

Palawaneuria, a new subgenus of *Compsoeuria* and new species of *Compsoeuria* and *Afronurus* (Ephemeroptera, Heptageniidae) from Palawan, Philippines

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Abstract

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A new subgenus and four new species of Heptageniidae are described from streams of the Philippine island of Palawan: *Compsoeuria* (*Palawaneuria*) *cabayuganensis* subgen. n., sp. n. (♂, ♀, ♂-SI, ♀-SI), *Compsoeuria* (s. str.) *tagbanua* sp. n. (♂, ♀, ♂-SI, nymph), *Afronurus palawanensis* sp. n. (♂-Ny, ♂-SI) and *Afronurus zerningi* sp. n. (♂-Ny). The new subgenus shares with imagos of *Compsoeuria* (s. str.) markings of body, legs and wings and is separated from it by absence of apico-medial hooks and discal spines of penis lobes and by having brown-coloured wings in subimagos. The genus *Compsoeuria* Eaton is recorded the first time from the Philippines. The taxonomic status of *Compsoeuria* Eaton and the synonymization of *Cinygmmina* Kimmins with *Afronurus* Lestage are discussed.

Introduction

No data on Heptageniidae of Palawan are available so far. Nine species of the family have been listed for other Philippines islands up to now: *Afronurus lobatus* (Ulmer, 1920: ♂) (Mindanao), *A. mindoroensis* Braasch, 2005 (♂, ♀: Mindoro), *A. philippinensis* Flowers & Pescador, 1984 (♂, L: Luzon), *A. sibuyanensis* Mol, 1987 (♂, ♀, ♂-SI: Sibuyan), *Atopopus meyi* Braasch, 2005 (♂, ♀, L: Leyte, Mindanao), *A. tibialis* Ulmer, 1920 (♂: Luzon, Negros), *Ecdyonurus illotus* (Navás, 1933) (♀: Luzon, Haightplace), *Thalerosphyrus torridus* (Walker, 1853) (♀: Luzon) and *T. sinuosus* Navás, 1933 (Wang & McCafferty, 2004: L: Philippines).

The comparatively small number of four confirmed Heptageniidae genera on the Philippines – *Ecdyonurus* and *Thalerosphyrus* are still questionable (s. below) – contrasts with genera numbers of adjacent islands like Borneo (6), Sundaland (7), and continental Southeast

Asia (Vietnam: 9, Thailand: 11, Southern China: 9, Peninsular Malaysia: 7) (Braasch 1990, 2005, 2006; Braasch in prep. a, b; Braasch & Soldán 1984a, b, c; 1986a, b, 1988; Edmunds & Polhemus 1990; Nguyen & Bae 2004; Soldán & Braasch 1986; Sangpradup et al. 2002; Sartori et al. 2003; Tong & Dudgeon 2003; Wang & McCafferty 1995, 2004).

The *Ecdyonurus* record by Wang & McCafferty (2004) is based on a larva from the Philippines. According to our knowledge the distribution of true *Ecdyonurus* Eaton, 1868 this genus is restricted to the Palearctic realm. Thus the aforementioned *Ecdyonurus* generally should be referred to this genus in a very broad concept of the authors, including *Afghanurus* Demoulin, 1964, *Rhithrogeniella* Ulmer, 1939, *Nixe* (s. str.) Flowers, 1980 and *Nixe* (*Akkarion*) Flowers, 1980. Navás (1933, p. 91) remarks that *Ecdyonurus illotus* is similar to the former *Ecdyonurus lobatus* Ulmer (“*Similis lobato* Ulm.”, see above) and “*Ala anterior* (fig. 81) angusta,

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apice elliptica, areis costali et subcostali obscuribus". This description provides a hint to the colour pattern in the costal and subcostal field of *Afronurus* spp. of the Philippines (Braasch, in prep. a; Flowers & Pescador 1984; Mol 1987).

The Philippine *Thalerosphyrus torridus* is problematic, because Ulmer (1924) associated a ♂ from Sumatra with a ♀ from northern Luzon. Referring to the female specimen studied (No. 101, Majajay, Luzon, 04. 04. 1860, Coll. Selys, ISNB), Ulmer (1924) pointed out that the forewings are alike of those of *T. determinatus* (Walker, 1853), i.e. with pitch-brown to umbra-brown costal and subcostal field in forewing. It might rather be supposed that the female is an *Afronurus* with C- and SC-field in forewings tinged as in *Afronurus philippinensis* (Flowers & Pescador 1984: p. 362) or *A. sibuyanensis* (Mol 1987: p. 3, fig. 1).

Borneo was even reached by *Thalerosphyrus* (Braasch, in prep. b). Thus further immigration steps to the eastern Philippine islands that do not belong to Sundaland (Heaney 1985) are rather unlikely. At no case, a report of larval occurrence of *Thalerosphyrus sinuosus* in the Philippines has been confirmed (Webb, c. l.).

The circumstances mentioned reflect the unsatisfying knowledge of this family in the Philippines.

Material and methods

Material. The material treated herein was mostly obtained from collections of the AQUA Palawana Project by the junior author at the Cabayugan River (CR) at 10°09'–10°12' N, 118°49'–118°55' E and Panaguman (PR) at 10°14'–10°15' N, 118°56'–118°58' E, both draining into the South Chinese Sea at the Saint Paul's Subterranean River National Park, Puerto Princesa City (Freitag 2004b, 2005).

Benthic specimens were captured by means of substrate-filled baskets with monthly exposition in current waters. Here-upon specimens were brushed resp. washed off from the substrate. Further specimens (prevalingly larvae) were caught by nocturnal exposition of drift nets (for details see Freitag 2005). Imagos and subimagos were obtained by specially modified emergence traps (Freitag 2004a). Samples were taken between 16.05.2000–26.11.2001.

Collecting sites were along a section (16 km) of the Cabayugan River: from the headwater site CR1 (1–4 m width, 0.2–0.5 m depth, 80 m a.s.l.), followed by the sites CR2 to CR4 (3–8 m width, 0.2–1.1 m depth, altitude (28–37 m), upstream of an underground cave of 8 km. The Cabayugan River runs through secondary forest (CR1–CR2), paddy fields (CR3) and primary forest (CR4).

An additional collecting site was situated at the Panaguman River (PR) in a course of about 6 km (PR1: 3–13 m width, 0.2–0.4 m depth, 8 m a.s.l.; PR2: estuary 29 m width, 0.5 m depth, altitude 0 m). No Heptageniidae were recorded at the estuaries, the subterranean section and limestone tributaries, which were sampled during the same time period.

Supplementary material of *Afronurus* spp. and *Compsoeuria* sp. used for this study was collected on Palawan between 05.–16.04.1992 by Michael Zerning (Potsdam, Germany), who obtained larval/nymphal specimens by kick sampling and few subimagos by a handled net to scour off the vegetation.

Terminology. The morphological terminology used herein follows mainly Braasch & Soldán (1986c) and Webb et al. (2006). In the genus *Afronurus* we accept the position of Kluge (2004) and Wang &

McCafferty (2004). The generic and specific terms were compared with those in Hubbard (1990) and Kluge (2004).

Genital and larval preparations. For checking the genitalia of males, last segment of specimens were separated by a needle or fine forceps. The penis was carefully taken off from the styli and transferred into glycerin, what guarantees the immobility of object for drawings.

Wings, legs and caudal filaments were obtained in similar way for detailed study.

Larvae were prepared by curved needle for partitioning off head, pronotum, abdomen and legs. Removing of the gills occurred with a fine scalpel, as a rule of first, third and seventh lamella with their tufts of filaments.

All described material was transferred into 70% alcohol and separately preserved in vials.

Abbreviations. ♂ = male; ♀ = female; L = larva, -ae; Ny = nymph (last instar larva with fully grown wing pads and often with prospective male genitals), -s; SI = Subimago; HR = Head Ratio (head width: head length in mm); LR = Leg ratios femur: tibia: tarsus (tarsal segments I–V) in mm; CR = Cabayugan River; PLW = Penis ratios length : width; PR = Panaguman River; E = East; N = North; NW = Northwest; SW = Southwest.

Depositories. CBP = Collection D. & H. Braasch, Potsdam, Germany; IMRL = Institut und Museum für Regenwaldökologie Leipzig, Phylodrom e. V.; ISNB = Institute Royal des Sciences Naturelles de Belgique, Bruxelles; MNHU = Museum für Naturkunde der Humboldt-Universität Berlin; WPU = Western Philippines University, Aquatic and Marine Biology Section, Puerto Princesa City, Philippines.

Results

Compsoeuria (s. str.) Eaton, 1881

Type species. *Compsoeuria spectabilis* Eaton, 1881: p. 23.

The genus *Compsoeuria* is accepted here in the sense of Braasch & Soldán (1986a) and Webb et al. (2006). It belongs to the subfamily Ecdyonurinae s. str. and tribe Compsoeuriini Webb et al. 2006. The genus is characterized by parallel-sided medial margins of the mesothoracic furcasternum, forewings with a reduced number of variously thickened and shaded crossveins, slightly sigmoidally bent costae and subcostae, stippled femora. The penes are slightly expanded laterally, only partially fused medially, display distinct dorsal sclerites (apically and laterally), ventral and dorsolateral spines, as well as typical, conspicuous hooks at base of incision medially on both apical lobes.

Subimagos are very similar to imagos in body and leg patterns, and display grey-clouded wings. Penis contours resemble those of imagos by the characteristic penial hooks.

Larvae of the genus generally have picturesque patterns on head and abdomen, short posterolateral spines on abdominal segments, acute supracoxal spurs of mid- and hindlegs, fimbriate setae on the inner surface of the hind tibiae, absence of posterolateral extensions of the pronotum, slender (not widened) anterior margin of the head capsule, numerous black spots at head and femora, narrow mouthparts, and apically pointed glossae (Braasch & Soldán 1986: fig. 14.2, p. 44; Ulmer 1939).

***Componeuria* (s. str.) *tagbanua* sp. n.**

Figures 1–17

Holotype ♂ (MNHU). Philippines, Isl. Palawan, Puerto Princesa City, Cabayugan River, CR3, "PHIL.: Palawan, P. Princesa S Manturon, Cabayugan R. 10°09'16" N 118°52'30" E 29.3.2001, leg. Freitag(CR3E)", specimen and genital in 70% alcohol.

Paratypes. 1 ♂ (UPLB), 1 SI ♂ (WPU), 1 SI ♀ (UPLB), same label as holotype; 1 ♂ (IMRL), 2 SI ♂ (MNHU, IRML), 1 ♀ (MNHU), 3 SI ♀♀ (MNHU, WPU, IMRL), "PHIL.: Palawan, P. Princesa S Manturon, Cabayugan R. 10°09'16" N 118°52'30" E 31.7.2001, leg. Freitag(CR3E)"; 1 Ny, 11 L (MNHU), 6 L (UPLB), "PHIL.: Palawan, P. Princesa S Manturon, Cabayugan R. 10°09'16" N 118°52'30" E 31.7.2001, leg. Freitag(CR3P)"; 3 L (WPU), "PHIL.: Palawan, P. Princesa S Manturon, Cabayugan R. 10°09'16" N 118°52'30" E 04.9.2000, leg. Freitag(CR3P)"; 2 L (IRML), "PHIL.: Palawan, P. Princesa S Manturon, Cabayugan R. 10°09'16" N 118°52'30" E 04.9.2000, leg. Freitag(CR3P)"; 1 Ny (CBP), "Philippines, SE Palawan, 7 km N Narra, Taritien River; at 9°19' N, 118°22' E, stony mountain stream (6–7 m width, up to 2 m depth, altitude 250 m) in forest, 05.04.92, leg. M. Zerning"; 2 L (CBP), "Philippines, SE Palawan, 3 km N Narra 9°18' N, 118°23' E, lowland stream, 2–3 m width, 0.2 m depth in paddy fields, partly forested, stony ground, along paddy fields, 10.04.92, leg. Zerning"; 2 Ny (CBP), "Philippines, NW Palawan, Puerto Princesa City, Sabang, Sabang River 10°11' N, 118°53' E, lowland river, 3–4 m width, 0.2 m depth, stony, rice fields, banks partly with trees, 16.04.92, leg. Zerning".

Additional material. Several immature larval stages of this species have been recorded from CR1, CR2, CR4 and PR1. Due to their less distinct characters we refrain from inclusion into the type series.

Etymology. The species is named after the native ethnic community of the *Tagbanua*, who live in the area the new species was found.

Male. Body length 5.0 mm; length of forewing 4.5 mm; length of hindwing 1.4 mm; caudal filaments > 12 mm long (incomplete).

Head with almost contiguous eyes (Fig. 1). Prothorax pale yellow, medially with dark patch (Fig. 1); mesothorax marginally with two darker, parallel lines; posterior third pale yellow with two black curved streaks and dark edges; dorsal abdominal terga with dark brown patches on yellow ground (Fig. 2); sterna pale yellowish.

Forewings transparent with 10–11 brown crossveins between C, SC and R1; crossveins brownish shaded; SC and R1 in distal third of forewing form a sinuous curve (comp. Gillies 1984: p. 22, fig. N, C); pterostigmal area opaque; single crossband of basal third in forewing marked by dark brown crossveins almost reaching outer margin of wing; distal half of forewing with inconspicuous colourless veins.

Femora (Fig. 4) without distinct crossbands, but completely stippled; tibiae with three distinct dark crossbands (Fig. 4); tarsal segments distally slightly darkened; LR in foreleg 1.2 : 1.3 : 1.8 (0.3 : 0.6 : 0.5 : 0.2 : 0.2), LR in hindleg 1.7 : 0.9 : 0.7 (0.2 : 0.1 : 0.1 : 0.2).

Genitalia. Penis dorsally somewhat twisted, stocky; stem basally slightly wider than long, slightly slenderer up to laterally enlarged lobes (Fig. 3); lobes approx. as wide as basal stem, fused up to basal 0.75 of penis; api-

cal third with broad V-shaped incision, submedially with small pointed hooks; face of apicolateral lobes with indistinct, outward directed spine (broken line) in each half; titillators strong, curved, with double-bulbous, slightly divergent basal roots; edge of styliger with shallow sockets and without separate swellings (Fig. 5); forcipes small, relatively short, curved, length 0.12 mm; length of segments in mm: I 0.13 (basal), II 0.79, III 0.17, IV 0.19 (distal). Caudal filaments pale, darker at distal third, articulations alternately narrowly bordered by black margins.

Female. Body length 5.2 mm; forewing length 6.0 mm; hindwing length 1.3 mm; caudal filaments > 11 mm long (incomplete).

Interocular distance 0.44 mm, four times as wide as ocellus.

Dorsal pattern of abdominal segments distinctly varying from that of male (Fig. 6); sterna pale yellowish; forewings with 14 expanded and shaded crossveins between C and Sc.

Femora stippled, without discernible bands, without distinctly fragmented patches; tibiae with three inconspicuous bands; LR in foreleg 1.3 : 1.1 : 1.0 (0.2 : 0.3 : 0.2 : 0.1 : 0.2), LR in hindleg 1.4 : 0.9 : 0.7 (0.2 : 0.1 : 0.1 : 0.1 : 0.2).

Subgenital plate with slightly arched distal margin; subanal plate spade-like bluntly rounded (Fig. 9). Caudal filaments whitish, annulated as in male.

Male SI. Body length 5.2 mm; forewing length 5.3 mm; caudal filaments lost.

Head, thorax, abdomen resemble imago to a great extent with the exception that the patterns are sometimes less expressed. Dorsal segments yellowish with brown patterns. Femora conspicuously stippled; tibiae with three narrow dark bands; first tarsal segment distally darker. LR: in foreleg 1.5 : 1.4 : 1.0 (0.2 : 0.3 : 0.2 : 0.1 : 0.2); LR in hindleg 1.8 : 1.1 : 0.7 (0.2 : 0.1 : 0.1 : 0.1 : 0.2).

Wings grey clouded; expanded and shaded crossveins faintly expressed.

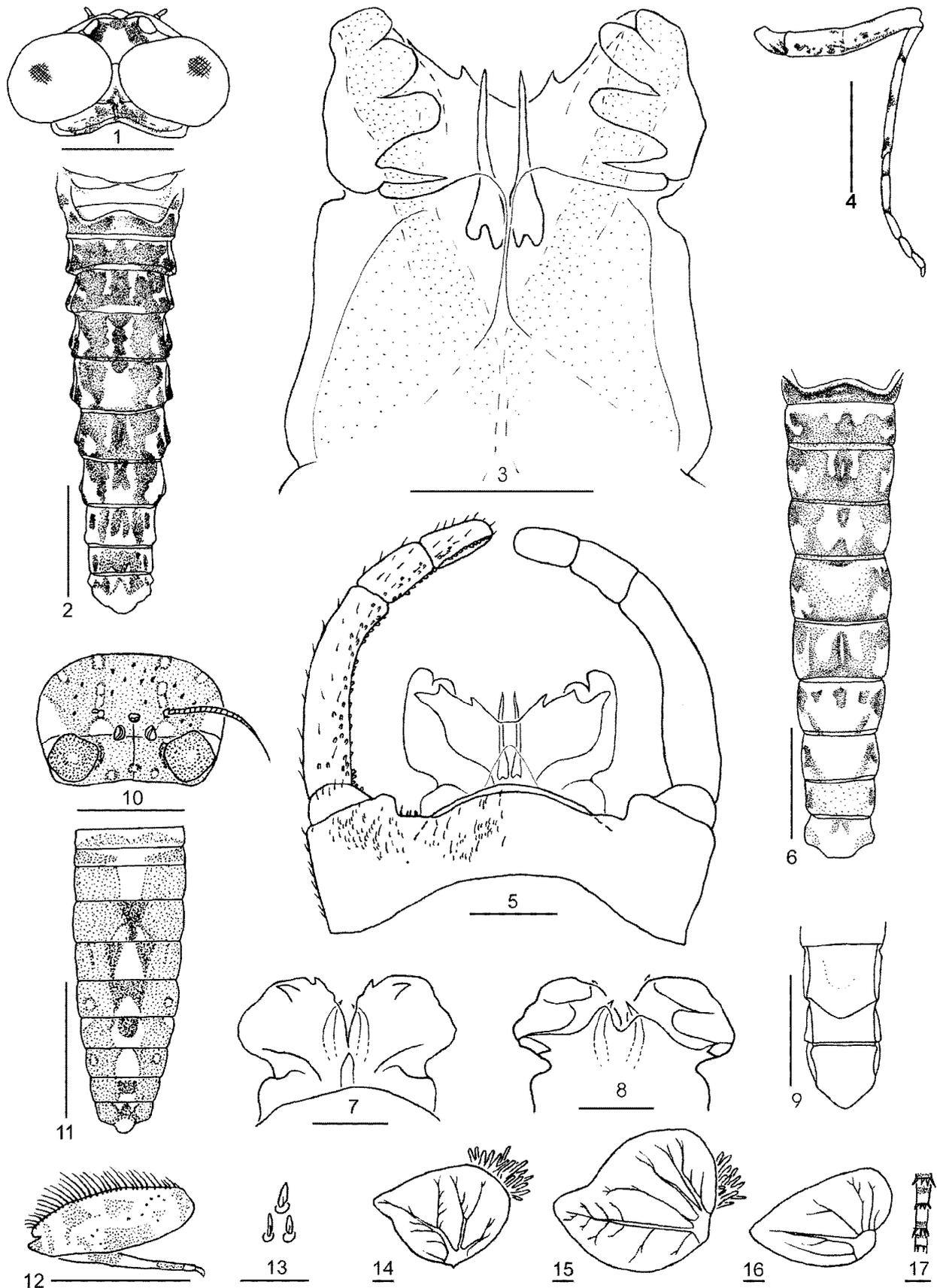
Genitalia (Figs 7, 8). Weakly differentiated, but species-characteristic sclerotisations fairly visible in dorsal penis (Fig. 8). Caudal filaments whitish, annulated as in imagos.

Female SI damaged, we refrain from formal description.

Male Ny. Body length 4.9 mm; caudal filaments 10 mm long. (♀-Ny. Body length 7.8 mm, caudal filaments lost).

Head dark brown, with characteristic pattern of four big, pale dots at front margin and two subparallel, interrupted longitudinal pale bands (Fig. 10), HR 1.5 (1.8 : 1.2); abdomen (2.3 mm).

Terga with dark brown pattern in the middle (Fig. 11) underlined by a whitish longitudinal band, distal margin with row of somewhat regular arrangement of small pointed bristles (0.02–0.04 mm).



Figures 1–17. *Compsoeuria* (s. str.) *tagbanua* sp. n. ♂ (scale 1 mm): 1. Dorsal head and prothorax; 2. Dorsal abdomen; (scale 0.1 mm); 3. Dorsal penis; (scale 1 mm); 4. Dorsal foreleg; (scale 0.1 mm); 5. Ventral genital segment; ♀ (scale 1 mm); 6. Dorsal abdominal pattern; ♂-SI (scale 0.1 mm); 7. Ventral penis; 8. Dorsal penis; ♀ (scale 1 mm); 9. Subgenital and subanal plates; ♂-Ny (scale 1 mm); 10. Dorsal head; 11. Dorsal abdomen; 12. Dorsal foreleg; (scale 0.1 mm); 13. Bristles at face of foreleg femur; 14. Gill I; 15. Gill III; 16. Gill VII; 17. Annulation and whorls of spines of caudal filaments.

Femur of foreleg (Fig. 12) ca. 0.56 mm wide, with dissolved large patches, speckled with dark brown spots, densely covered with ca. 0.04 mm long, pointed bristles (Fig. 13); hind margin with long stiff (swimming) hairs (length 0.1–0.3 mm); LR in foreleg 1.27 : 1.21 : 0.46; claw with darkened tip, subapical tooth and three denticles; meso- and metathoracic supracoxal spurs acutely pointed.

Gills bulged and pointed, with prominent dark tracheation and tufts of filaments at gill I–VI (Figs 14–16); length of gills: I 0.63 mm, III 0.77 mm and VII 0.59 mm.

Caudal filaments annulated as in Fig. 17; distance between two whorls of big spines subbasally 0.2 mm.

Differential diagnosis. The male imago of *C. (s. str.) tagbanua* sp. n. is similar to that of *C. (s. str.) flowersi* Braasch & Soldán; 1986. However, titillators are basally bilobed and contours of apical lobes are less conspicuous than in *C. (s. str.) flowersi*. Apparently, penis lobes lack discal spines. Together with the latter species and other Southeast Asian *Compsoeuria* (s. str.) spp. like *C. (s. str.) diehli* Braasch & Soldán, 1986 and *C. (s. str.) thienemanni* (Ulmer, 1939) they represent a group of species with stippled femora by lack of clearly visible femur bands. For further comparison of the copulatory apparatus see Braasch & Soldán (1986a, b: figs 1–6, p. 43, 8–13, p. 61).

Biological notes. Imagos and subimagos of *Compsoeuria* (s. str.) *tagbanua* sp. n. were exclusively found in the rhithral at low altitude along moderately anthropogenically altered sections (paddy fields) of the Cabayugan River. However, larvae could be recorded from various river courses including headwaters by drift and kick sampling.

Compsoeuria (Palawaneuria) subgen. n.

Type species ♂. *Compsoeuria (Palawaneuria) cabayuganensis* subgen. n., sp. n.

Differential diagnosis. The imagos of *C. (Palawaneuria)* subgen. n. share the following characters with *Compsoeuria* (s. str.): similar body patterns in males and females (except of small differences in pattern of femora), analogous pattern in forewings of imagos, crossveins in costal and subcostal fields thickened, shaded, slightly sigmoidly curved; other crossveins slightly shaded; the first foretarsal segment in *C. (Palawaneuria)* subgen. n. 0.5 times as long as second segment in *Compsoeuria* (s. str.) spp.: first segment 0.3–1.0 times as long as the second segment; spade-like subanal plates of subimago females; alternately annulated caudal filaments.

Compsoeuria (Palawaneuria) subgen. n. differs by clear brown wings in subimaginal stages from *Compsoeuria* (s. str.) spp. with grey-clouded wings. The simple predistal crossband at the tibiae of *C. (Palawaneuria)* contrasts with the triple-banded tibiae of *Compsoeuria*

(s. str.). While the penes in Asiatic species of *Compsoeuria* (s. str.) are stocky-shaped (*C. (s. str.) thienemanni* 0.83, *C. (s. str.) spectabilis* 0.85), with strong, curved titillators and with spines on the top of the lobes, *C. (Palawaneuria)* subgen. n. displays a subcordiform lobal head and a more elongated copulatory organ with contiguous and attenuate titillators, but without discal spines and submedial hooks. Its styliiger displays swellings (protuberances) aside of the moderately elevated sockets (most conspicuously in SI), whereas it is in *Compsoeuria* (s. str.) without swellings and elevated sockets.

Larval stages of *C. (Palawaneuria)* subgen. n. are unknown.

Compsoeuria (Palawaneuria) cabayuganensis subgen. n., sp. n.

Figures 18–33

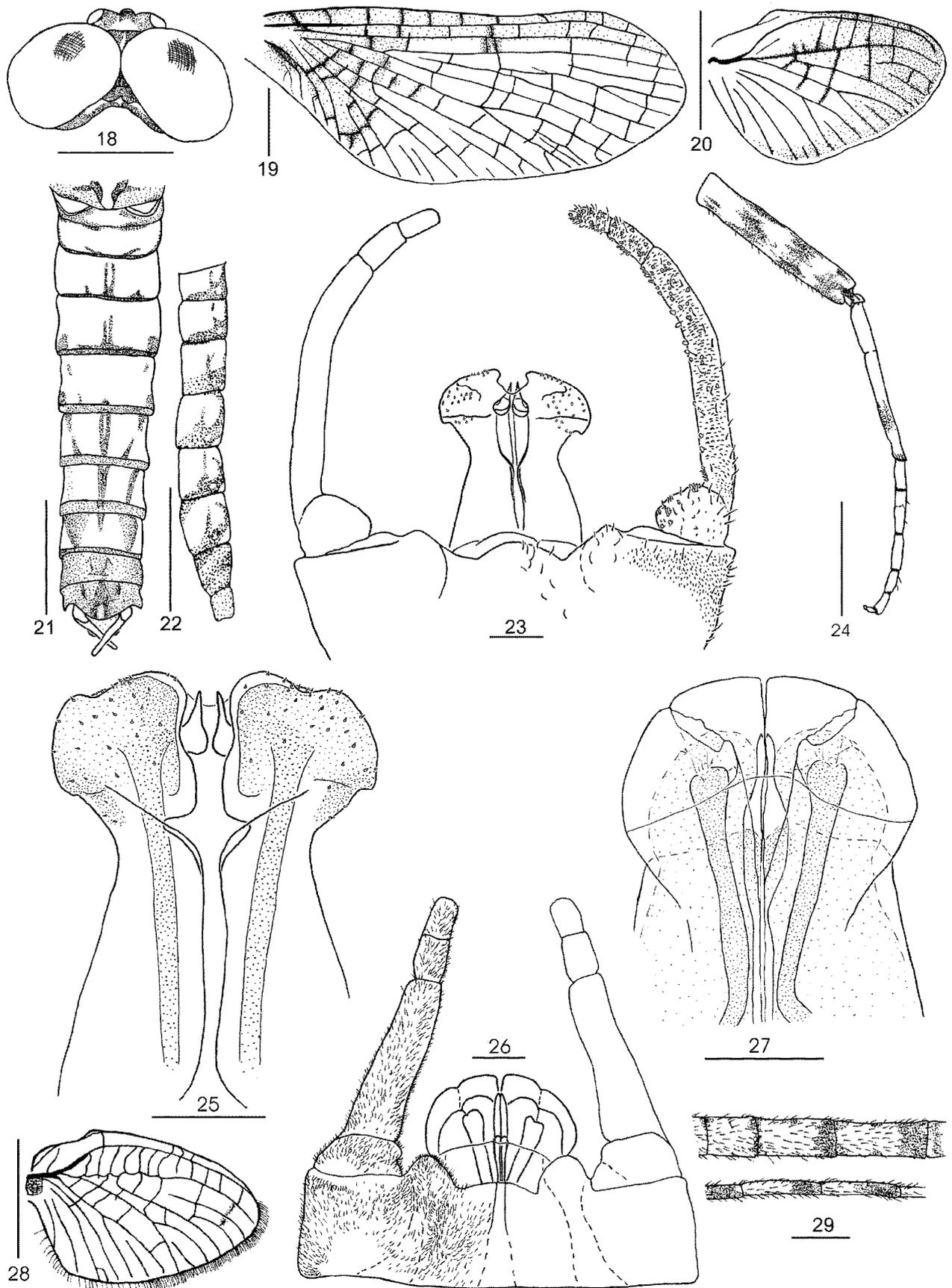
Holotype ♂ (MNHU). Philippines, Isl. Palawan, Puerta Princesa City, Cabayugan River (CR1), “Phil.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 12.08.2001, leg. Freitag(CR1E)”, specimen and genital in 70% alcohol.

Paratypes. 1 ♀ (MNHU) same label as holotype; 1 SI ♂ (MNHU). “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 21.10.2000, leg. Freitag(CR1E)”, 9 SI ♂♂, 3 SI ♀♀ (UPLB) same label as holotype; 6 SI ♂♂, 2 SI ♀♀ (UPLB), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 21.10.2000, leg. Freitag(CR1E)”; 3 SI ♂♂, 1 SI ♀ (UPLB), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 03.11.2000, leg. Freitag(CR1E)”; 1 SI ♂, 2 SI ♀♀ (UPLB), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 16.11.2000, leg. Freitag(CR1E)”; 6 SI ♂♂, 1 SI ♀ (UPLB), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 11.12.2000, leg. Freitag(CR1E)”; 3 SI ♂♂, 1 SI ♀ (WPU), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 15.1.2001, leg. Freitag(CR1E)”; 4 SI ♂♂, 4 SI ♀♀ (WPU), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 21.3.2001, leg. Freitag(CR1E)”; 6 SI ♂♂, 3 SI ♀♀ (WPU), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 30.4.2001, leg. Freitag(CR1E)”; 6 SI ♂♂, 4 SI ♀♀ (IRML), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 06.5.2001, leg. Freitag(CR1E)”; 9 SI ♂♂, 5 SI ♀♀ (MNHU), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 17.6.2001, leg. Freitag(CR1E)”; 6 SI ♂♂, 5 SI ♀♀ (MNHU), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 15.7.2001, leg. Freitag(CR1E)”; 1 SI ♂ (MNHU), “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'47" N 118°50'37" E 30.9.2000, leg. Freitag(CR2E)”.

Etymology. The specific name refers to the Cabayugan River where the new species occurs.

Male. Body length 6.0 mm, forewing length 6.9 mm, hindwing length 1.5 mm, caudal filaments > 12 mm long (incomplete).

Head slightly damaged, pigmentation as in Figure 18 (♂-SI); eyes contiguous. Prothorax medially with large, dark bands; mesothorax with dark brown scutellum; medioscutum grey brown, submedioscutum pale yellow; lateroscutal clasp brown, distally truncate, distinctly wi-



Figures 18–29. *Compsoeuria (Palawaneuria) cabayuganensis* sp. n. ♂-SI (scale 1 mm): **18.** Dorsal head and prothorax; ♂ (scale 1 mm); **19.** Forewing; **20.** Hind wing; ♂-SI (scale 1 mm); **21.** Dorsal abdomen; ♂ (scale 1 mm); **22.** Lateral abdomen; (scale 0.1 mm); **23.** Ventral genital segment, dorsal penis; ♂-SI (scale 1 mm); **24.** Dorsal foreleg; ♂ (scale 0.1 mm); **25.** Ventral penis; ♂-SI (scale 0.1 mm); **26.** Ventral genital segment; **27.** Dorsal penis; (scale 1 mm); **28.** Hindwing; (scale 0.1 mm); **29.** Annulation of caudal filaments.

dened. Forefemur brownish with rather indistinct dark, longitudinal bands interspersed with stipples; tibiae with dark predistal crossband. LR of foreleg 1.7 : 1.98 : 2.4 (0.33 : 0.76 : 0.60 : 0.43 : 0.28); LR of hindleg 2.0 : 1.4 : 0.59 (0.21 : 0.12 : 0.10 : 0.05 : 0.11). Forewing (Fig. 19) transparent with strong, dark brown C, SC and R1; other longitudinal veins distinctly weaker; costal field with 11 crossveins, brown shaded crossveins only in anterior part of wing; a conspicuously brown patch beside bulla between fifth and sixth crossveins; in last two thirds crossveins thin and partly extinct; almost entire hind wing brownish tinged (Fig. 20).

Abdomen pale with dark brown dorsal and lateral pattern; terga with dark brown midline pattern (as in Fig. 21, SI ♂), laterally with markings on segments II–VII (Fig. 22); hind margins of segments broadly dark brown bordered; sterna pale without any conspicuous patches. Styliger ventrally (Fig. 23) 0.68 mm wide, with “swellings” (Harker 1989) aside of moderately elevated sockets, forcipes pale, relatively short (segments 0.11, 0.46, 0.09, 0.07 mm long). Penis longer than broad (PLW 0.36 mm : 0.26 mm = 1.4), waisted beneath rounded bulb, without latero-dorsal and discal spines all over ventral and dorsal lobes, without apico-medial hooks, but in dorsal view with lateral sclerites (Fig. 23); ventrally (Fig. 25) penis stem fused up to basal 0.85, lobes with enlarged ventral sclerites; and with a shallow medio-apical emargination (Fig. 25); dorsally (Fig. 23) with acute median incision; titillators almost straight, slender conical, contiguous.

Caudal filaments alternately annulated, damaged.

Female. Body length 5.4 mm, forewing length 6.9 mm, hind wing length 1.98 mm, caudal filaments > 11 mm long, incomplete.

Head, prothorax and last segments of abdomen damaged, almost as in Figure 30 (♀-SI); general colour orange brown; abdominal pattern as in Figure 31 (♀-SI), laterally conspicuously marked on segments III–VII (Fig. 32); region of subgenital and subanal plate defect, sterna without any markings. Forewing transparent, with strong dark brown longitudinal veins C, SC and R1, crossveins thick and faintly shaded in costal and subcostal fields; ca. 17 crossveins in costal field; conspicuous cross band over 6 rows near bulla; shaded crossveins in anterior part of wing weakly expressed; distal wing portion with faint crossveins. Hind wing with brownish tinge around distal margin. Femora pale with three indistinct longitudinal brown patches, in-between slightly speckled, arrangement of patches as in Figure 24, tibiae pale with predistal brown crossband, tarsal segments pale; LR of hindleg (forelegs missing), 3.1 : 1.1 : 0.7 (0.2 : 0.1 : 0.1 : 0.1 : 0.2).

Male SI. Body length 6.8 mm; forewing length 7.0 mm; hind wing length 1.2 mm, caudal filaments ca. 13 mm long.

Entire dorsal body pale brown; head with almost contiguous compound eyes (Fig. 18); prothorax

(Fig. 18) as described in imago; abdominal terga with dark brown midline pattern (Fig. 21); sterna pale brown without any conspicuous patches.

Wings clear brown, 14 dark shaded crossveins in forewing between C and SC, partly forming four darker crossbands on the posterior face of wing, curve in SC and R1 only slightly sinuous; hind wing brown with smoothed angle (Fig. 20).

Femora pale brown, colour patterns as in Figure 24, with three somewhat fragmented dark brown bands and few stipples in-between; tibiae slightly brown with indistinctly extended band at distal half, tarsal segments pale brownish.

LR of foreleg 1.6 : 1.4 : 1.2 (0.2 : 0.4 : 0.3 : 0.2 : 0.1); LR of hindleg 1.8 : 1.2 : 0.7 (0.2 : 0.1 : 0.1 : 0.1 : 0.2).

Ventral segment with styliger as in Figure 26. Penis with subcordiform pair of fused lobes, small, with somewhat straightly pointed titillators and apparently without spines or hooks, with distinctly conspicuous gonoducts and gonopores; penis in most SI specimens studied well developed, similar to that of imago. Dorsal penis as in Figure 27.

Caudal filaments grey, dark annulated alternately (Fig. 29).

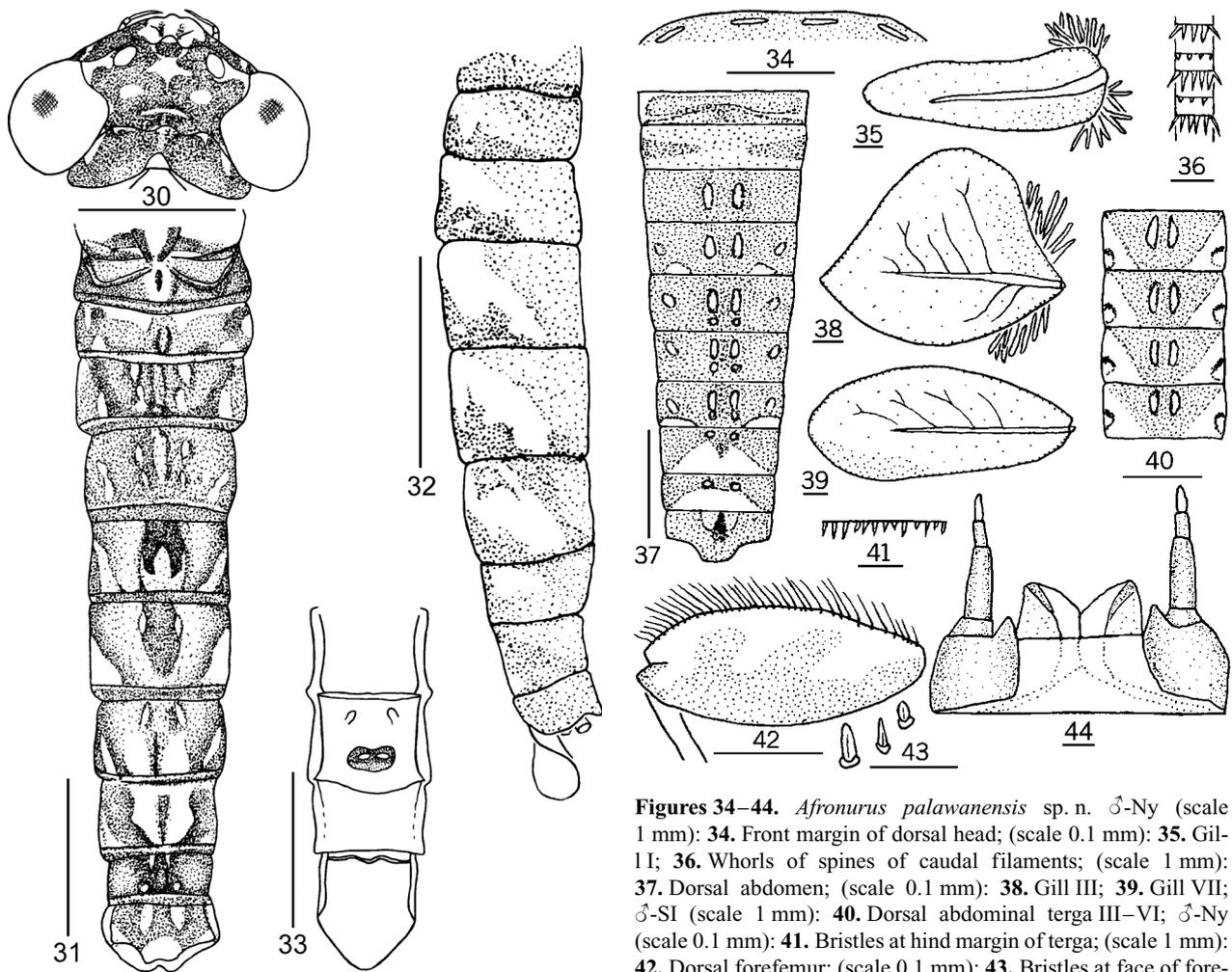
Female SI. Body length 6.8 mm, forewing length 8.1 mm, caudal filaments > 10 mm long, incomplete. Head with interocular distance 4.2 times as wide as median ocellus (Fig. 30); forewing with 15 crossveins; abdominal pattern of terga generally darker than in males (Fig. 31), sterna without conspicuous patches; legs similar to that of male; LR in foreleg 1.7 : 1.4 : 0.9 (0.1 : 0.3 : 0.2 : 0.1 : 0.2). Subgenital plate with flatly arched distal margin; subanal plate spade-like (Fig. 33).

Larvae. Unknown.

Differential diagnosis. The species resembles superficially some species of *Compsoeuria* (s. str.). While wings in subimagos of *Compsoeuria* (s. str.) are grey-clouded, that of *Compsoeuria* (*Palawaneuria*) are brown. In male, the hind wing of *C. (Palawaneuria) cabayuganensis* subgen. n., sp. n. is similarly brownish tinged as in that of *C. (s. str.) lieftincki* (Ulmer, 1939: p. 573: Fig. 163), but differs from the latter by body pattern and genital characters. Unlike as in the sympatric *C. (s. str.) tagbanua* sp. n., the forewing in *C. (Palawaneuria) cabayuganensis* subgen. n., sp. n. displays only a slightly sinuous curve in SC and R1.

Biological notes. Larvae clearly affiliated to the imagos of *Compsoeuria (Palawaneuria) cabayuganensis* subgen. n., sp. n. could not be found, although material was collected in almost every month between May 2000 and August 2001.

Emergence catches of imagos and subimagos were restricted to the headwaters of Cabayugan River.



Figures 30–33. *Compsoeuria (Palawaneuria) cabayuganensis* sp. n. ♀-SI (scale 1 mm): **30.** Dorsal head and prothorax; **31.** Dorsal abdomen; **32.** Lateral abdomen; **33.** Subgenital and subanal plates.

***Afronurus palawanensis* sp. n.**

Figures 34–44

Holotype ♂-Ny (MNHU). Philippines, Isl. Palawan, Municipality of Narra, Estrella Falls, “Philippines, SE Palawan, 7 km north of Narra, Estrella Falls, 9°18' N, 118°23' E; altitude 100–200 m, width 3–4 m, stony, fast current, secondary forest; 12.04.92; leg. Zerning”; specimen in 70% alcohol.

Paratypes. 1 ♂-SI (MNHU), 1 ♀-SI (MNHU), 8 Ny (UPLB; WPU, IRML) same label as holotype. 2 Ny, 3 L (CBP), “Philippines, SE Palawan, 7 km N Narra, Taritien River, 9°19' N, 118°22' E, stony mountain stream (6–7 m width, up to 2 m depth, altitude 250 m) in forest, 05.04.92, leg. M. Zerning”; 1 L (MNHU), “Philippines, NW Palawan, Puerto Princesa City, Sabang, Sabang River 10°11' N, 118°53' E, lowland river, 3–4 m width, 0.2 m depth, stony, rice fields, banks partly with trees, 16.04.92, leg. Zerning”; 1 Ny (NMW) “PHIL.: Palawan, P. Princesa, Sabang Waterfall (upper, 30 m asl); 10°13' N 118°53' E 21.12.1994, leg. Freitag (19 a) M”; 7 Ny, 27 L “PHIL.: Palawan, P. Princesa SSW Martarpi, Cabayugan R. 10°09'46" N 118°49'29" E 03.11.2000, leg. Freitag (CR1)”. Additional material: 4 L (UPLB), “PHIL.: Palawan, P. Princesa S Martarpi, Cabayugan R. 10°09'47" N 118°50'37" E 05.09.2000, leg. Freitag (CR2R)”; 4 L (MNHU), “PHIL.: Palawan, P. Princesa S Martarpi, Cabayugan R. 10°09'47" N 118°50'37" E 21.10.2000, leg. Freitag (CR2P)”; 1 L (WPU), “PHIL.:

Figures 34–44. *Afronurus palawanensis* sp. n. ♂-Ny (scale 1 mm): **34.** Front margin of dorsal head; (scale 0.1 mm); **35.** Gill I; **36.** Whorls of spines of caudal filaments; (scale 1 mm); **37.** Dorsal abdomen; (scale 0.1 mm); **38.** Gill III; **39.** Gill VII; ♂-SI (scale 1 mm); **40.** Dorsal abdominal terga III–VI; ♂-Ny (scale 0.1 mm); **41.** Bristles at hind margin of terga; (scale 1 mm); **42.** Dorsal forefemur; (scale 0.1 mm); **43.** Bristles at face of forefemur; SI-♂ (scale 0.1 mm); **44.** Ventral genital segment.

Palawan, P. Princesa S Martarpi, Cabayugan R. 10°09'47" N 118°50'37" E 21.10.2000, leg. Freitag (CR2P)”; 1 L (IRML), “PHIL.: Palawan, P. Princesa Panaguman R., Marofinas 10°15'09" N 118°58'03" E 20.10.2000, leg. Freitag (PR1P)”.

Etymology. The name refers to the origin of the species from Palawan.

Male Ny. Body length 9.4 mm (length of ♀-Ny 14.0 mm); caudal filaments > 7.0 mm long, incomplete.

Head prevailing grey-brown, anterodorsally with four narrow indistinct pale spots (Fig. 34); ocellar area dark brown; anterior part of head distinctly speckled; posterior margin slightly concave; head width 2.9 mm, length 2.0 mm (Ratio: 1.4); mouthparts generally as in *Afronurus philippinensis* (Flowers & Pescador 1984: p. 363: 1a,b–5a,b); maxillae with 20 comb-like bristles.

Abdomen length 4.2 mm; dorsal colour pattern as in Figure 37; hind margin of terga with small acute bristles of 0.02–0.04 mm length (Fig. 41) and with short acute lateral projections on terga II–VIII.

Forefemur (Fig. 42) 2.7 mm long, 1.2 mm wide, dorsally with broad, irregular patches; hind margin with row of stiff hairs, scattered with numerous bristles of about 0.03–0.05 mm length (Fig. 43).

Most gills with dense tufts of filaments; gill lamella I slightly banana-shaped, with roundly ends, length 0.85 mm (Fig. 35); gills III–VI subtriangular and pointed; gill III 0.85 mm (Fig. 38); gill VII elliptical, without tufts of filaments (Fig. 39), length 0.97 mm.

Caudal filaments with whorls of equally large spines at articulations and in-between with smaller spines (Fig. 36); distance of main whorls ca 0.18 mm.

Male SI. Body length 10.4 mm; forewing length 9.4 mm; caudal filaments > 15.5 mm long, incomplete.

Eyes contiguous; wings pale grey; forewings in costal and subcostal field slightly yellowish coloured; abdominal terga III–VI with pattern as in Fig. 40; legs with inconspicuous colour pattern; femora slightly reddish; LR of foreleg 2.3 : 3.5 : 1.8 (0.4 : 0.5 : 0.4 : 0.2 : 0.3); LR of hindleg 2.9 : 2.4 : 0.7 (0.1 : 0.1 : 0.1 : 0.1 : 0.3).

Genital segment (Fig. 44) 0.88 mm wide; apical ends of penial lobes outwards directed, without titillators; styliger with relatively low sockets.

The subimago was associated with the nymph due to size and similarity in tergal pattern.

Differential diagnosis. The subimaginal penial apparatus of *Afronurus palawanensis* sp. n. resembles that of *A. malaysianus* Braasch 2005 with its convergent, rounded lobes. However, it differs by the more tapered lobes less approached to each other and its forewings without reddish tinge in the costal field. It differs from the other known *Afronurus* spp. in the Philippines by the lower sockets in styliger and different colour patterns.

Afronurus zerningi sp. n.

Figures 45–56

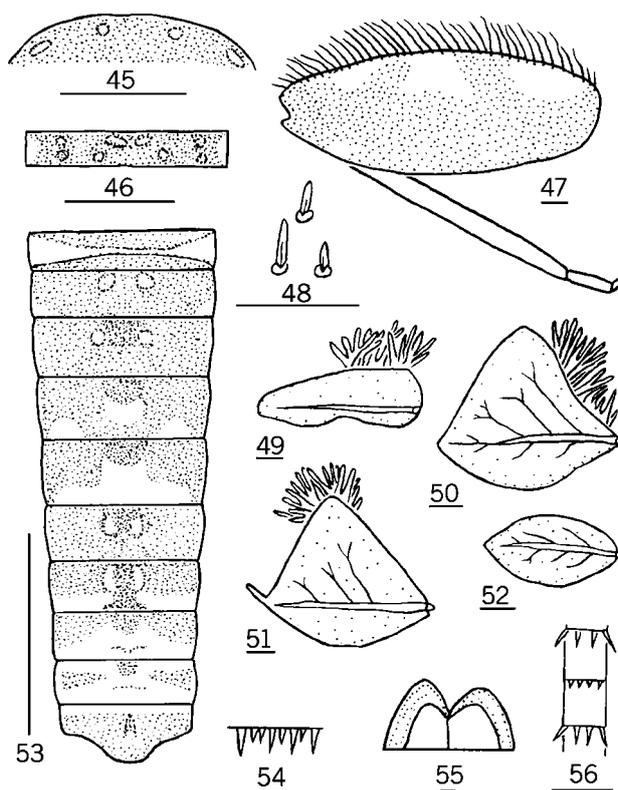
Holotype. ♂-Ny. (MNHU). Philippines, Isl. Palawan, Municipality of Narra, Taritien River, “Philippines, SE Palawan, 7 km N Narra, Taritien River, 9°19' N, 118°22' E, stony mountain stream (6–7 m width, up to 2 m depth, altitude 250 m) in forest, 05.04.92, leg.M. Zerning”; specimen in 70% alcohol.

Paratypes. 8 Ny (UPLB, WPU, IMRL, CBP), 6 L (CBP), same label as holotype.

Etymology. The species is dedicated to its collector Michael Zerning, Potsdam, Germany.

Male Ny. Body length 6.2 mm, caudal filaments 8.1 mm long.

Head 2.1 mm wide, 1.5 mm long (HR 1.4), anterodorsally with two pairs of inconspicuous, pale spots on darker ground, one of them elongate, one round, (Fig. 45); face of head finely speckled with numerous dark spots. Mouthparts: essentially shaped as in *Afronurus philippinensis* (Flowers & Pescador 1984: p. 363: 1a,b – 5a,b); labrum almost half as long (1.0 mm) as head wide; labium with glossae apically rounded, 0.6 mm long; distance of glossae 1.0 mm; hypopharynx distally bent; maxillae with scattered setae on ventral



Figures 45–56. *Afronurus zerningi* sp. n. ♂-Ny (scale 1 mm): 45. Front margin of dorsal head; 46. Dorsal pronotum; (scale 0.1 mm); 47. Dorsal foreleg; 48. Bristles at face of forefemur; 49. Gill I; 50. Gill III; 51. Gill VI; 52. Gill VII; (scale 1 mm); 53. Dorsal abdomen; (scale 0.1 mm); 54. Bristles of hind margin of dorsal tergum; 55. Prospective penis; 56. Whorls of spines of caudal filaments.

surface as usual in subfamily Ecdyonurinae Ulmer 1920, apically with 16–17 comb-like bristles.

Pronotum (Fig. 46) 1.8 mm wide, with a number of pale dots.

Abdomen 2.6 mm long, with dorsal pattern as in Figure 53; hind margin of terga with moderately large acute bristles of 0.03–0.06 mm length (Fig. 54).

Forefemur 1.4 mm long, 0.6 mm wide, dorsally with broad colour patches (Fig. 47) and small bristles of 0.01–0.04 mm length (Fig. 48); foretibia 1.7 mm long, pale yellow; tarsal segments pale brown; precoxal spurs suboval or subtriangular; claws with 3–4 denticles.

Gill lamella I narrow with tapered apex (Fig. 49), length 0.60 mm; lamella III subtriangular, length 0.55 mm (Fig. 50); gill lamellae V and VI subtriangular, apically elongated as in *Afronurus* spp. formerly assigned to *Cinygmina* (Braasch & Soldán 1984, 1987), length 0.55 mm (Fig. 51); lamella VII elongately elliptical, slightly pointed, length 0.44 mm (Fig. 52).

Prospective penis upright (Fig. 55); lobes apically rounded with upright directed tips. Caudal filaments brown, with whorls of moderately long spines at articulations and whorls of smaller spines in-between (Fig. 56); distance between main whorls ca. 0.15 mm.

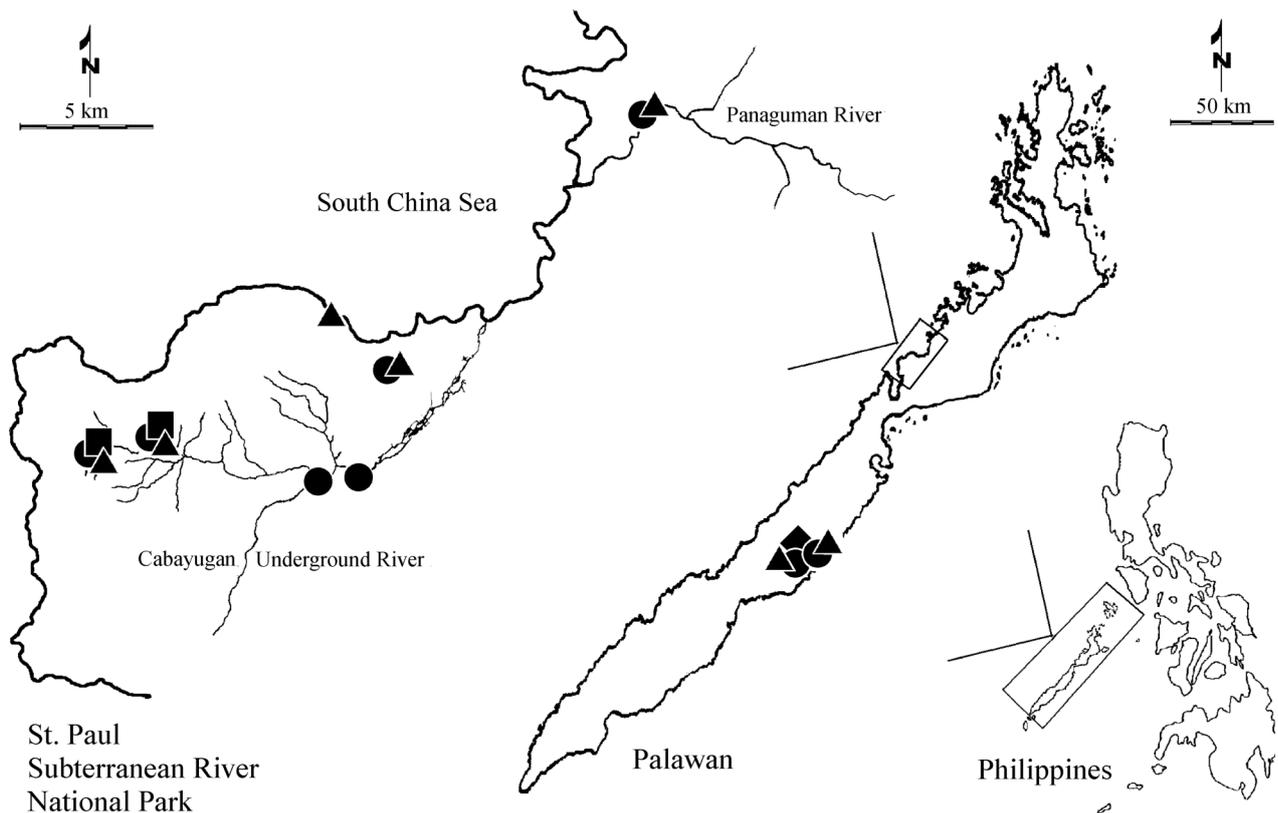


Figure 57. Collecting sites and geographical distribution of the new species on Palawan and in the St. Paul National Park: ● *Compsoeuria* (s. str.) *tagbanua* sp. n., ■ *C. (Palawaneuria) cabayuganensis* sp. n., ▲ *Afronurus palawanensis* sp. n., ◆ *A. zeringi* sp. n.

Differential diagnosis. Larvae of the species can be distinguished from all other *Afronurus* spp. and from the coexistent species *A. palawanensis* sp. n. by a pair of narrow, sublateral pale spots and enclosing a pair of roundish, pale spots at anterior dorsal head, the lack of conspicuous posterolateral projections of the terga and by the elongated gill lamellae V and VI. The species additionally varies by the upright directed, rounded lobes of the prospective penis from larvae of *A. malaysianus* Braasch, 2005 with inwardly directed penial lobe tips.

Comments

Compsoeuria Eaton, 1881

The genus *Compsoeuria* was misinterpreted by Wang & McCafferty (2004), because Ulmer's "*Compsoeuria*" larva (Ulmer, 1939) is a genuine Heptageniinae, whereas the *Compsoeuria* male type (Eaton 1881, p. 275: fig. 42, pl. XXIII + XXIV) represents an Ecdyonurinae species by body colour pattern, venation in forewing with rather small number of shaded crossveins in costal, subcostal field with crossbands and by other characters (Braasch & Soldán 1986; Webb et al. 2006). On the other hand, the larva of *Compsoeuria spectabilis* is still unknown. Kluge (2004) placed *Compsoeuria* spp. into *Ecdyonurus*/fg1 INCERTAE SEDIS,

while *Compsoeuria* Ulmer is regarded to be „probably ... an older name for *Afghanurus*/fg1.“ Contemporarily, Wang & McCafferty (2004) transferred *Afghanurus* Demoulin into *Ecdyonurus* Eaton, while *Compsoeuria* Ulmer was placed into *Thalerosphyrus* Eaton. Recently, the nomenclatural problems have been elucidated by re-evaluation of *Compsoeuria* Eaton, *Compsoeuria* Ulmer and *Trichogenia* Braasch & Soldán (Webb et al. 2006), and at the same time, the Ecdyonurinae generic entities *Compsoeuria* Eaton, 1881 and *Thalerosphyrus* Eaton, 1881 were re-established: "*Compsoeuria* can no longer be included in the Heptageniinae and is placed in Ecdyonurinae with the tribe Compsoeurini accompanying its type genus to Ecdyonurinae". In addition the possible relationships of Compsoeurini to other tribes are discussed suggesting that "the phylogenetic position of *Compsoeuria* (and Compsoeurini) within the Ecdyonurinae is unclear. The possession of ventral spines on the penes, the general shape and the sclerotization of the penes, and the possession of black spotting on the head capsule suggest that *Compsoeuria* may be related to members of the tribe Leucrocotini Wang & McCafferty. However, unlike other members of the Leucrocotini, the apical setae on the ventral side of the galealacinae are simple rather than fimbriate, and the distal dentisetae on the maxillae are branched rather than simple, indicating a closer relationship to the Notacanthurini Wang & McCafferty and Atopopini Wang & McCaff-

erty (Webb et al. 2006). *Compsoeuria* (s. str.) and the new subgenus *C. (Palawaneuria)* share many characters, except for penial sclerotizations, characters of styliger and general shape. The latter characters suggest affinities to tribe Notacanthurini. However, we refrain from a formal placement into any tribe due to the lack of larval stages in *C. (Palawaneuria)* subgen. n.

Compsoeuria, which is abundant in lowland rivers of Sundaland and mainland of Southeast Asia, could not yet be found on the eastern Philippine islands. The first discovery in the western Philippines occurred by the recent study on Palawan, which belongs to Greater Sunda (Heany 1985). This island was connected to the Asian mainland during the Pleistocene, which is the assumed distributional centre of *Compsoeuria*. The genus has presumably reached Palawan by dispersal in times of ocean regression.

Afronurus Lestage, 1924

Wang & McCafferty (2004) as well as Kluge (2004) have synonymized *Cinygmima* with *Afronurus*. Furthermore, the eggs of these groups are not clearly distinguishable (Belfiore et al. 2003; Flowers & Pescador 1984). Therefore, species previously considered as *Cinygmima* spp. (s. Braasch & Soldán 1988) are now regarded as *Afronurus levis* (Navás, 1912) and *A. yoshi-dae* (Takahashi, 1924) by Kluge (2004). One of the Palawan species described herein, *Afronurus zerningi* sp. n., displays pointed elongations of the gill lamellae V and VI as characteristic in many former *Cinygmima* spp. (Braasch, 1990; Braasch & Soldán, 1984a). However, its prospective genital characters indicate the affiliation with *Afronurus* s. str. (penis without titillators), not with former *Cinygmima* (penis with reduced titillators). This is suggestive to consider *A. zerningi* a primitive ancestral species of the genus.

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