cannot be found, but based on the forewing illustration provided by HARKER (1950), this species keys to the family Leptophlebiidae using PETERS and CAMPBELL (1991). Other described characteristics are also compatible with this latter family, except for Harker's intimation that all tarsi were five-segmented. We place Harker's species in the family

Leptophlebiidae in a *genus inquirenda* quite possibly representing a new, undescribed genus. The genus *Poya* PETERS and PETERS (1980) from New Caledonia, appears to have relatively similar venation to that depicted by Harker's species in Australia. If the material upon which Harker's name was based is never found, her description will remain an anomaly.

Although the male adult tarsal ratios of *Atopopus*, first described by EATON (1881) and illustrated by EATON (1885), are distinctive within the family Heptageniidae, the absence of any knowledge of the larval stage has prevented any assessment of intergeneric relationships and has led to a general consideration of the genus as an enigma. Recently, we have received valuable specimens of heptageniids from Malaysia and the Philippines donated by George Edmunds of Salt Lake City, Utah. These materials proved to contain both larvae and adults of *Atopopus*, including both stages of *A. tibialis* and a new species we dedicate to Professor Edmunds. In this paper we redescribe *Atopopus*, provide the first larval descriptions of the genus, describe a new species, and phylogenetically compare the adults of the three valid species. All material upon which the present study is based

is deposited in the Purdue Entomological Research Collection (PERC). The type material of *A. tarsalis* was kindly examined under our auspices by Mr. David GOODGER at the British Museum due to the fragile condition and thus intransportability of the material.

RESULTS

1. *Atopopus* Eaton

Type species : *Atopopus tarsalis* Eaton, 1881, by original designation.

Larval diagnosis : Head capsule (Fig. 1) with posterior margin emarginate laterally, and with anterior margin thickened ventrally (Fig. 2). Mandibles with outer incisor serrate medially for entire length but not furcated apically (Fig. 3,4). Ventral surface of galealacinae of maxillae (Fig. 5) with scattered setae; maxillary palpi apparently two segmented, with long setae basally, and pointed apex (Fig. 5). Superlinguae of hypopharynx (Fig. 6) moderately narrow and curved, with pointed laterobasal oriented apex. Lingua (Fig. 6) thick, with somewhat variable medial depression along outer margin. Glossae (Fig. 2) subquadrate and with

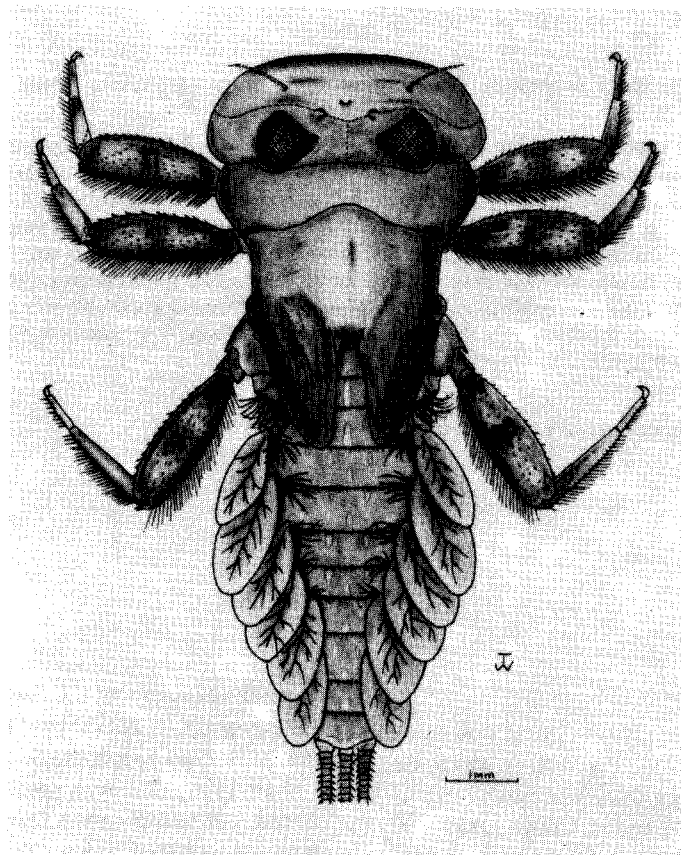


Fig. 1. *Atopopus edmundsi*, n. sp. mature larva, dorsal view.
Fig. 1. *Atopopus edmundsi* n. sp., larve mature en vue dorsale.

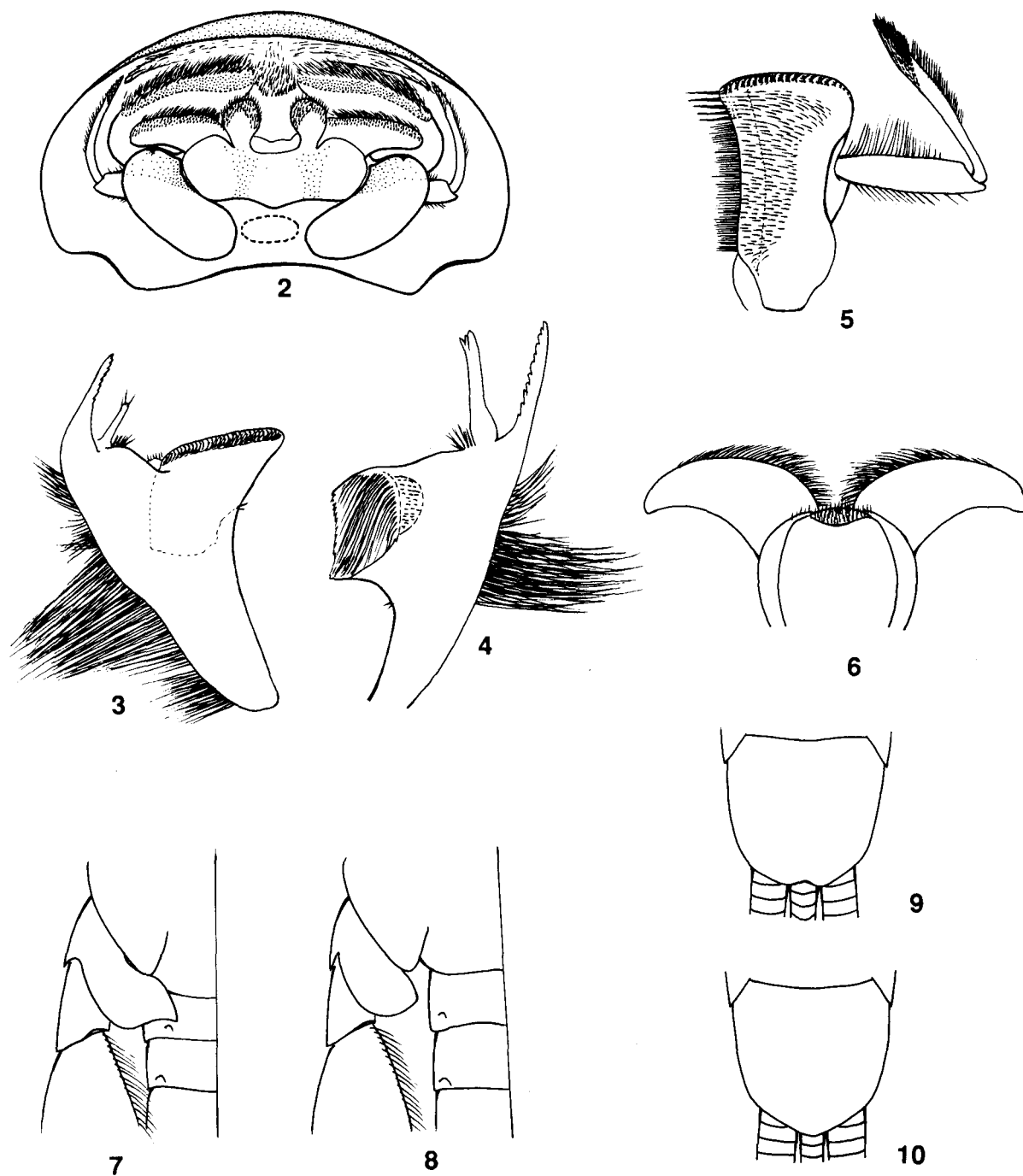


Fig. 2 - 10. *Atopopus* spp. mature larvae.

Fig. 2 : *A. edmundsi* head in ventral view. Fig. 3 : *A. edmundsi* right mandible. Fig. 4 : *A. edmundsi* left mandible. Fig. 5 : *A. edmundsi* left maxilla. Fig. 6 : *A. edmundsi* hypopharynx. Fig. 7 : *A. edmundsi* hindcoxa and supercoxal sclerite. Fig. 8 : *A. tibialis* hindcoxa and supercoxal sclerite. Fig. 9 : female *A. edmundsi* terminal abdominal sternite. Fig. 10 : female *A. tibialis* terminal abdominal sternite.

Fig. 2 à 10. Larves matures d'*Atopopus* spp.

Fig. 2 : tête d'*A. edmundsi* en vue ventrale. Fig. 3 : mandibule droite d'*A. edmundsi*. Fig. 4 : mandibule gauche d'*A. edmundsi*. Fig. 5 : maxille gauche d'*A. edmundsi*. Fig. 6 : hypopharynx d'*A. edmundsi*. Fig. 7 : coxa postérieure et sclérite supercoxal d'*A. edmundsi*. Fig. 8 : coxa postérieure et sclérite supercoxal d'*A. tibialis*. Fig. 9 : sternite abdominal terminal femelle d'*A. edmundsi*. Fig. 10 : sternite abdominal terminal femelle d'*A. tibialis*.

broad U-shaped separation between glossae; paraglossae and glossae with dense setae apically. Pronotum (Fig. 1) narrower than head capsule, with posterior margin concave medially and lacking posterolateral processes or development. Mid- and hindsupercoxal sclerites (Fig. 7, 8) somewhat produced posteriorly; mid- and hindcoxae (Fig. 7, 8) well developed and sometimes pointed posteriorly. Femora, tibiae, and tarsi (Fig. 1) with row of long setae along posterior margins; surface of femora with scattered spatulate setae. Tarsal claws with only one large basal denticle. Abdomen (Fig. 1) with lateral gills on segments 1-7; gills 1 with lamella highly reduced and much smaller than other gill lamellae. Abdominal terga with short and pointed posterolateral projections. Median terminal filament well developed; caudal filaments with whorls of spinelike setae and lacking intersegmental hairlike setae.

Adult diagnosis: Male head with relatively large compound eyes, separated dorsally by more than width of median ocellus, or contiguous. Frontal margin of head (Fig. 11) moderately produced medially, with slight emargination. Tarsal segments of male forelegs (Fig. 12, 15, 18) in order of diminishing lengths = 1, 2, 3, 4, 5; tarsal segment 1 of male mid- and hindlegs > 2.8 times as long as tarsal segment 2 (Fig. 13, 14, 16, 17, 19, 20). Claws of each claw pair dissimilar. Median depression of mesothoracic furcasternum (Fig. 21) parallel sided. Forewings with costal and posterior-most margin pigmented (Fig. 22, 24, 26). Hindwings with blunt to acute costal projection, and with apical costal and entire outer margin pigmented (Fig. 23, 25, 27). Male genitalia (Fig. 28) with subgenital plate broadly emarginate; penes fused in basal half, lacking dorsolateral spines, nearly rounded apically, and with median titillators small or moderately developed.

Species included: *Atopopus edmundsi* WANG & McCAFFERTY, n.sp.; *A. tarsalis* Eaton, 1881; and *A. tibialis* Ulmer, 1920.

Distribution: Southeast Asia.

Affinities: Such characteristics as the mesothoracic furcasternum of the adult, the adult penes, the subquadrate glossae of the larval labium, and apical furcation of the outer incisor of the mandible of the larvae clearly place *Atopopus* with a group of heptageniid genera that includes *Ecdyonurus*. Elongation of the first segment of the male adult foreleg and setation of the larval caudal filaments further places *Atopopus* in a subgroup containing such genera as *Thalerosphyrus* and *Afronurus*. The monophyletic nature of the *Atopopus* taxon is demonstrated by several apomorphic character states: posteriorly well-developed larval coxae, elongated tarsal segment 1 of all male adult legs, and tinted marginal bands on both the fore- and hindwings.

2. *A. edmundsi*, n.sp.

— Description

Mature larva

Body: length 13-15 mm. General coloration yellowish brown to dark brown.

Head: vertex (Fig. 1) with pair of narrow transverse dashes appearing anteromedially of antennal bases and additional pair of narrow transverse dashes appearing postero-

medially of antennal bases. Head width: pronotal width ratio = 27.0:23.0. Galealacinae of maxillae (Fig. 5) with 16-20 comblike apical spines, and setae of medial row becoming very thick in apical fifth. Lingua of hypopharynx (Fig. 6) rounded apically, with sparse, short marginal setae laterad of median marginal depression.

Thorax: Mid- and hind coxae (Fig. 7) well developed and pointed posteriorly. Dorsal surface of femora of all legs (Fig. 1) with basal, middle, and subapical dark transverse bands. Ratio of fore-: mid-: hindfemoral lengths = 12.0:12.5:14.0. Ratio of fore-: mid-: hindtibial lengths = 10.0:10.5:11.5. Ratio of fore-: mid-: hindtarsal length = 1.0:1.0:1.0. All tarsal claws with only one large basal denticle. R_1 crossveins of forewing pads not margined with brown.

Abdomen: Lamellate gills present on segments 1-7; fibrilliform gills present on segments 1-6; fibrilliform gills darker pigmented in apical half. Segments 1-10 with short and pointed posterolateral projections. Light yellowish medial markings extending from posterior margin of terga 1-9 (Fig. 1) (progressively more developed on anterior terga); pair of submedial light spots most apparent on terga 3-8. Caudal filaments with ventral spinelike setae smaller than dorsal setae. Female terminal sternite (Fig. 9) with narrow emargination apically.

Male adult

Body: length 8.0 mm. Forewing length 11.0 mm; forewing width 3.0 mm. General color brown to dark brown.

Head: with large compound eyes separated dorsally by more than width of median ocellus (Fig. 11).

Thorax: Forewings (Fig. 22) relatively narrow-elongate; costal and subcostal area of forewing tinted brownish; weakest in basal costal area; costal crossveins numbering about 40; crossveins below R_1 not margined; stigmatic crossveins not anastomosed; both veins of second pair of cubital intercalaries originating basad of MP fork; posterior margin of wing between MP_2 and A_1 very thinly tinted, and marginal intercalaries relatively short in this area. Hindwings (Fig. 23) with blunt costal projection; margin of wing tinted brownish from end of costal projection to anal region, narrowly in costal margin; cubital area with single intercalary vein. Forelegs (Fig. 12) subequal in length to body; tibia length 1.2 times that of femora; tarsi length 1.5 times that of femora; tarsal segment 1 length 1.4 times that of tarsal segment 2. Hindlegs (Fig. 14) with tibiae length 0.6 times that of femora; tarsal length 0.7 times that of femora and 1.1 times that of tibia; tarsal segments in order of diminishing lengths = 1, 2, 5, 3, 4; tarsal segment 1 length 3.1 times that of tarsal segment 2.

Abdomen: Penes each with medial titillator becoming sharp apically and extended slightly beyond apical margin of penes (Fig. 28). Cerci length more than two times that of body.

Female subimago

Body: length 13.5 mm. Forewing length 14.0 mm; forewing width 5.0 mm. General characteristics similar to that described above for male adult, except for usual difference attributable to different sexes or different alate stages.

Thorax: with forelegs missing in specimen. Hindlegs with coxae slightly pointed posteriorly; tibiae length 0.6 times

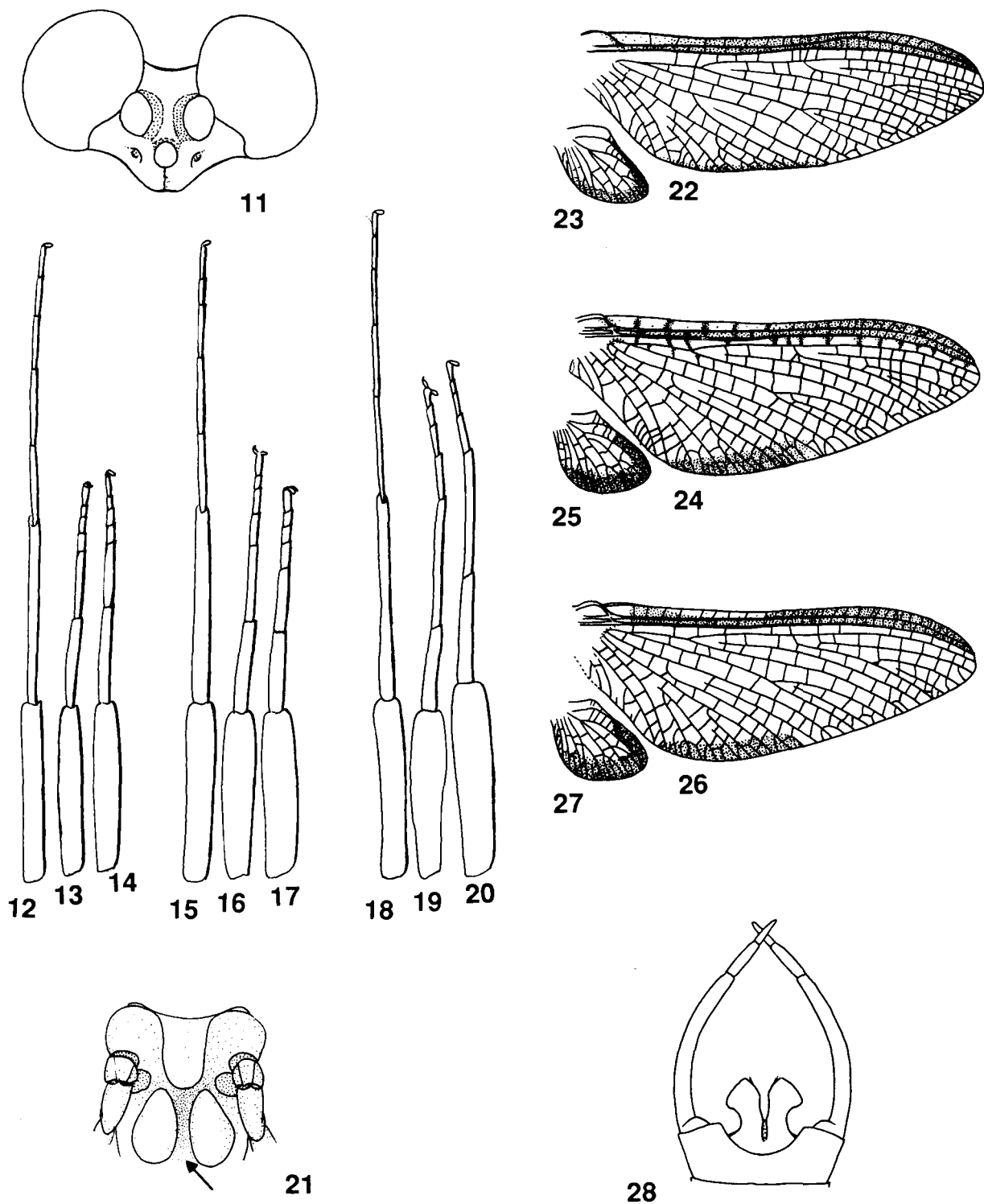


Fig. 11-28. *Atopopopus* spp. male adults

Fig. 11 : *A. edmundsi* head in frontal view. Fig. 12 : *A. edmundsi* foreleg. Fig. 13 : *A. edmundsi* midleg. Fig. 14 : *A. edmundsi* hindleg. Fig. 15 : *A. tibialis* foreleg. Fig. 16 : *A. tibialis* midleg. Fig. 17 : *A. tibialis* hindleg. Fig. 18 : *A. tarsalis* foreleg (after Eaton 1885). Fig. 19 : *A. tarsalis* midleg (after Eaton 1885). Fig. 20 : *A. tarsalis* hindleg (after Eaton 1885). Fig. 21 : *A. edmundsi* mesosternum (arrow to median depression of furcasternum). Fig. 22 : *A. edmundsi* forewing. Fig. 23 : *A. edmundsi* hindwing. Fig. 24 : *A. tibialis* forewing. Fig. 25 : *A. tibialis* hindwing. Fig. 26 : *A. tarsalis* forewing (after Eaton 1885). Fig. 27 : *A. tarsalis* hindwing (after Eaton 1885). Fig. 28 : *A. edmundsi* male genitalia in ventral view.

Fig. 11 à 28. Adultes mâles d'*Atopopopus* spp.

Fig. 11 : tête d'*A. edmundsi* en vue frontale. Fig. 12 : patte antérieure d'*A. edmundsi*. Fig. 13 : patte moyenne d'*A. edmundsi*. Fig. 14 : patte postérieure d'*A. edmundsi*. Fig. 15 : patte antérieure d'*A. tibialis*. Fig. 16 : patte moyenne d'*A. tibialis*. Fig. 17 : patte postérieure d'*A. tarsalis*. Fig. 18 : patte antérieure d'*A. tarsalis* (d'après Eaton 1885). Fig. 19 : patte moyenne d'*A. tarsalis* (d'après Eaton 1885). Fig. 20 : patte postérieure d'*A. tarsalis* (d'après Eaton 1885). Fig. 21 : mesosternum d'*A. edmundsi* (flèche sur la dépression médiane du furcasternum). Fig. 22 : aile antérieure d'*A. edmundsi*. Fig. 23 : aile postérieure d'*A. edmundsi*. Fig. 24 : aile antérieure d'*A. tibialis*. Fig. 25 : aile postérieure d'*A. tibialis*. Fig. 26 : aile antérieure d'*A. tarsalis* (d'après Eaton 1885). Fig. 27 : aile postérieure d'*A. tarsalis* (d'après Eaton 1885). Fig. 28 : genitalia mâles d'*A. edmundsi* en vue ventrale.

that of femora ; tarsi length 0.6 times that of femora, and subequal to that of tibiae ; tarsal segments in order of diminishing length = 1, 5, 2, 3, 4 ; tarsal segment 1 length 3.5 times that of tarsal segment 2.

Abdomen : with terminal sternite with narrow emargination posteriorly. Cerci missing in specimen.

— Material examined

Holotype : male adult (pinned), British N. Borneo, Tenompok, 1460 m, Jesselton, 30 mi., E., II-2-4-1959. *Paratypes* : one mature larva (female in alcohol), E. Malaysia, Sabah, Silau stream, N. of Kinabalu National Park Headquarters, 1585 m (S3e), 2-VIII-72, G.F. & C.H. Edmunds ; one mature larva (female in alcohol), East Malaysia, Sabah, Liwagu Riv. at bridge, Ranau, 335 m (S4e), 11-16-VIII-72, G.F. & C.H. Edmunds. Other material : one immature larva, same data as first listed paratype ; one female subimago (alcohol), Brit. N. Borneo : Ranau, 1700', open forest, 28-IX-1959, T. Maa.

— Etymology

It is an honor to name this species after Professor George F. Edmunds, Jr. for his consistent stimulation and contribution to basic research on Ephemeroptera.

— Diagnosis and discussion

Larvae of *A. edmundsi* can be distinguished from those of *A. tibialis* by the 16-20 comblike spines at the apex of the galealacinae of the maxillae, the more posteriorly produced mid- and hindcoxae, and the shape of the apical margin of the terminal abdominal sternite in the females. We do not yet know the larvae of *A. tarsalis*. The forewings of *A. edmundsi* adults are narrower, have a thinner posterior tint band, and have shorter marginal intercalaries than the adults of both *A. tarsalis* and *A. tibialis*. Other differences between the adults of these three species can be found using Table 1 and Fig. 29, discussed below.

Our association of the larval and adult stages of *A. edmundsi* is based on several specific characteristics that are common to both the adults and larvae. Dissection of the ultimate instar larval hindlegs of *A. edmundsi* revealed the same tarsal segment 1 : tibia length ratio as found in the adults of

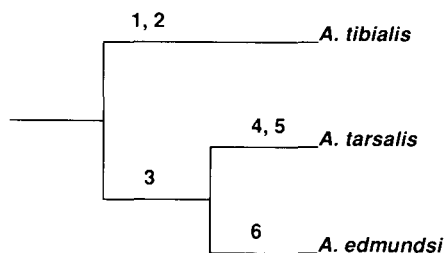


Fig. 29. Cladogram of *Atopopus* species (numbers refer to apomorphies in Table 1).

Fig. 29. Cladogramme des espèces d'*Atopopus* (les nombres se réfèrent aux apomorphies du Tableau 1).

APOMORPHY

- 1 - R₁ and R_s crossveins margined
- 2 - Hindwing costal projection acute
- 3 - Hindtarsal segment 1 length > 3.1 x segment 2 length
- 4 - Hindtarsal segment 1 longer than tibia
- 5 - Hindtarsal segment 1 length > 3.5 x segment 2 length
- 6 - Forewing narrow (length > 3.5 X width)

PLESIOMORPHY

- crossveins not margined
- costal projection blunt
- segment 1 < 3.0 X segment 2
- segment 1 shorter than tibia
- segment 3.1 - 3.4 X segment 2
- Forewing wide (length < 3.0 X width).

Table 1. Adult character states used to deduce cladogram of *Atopopus* species as depicted in Fig. 29.

Tableau 1. Caractères adultes pris en compte dans la déduction du cladogramme des espèces d'*Atopopus*, tel que représenté sur la Fig. 29.

this species (tarsal segment 1 shorter than tibia). This excludes the possibility of these larvae belonging to *A. tarsalis*, since that ratio is critically different in hindlegs of *A. tarsalis* (tarsal segment 1 longer than tibia). The larvae of *A. edmundsi* were excluded from consideration as those of *A. tibialis* by the fact that our examination of the wing venation evident in larval wingpads revealed that R₁ crossveins are not darkly margined as they are in the adults (and larvae) of *A. tibialis*. In addition, the narrow apical emargination of the terminal abdominal sternite matched in the female larva and female subimago.

3. *A. tibialis* Ulmer, 1920

— Description

Mature larva

Body : length 12-14 mm. General coloration yellowish brown.

Head : generally similar to that of *A. edmundsi*, described above, except for following. Vertex lacking transverse dashes. Apex of galealacinae with comblike spines numbering 13-15.

Thorax : generally similar to that of *A. edmundsi*, described above, except for following. Mid- and hindcoxae (Fig. 8) well developed posteriorly but not sharply pointed. R₁ crossveins of forewing pads margined with brown. Dorsal surface of femora unicolorous, without distinctive transverse bands.

Abdomen : generally similar to that of *A. edmundsi*, described above, except apical margin of terminal sternite of female entire, without any emargination (Fig. 10).

Male adult

Body : length 11-14 mm. Forewing length 13-16 mm ; hindwing length 4.0-5.0 mm. General coloration yellowish brown.

Head : generally similar to *A. edmundsi*, except compound eyes separated by less than the width of median ocellus.

Thorax : generally similar to that of *A. edmundsi*, except for following. Forewings (Fig. 24) subtriangular ; costal and

subcostal area tinted with brown, except basal half of costal area unpigmented, with only crossveins margined; some stigmatic crossveins anastomosed; R_1 and R_s crossveins margined; posterior tint band relatively broad; marginal intercalaries between MP_2 and A_1 relatively long. Hindwings (Fig. 25) with costal projection acute; marginal tint band relatively broad throughout (not present in basal costal area). Hindlegs (Fig. 17) with tarsal segment 1 less than three times that of tarsal segment 2.

Abdomen: generally similar to that of *A. edmundsi*.

— Material examined

One mature male and one mature female larva, Philippines, Negros Or., Fast stream, L. Balinsasayao, 3-X-1959 Yoshimoto; two male adults, Philippines, Camarines Sur, Mr. Isarog, 20 km E. of Naga 500-600 m, 7-IV-1963, H. M. Torrevillas.

— Diagnosis and discussion

Larvae of *A. tibialis* can be distinguished from those of *A. edmundsi* by the presence of 13-15 comblike spines at the apex of the galealaciniae of the maxillae, the less-developed (not sharply pointed) mid- and hindcoxae, and the apical margin of the terminal abdominal sternite in the female that lacks any emargination. The forewings of *A. tibialis* differ from those of both *A. edmundsi* and *A. tarsalis* by possessing margined basal costal, R_1 , and R_s crossveins. The hindwings differ from those of both other species by possessing an acute costal projection.

Our association of the larvae and adults of *A. tibialis* is based primarily on the possession of margined R_1 crossveins in adults and mature larval wingpads (also see discussion of association of stages of *A. edmundsi*, above).

Further description of the male adult of *A. tibialis* may be found in ULMER (1924).

Atopopus tibialis has been reported from both the Philippines (ULMER 1920, 1924) and Malaysia (Sabah) (ULMER 1939). We can confirm the report from the Philippines, but we suspect that the Sabah records are actually referable to *A. edmundsi*.

4. *A. tarsalis* Eaton, 1881

Description of the male adults of this species may be found in EATON (1885). Larvae and females remain unknown. Type material in the British Museum demonstrates that Eaton's (1885: Pl. XXII, Fig. 39) depiction of partial fusion of the segmentation between the tibia and tarsal segment 1 of the hindlegs is incorrect. These segments are not fused (Figs. 19, 20), but demarked as in *A. edmundsi* and *A. tibialis* and other Heptageniidae. Prior to our discovery of this, it could have been interpreted that the adults of *Atopopus* were unlike those of other Heptageniidae and instead similar to those of the heptagenioid family Pseudironidae (see WANG and McCafferty 1995).

The adults of *A. tarsalis* can be told easily from those of *A. edmundsi* and *A. tibialis* by a hindtarsal segment 1 that is longer than the hindtibia. Unlike the forewings of *A. tibialis*, those of *A. tarsalis* (Fig. 26) lack any crossvein margination; and unlike forewings of *A. edmundsi*, those of *A. tarsalis* (Fig. 26) possess a thick posterior tint band, and the marginal intercalaries are somewhat longer.

Atopopus tarsalis is known only from Malaysia (Sabah).

5. Species relationships

A hypothesized phylogeny of the three species of *Atopopus* treated herein is presented as a cladogram (Fig. 29). Numbers on branches of the cladogram refer to the synapomorphies and autapomorphies listed in Table 1. Because the larvae of *A. tarsalis* remain unknown, character states used to deduce the cladogram were limited to those of adults. Polarity of character states were determined by considering *Ecdyonurus* and related taxa as the outgroup. Character states described under numbers 3 and 5 represent a two-step phenocline, with the first tarsal segment of the hindleg becoming progressively longer.

We deduce that *A. tarsalis* and *A. edmundsi* are sister species whose immediate common ancestor was derived from a common ancestor with *A. tibialis*. Distributions would further indicate that *A. tibialis* and common ancestor to *A. tarsalis* and *A. edmundsi* paralleled a vicariant or dispersalist event involving Borneo and the Philippines.

ACKNOWLEDGMENTS

We thank George F. EDMUNDS, Jr., Salt Lake City, Utah, for donating material of *Atopopus* for this study and Mr. David GOODGER, London, England, for examining type material of *A. tarsalis* in the British Museum. We also thank Steve JENSEN, Springfield, Missouri, for making comparative material available to us, and Alain THOMAS, Toulouse, France, for preparing the French resumé. This paper has been assigned Purdue Agricultural Research Program Journal n°. 14743.

REFERENCES

- Eaton (A.E.). 1881. — An announcement of new genera of the Ephemeroidea. *Entomol. monthly mag.*, 17: 21-27.
- Eaton (A.E.). 1883-88. — A revisional monograph of recent Ephemeroidea or mayflies. *Trans. Linn. Soc. London, Sec. Ser. Zool.*, 3: 1-352.
- Campbell (I.). 1988. — Ephemeroptera, pp. 1-22, in: D.W. Walton, ed, *Zoological Catalogue of Australia, Volume 6. Ephemeroptera, Megaloptera, Odonata, Plecoptera, Trichoptera*, Brown Prior Anderson, Carlton, Victoria.
- Harker (J.E.). 1950. — Australian Ephemeroptera. Part I. Taxonomy of New South Wales and evaluation of taxonomic characters. *Proc. Linn. Soc. Wales*, 75: 1-34.
- McCafferty (W.P.) & Edmunds (G.F.). 1979. — The higher classification of the Ephemeroptera and its evolutionary basis. *Ann. Entomol. Soc. Am.*, 72: 5-12.
- Peters (W.L.) & Campbell (I.). 1991. — Ephemeroptera (mayflies), pp. 279-293, in I.D. Naumann et al., eds, *The Insects of Australia, 2nd Ed.*, Melbourne Univ. Press, Melbourne.
- Peters (W.L.) & Peters (J.G.). 1979-80. — The Leptophlebiidae of New Caledonia (Ephemeroptera). Part II. Systematics. *Cah. O.R.S.T.O.M., sér. Hydrobiol.*, 13: 61-82.
- Riek (E.F.). 1970. — Ephemeroptera (mayflies), pp. 224-240 in D.F. Waterhouse et al., eds, *The Insects of Australia*, Melbourne Univ. Press, Carlton, Victoria.
- Ulmer (G.). 1920. — Neue Ephemeropteren. *Arch. Naturgesch.*, 85: 1-80.
- Ulmer (G.). 1924. — Ephemeropteren von den Sunda-Inseln und den Philippinen. *Treubia*, 6: 28-91.
- Ulmer (G.). 1939. — Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. *Arch. Hydrobiol. Suppl.*, 16: 443-692.
- Wang (T.-Q.) & McCafferty (W.P.). 1995. — Relationships of the Arthropodea, Heptageniidae, and Pseudironidae (Ephemeroptera: Heptagenioidea). *Entomol. News*, in press.