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## New tribe, new genera, and new species of the family Issidae (Hemiptera: Fulgoroidea) from Southeastern Asia and New Guinea, with notes on morphology and evolution of the family

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### ABSTRACT

Eupilisini trib. nov. is erected for the genera *Eupilis* Walker, 1857, *Gabaloeca* Walker, 1870, *Syrgis* Stål 1870, and *Bornepilis* gen. nov. (type species: *Bornepilis longipennis* sp. nov.) in the subfamily Issinae of the family Issidae. *Bornepilis longipennis* sp. nov. is described from Sabah State of Malaysia in northern Borneo. Two new species of the genus *Eupilis* are described from northwestern Borneo – *E. borneoensis* sp. nov. and *E. walkeri* sp. nov. *Eupilis hyalinocosta* Melichar, 1914 is redescribed and together with *E. rubrovenosa* Melichar, 1914 is transferred to *Bornepilis* gen. nov. *Eupilis albilineola* Walker, 1857, *E. hebes* Walker, 1857, and *Gabaloeca retifera* Walker, 1870 are redescribed. *Eupilis nigrinervis* Stål, 1870 is redescribed and transferred to the genus *Gabaloeca*. Three new combinations are formed: *Bornepilis hyalinocosta* (Melichar, 1914), comb. nov., *B. rubrovenosa* (Melichar, 1914), comb. nov., and *Gabaloeca nigrinervis* (Stål, 1870), comb. nov. *Paguinella ramosa* gen. et sp. nov. is described from the canopies of Madang Province in Papua New Guinea. This new genus is closely related to New Guinean genus *Papunega* Gnezdilov et Bourgoin, 2015, but well distinguished by ventral aedeagal hooks each with two long branches and wide neck of capitulum of style. Morphology of hind wing and male genitalia of the members of issid tribes Eupilisini trib. nov., Issini, Sarimini, Chimetopini, and Kodaianellini are discussed and illustrated in accordance to evolution and historic distribution of the family Issidae from southeastern Asia to America and tropical Africa. New data on distribution of *Bornepilis hyalinocosta* and *Gabaloeca nigrinervis* in the Philippines are given.

**Key words:** biogeography, Chimetopini, evolution, Issini, Kodaianellini, morphology, new combination, new genus, new species, new tribe, Oriental Region, Sarimini, systematics

## Новая триба, новые роды и новые виды семейства Issidae (Hemiptera: Fulgoroidea) из Юго-Восточной Азии и Новой Гвинеи с замечаниями по морфологии и эволюции семейства

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### РЕЗЮМЕ

Новая триба, Eupilisini trib. nov., установлена в подсемействе Issinae семейства Issidae для родов *Eupilis* Walker, 1857, *Gabaloeca* Walker, 1870, *Syrgis* Stål 1870 и *Bornepilis* gen. nov. (типовой вид: *Bornepilis longipennis* sp. nov.). *Bornepilis longipennis* sp. nov. описан из малазийского штата Сабах на севере Борнео. Два новых вида рода *Eupilis* описаны с северо-западного Борнео – *E. borneoensis* sp. nov. и *E. walkeri* sp. nov. *Eupilis hyalinocosta* Melichar, 1914 переописан и вместе с *E. rubrovenosa* Melichar, 1914 перенесен в род *Bornepilis* gen. nov. *Eupilis albilineola* Walker, 1857, *E. hebes* Walker, 1857 и *Gabaloeca retifera* Walker, 1870 переописаны.

*Eupilis nigrinervis* Stål, 1870 переописан и перенесен в род *Gabaloeca*. Предложены три новые комбинации: *Bornepilis hyalinocosta* (Melichar, 1914), comb. nov., *B. rubrovenosa* (Melichar, 1914), comb. nov. и *Gabaloeca nigrinervis* (Stål, 1870), comb. nov. Описан новый род и вид, *Paguinella ramosa* gen. et sp. nov., с крон деревьев из провинции Маданг в Папуа Новой Гвинее. Этот новый род близок к новогвинейскому роду *Papunega* Gnezdilov et Bourgoin, 2015, но хорошо отличается строением вентральных крючков эдегуса, каждый с двумя длинными отростками, и широкой шейкой головки стилуса. Проиллюстрированы и обсуждены морфологические особенности заднего крыла и гениталий самцов представителей иссидных триб Eupilisini trib. nov., Issini, Sarimini, Chimetopini и Kodaianellini в контексте эволюции и исторического распространения семейства Issidae из Юго-Восточной Азии в Америку и тропическую Африку. Приведены новые данные по распространению *Bornepilis hyalinocosta* и *Gabaloeca nigrinervis* на Филиппинах.

**Ключевые слова:** биогеография, Chimetopini, эволюция, Issini, Kodaianellini, морфология, новые комбинации, новые роды, новые виды, новая триба, Ориентальная область, Sarimini, систематика

## INTRODUCTION

Oriental genera *Eupilis* Walker, 1857 and *Gabaloeca* Walker, 1870 are never been in a focus of taxonomic studies since their description by F. Walker (1857a, 1870), except the redescription of *Eupilis nigrinervis* Stål, 1870 by Hori (1971) and recent placement of these genera in the tribe Colpopterini Gnezdilov (currently Nogodinidae) (Gnezdilov et al. 2004) corrected later by its transfer back to Issidae (Gnezdilov 2012). Otherwise my study of several European and American collections revealed that these genera are well represented in the Oriental Region and more new species have to be described in the future. From the other hand my examination of the type series of *Eupilis albilineola* Walker, 1857, *E. hebes* Walker, 1857, and *Gabaloeca retifera* Walker, 1870, deposited in the Natural History Museum in London (United Kingdom), and unidentified C.F. Baker's materials from the Smithsonian Institution in Washington (USA) showed that *E. nigrinervis*, described from the Philippines (Stål 1870), have to be transferred to the genus *Gabaloeca*, while *Eupilis hyalinocosta* Melichar, 1914 and *E. rubrovenosa* Melichar, 1914, both described from Luzon Island in the Philippines (Melichar 1914), do not belong to *Eupilis sensu stricto*, but closely related in male genitalia structure to the new species, described below from northern Borneo, and have to be accommodated altogether in a new genus, *Bornepilis* gen. nov., which is erected here as well.

Comparative study of wing structure and venation discovered distinct position of the genera *Eupilis* Walker, *Gabaloeca* Walker, *Syrgis* Stål, 1870, and *Bornepilis* gen. nov. within the subfamily Issinae *sensu* Gnezdilov et al. (2020) and showed

that these taxa do not belong to the tribe Sarimini Wang, Zhang et Bourgoin as the mentioned above genera are characterized by hindwings with weak clefts of its lateral margins, with *CuA* and *CuP* fused apically, but not flattened as opposed to Sarimini *sensu* Wang et al. (2016) with deep cubital cleft and usually distinctly flattened apically *CuA* and *CuP* in shape of a plaque.

Also the description of the Issidae fauna of New Guinea is still in its initial stage, with 16 species of 7 genera recorded so far (Walker 1870; Melichar 1906; Gnezdilov 2013; Gnezdilov et al. 2015), with half of these species belongs to the tribe Hemisphaeriini Melichar and six species are from the tribe Sarimini. The position of another New Guinean genus and species, *Gilda vittiventris* Walker, 1870, remains uncertain as the type specimen is not located and is not reexamined since Walker's original description. Below I describe one more genus and species of Sarimini from the canopies of Madang Province of Papua New Guinea which is important for our understanding of evolution and dispersal of the family Issidae from southeastern Asia to other parts of the World hypothesized by Gnezdilov (2016a, 2016b, 2019), with discussion of hind wing venation and male genitalia structure in some groups of the family.

## MATERIAL AND METHODS

Taxonomy of the family Issidae follows Gnezdilov et al. (2020). Morphological terminology follows Anufriev and Emeljanov (1988) and Emeljanov (1995) for the head and Bourgoin (1993), Gnezdilov (2002, 2003, 2017), Gnezdilov et al. (2014), and Gnezdilov and Bartlett (2018) for wing venation and male and female genitalia structure including

the terms “anal tube” refers to X segment and “anal column” refers to paraproct.

Photographs were taken using a Leica MZ9.5 stereomicroscope and a Leica DFC 490 camera. Images were produced using Helicon Focus v. 6.7.1 and Adobe Photoshop software. The genital segments of male and female specimens examined were macerated in 10% KOH and figured in glycerine jelly (Brunel Micro Ltd, UK) using the same stereomicroscope with a camera lucida. Label information is quoted, with ‘/’ indicating new line and ‘//’ indicating next label.

The material studied including the species described below are deposited in the following collections: BMNH – the Natural History Museum (London, United Kingdom); OXUM – Oxford University Museum (United Kingdom); RBINS – the Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SNSD – Staatliche Naturhistorische Sammlungen, Dresden, Germany; USNM – Smithsonian Institution, National Museum of Natural History, Washington, D.C., USA; ZIN – Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

## TAXONOMY

### Family Issidae Spinola, 1839

#### Subfamily Issinae Spinola, 1839

#### Tribe Sarimini Wang, Zhang et Bourgoïn, 2016

#### Genus *Paguinella* gen. nov.

**Type species:** *Paguinella ramosa* sp. nov., by original designation.

**Etymology.** The generic name is a combination of the words “Papua” and “Guinea” and refers to the distribution of the genus. Feminine in gender.

**Diagnosis.** Coryphe weakly transverse. Metope wide, with well developed median and sublateral carinae; last ones joint below its upper margin. Forewings without hypocostal plate; basal cell narrowly oval;  $R$  2,  $M$  4,  $CuA$  2; clavus  $\frac{3}{4}$  as long as whole wing. Hind wings 3-lobed, with  $Pcu$  and anterior branch of first anal vein ( $A_{1,1}$ ) fused medially, second anal vein ( $A_2$ ) simple or branchy. Aedeagus with long ventral hooks arising subapically, each with two long branches.

**Description** (Figs 1–11). Metope weakly convex, wide, slightly enlarged above clypeus, with almost

straight upper margin (Figs 1, 3). Metope with distinct median carina running from its upper margin to lower level of eyes and with distinct sublateral carinae joint below its upper margin and curved above metopoclypeal suture which is distinct laterally (Figs 3, 7). Postclypeus flattened dorso-ventrally, without carina. Ocelli absent. Rostrum short, reaching just middle coxae; 3rd segment not narrowing apically. Pedicell weakly elongately cylindrical. Coryphe and metope joint at obtuse angle (nearly  $130^\circ$ ) (in lateral view) (Fig. 2). Coryphe weakly transverse, 1.5 times as wide as long at midline, without carinae; anterior margin convex; lateral margins subparallel, posterior margin obtusely angulate (Fig. 8). Pronotum slightly shorter than coryphe at midline, without carinae; posterior margin straight. Paradiscal fields of pronotum narrow behind the eyes. Paranotal lobes of pronotum short and wide, semirounded. Mesonotum twice as long as pronotum at midline, with median and lateral carinae. Tegulae small. Forewings covering abdomen, slightly narrowing apically, without hypocostal plate. Clavus  $\frac{3}{4}$  as long as whole wing,  $Pcu$  joined  $A_1$  at wing middle and running into its apex. Basal cell narrowly oval. Forewing veins sequence:  $R$  2, furcating closely to basal cell;  $M$  4, firstly furcating at wing middle and anterior branch ( $R_1$ ) furcating twice in apical third of the wing;  $CuA$  2, furcating at wing middle (Figs 2, 9). Transverse veins present in subcostal area and in distal half of corium. Hindwings with concave costal margins, 3-lobes, each with deep cubital cleft and weak vannal cleft of lateral margin; coupling lobe present. Remigial and remigio-vannal lobes are almost equal in width, anal lobe narrower. Basal cell widely oval. Hindwing veins sequence:  $R$  2, furcating right after coupling lobe;  $r-m$  1;  $M$  1;  $m-cua$  1;  $CuA$  2;  $cua-cup$  1;  $CuP$  1;  $cup-pcu$  1;  $Pcu$  2, furcating apically;  $A_1$  2;  $A_2$  1–3 (Figs 4, 5, 10, 11).  $CuA$  joined  $CuP$  at cubital cleft, not flattened.  $Pcu$  and  $A_{1,1}$  fused medially. Hind tibia with two lateral spines distally and 6 apical spines. First metatarsomere twice as long as second one, with two latero-apical and five intermediate spines in a row: 3 + 1 + 1. Second metatarsomere with only two latero-apical spines. First and second metatarsomeres with dense hair-shaped setae ventrally. Arolium of pretarsus with strongly convex margin surpassing the apices of claws (in dorsal view).

**Composition.** The genus is so far only represented by the type species.

**Distribution.** Papua New Guinea.

**Differential diagnosis.** The new genus clearly differs from the genus *Tetrica* Stål, 1866 (based on its type species *T. fusca* Stål, 1870), by its postclypeus without median carina and forewings without hypostale plate, but with *CuA* with two branches [*T. fusca* has a strong median carina running throughout metope and clypeus and forewings with wide hypostale plate and *CuA* with three branches (Gnezdilov et al. 2015, figs 21, 22)] and from both *Sarima* species known from New Guinea by dark metope, with pale band (*Sarima notata* Melichar, 1906 and *S. bimaculata* Melichar, 1906 have metope regularly pale). New genus is closely related to *Papunega* Gnezdilov et Bourgoïn, 2015 according to metope with pale band, aedeagus with pair of hook-shaped processes subapically and ventral aedeagal hooks arising subapically (Gnezdilov et al. 2015, figs 8, 12, 19). The new genus is well distinguished by ventral aedeagal hooks each with two long branches and wide neck of capitulum of style in opposite to *Papunega* species with aedeagal hooks with short second branches and long narrow neck of capitulum (Gnezdilov et al. 2015, figs 6, 8).

***Paguinella ramosa* sp. nov.**

(Figs 1–18)

**Etymology.** Species name is derived from Latin “ramósus” (branchy) meaning furcated referring to ventral aedeagal hooks each with two long branches.

**Type material.** Holotype, male, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta 10.V. / 1995 Fogging AR 5 / Leg. Olivier Missa” (RBINS). Paratypes: Papua New Guinea: 1 male, 1 female, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta 10.V. / 1995 Fogging AR 5 / Leg. Olivier Missa” (ZIN); 1 female, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta 20.VII. / 1995 Fogging AR 33 / Leg. Olivier Missa” (RBINS); 2 males, 1 female, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta / 24.V.1995 Fogging AR 7 / Leg. Olivier Missa” (RBINS); 1 female, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta / 29.VII.1995 Fogging AR 68 / Leg. Olivier Missa” (RBINS); 1 male, 1 female, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta 1995 / Fogging AR 14 / Leg. Olivier Missa” (RBINS); 4 males, 2 fe-

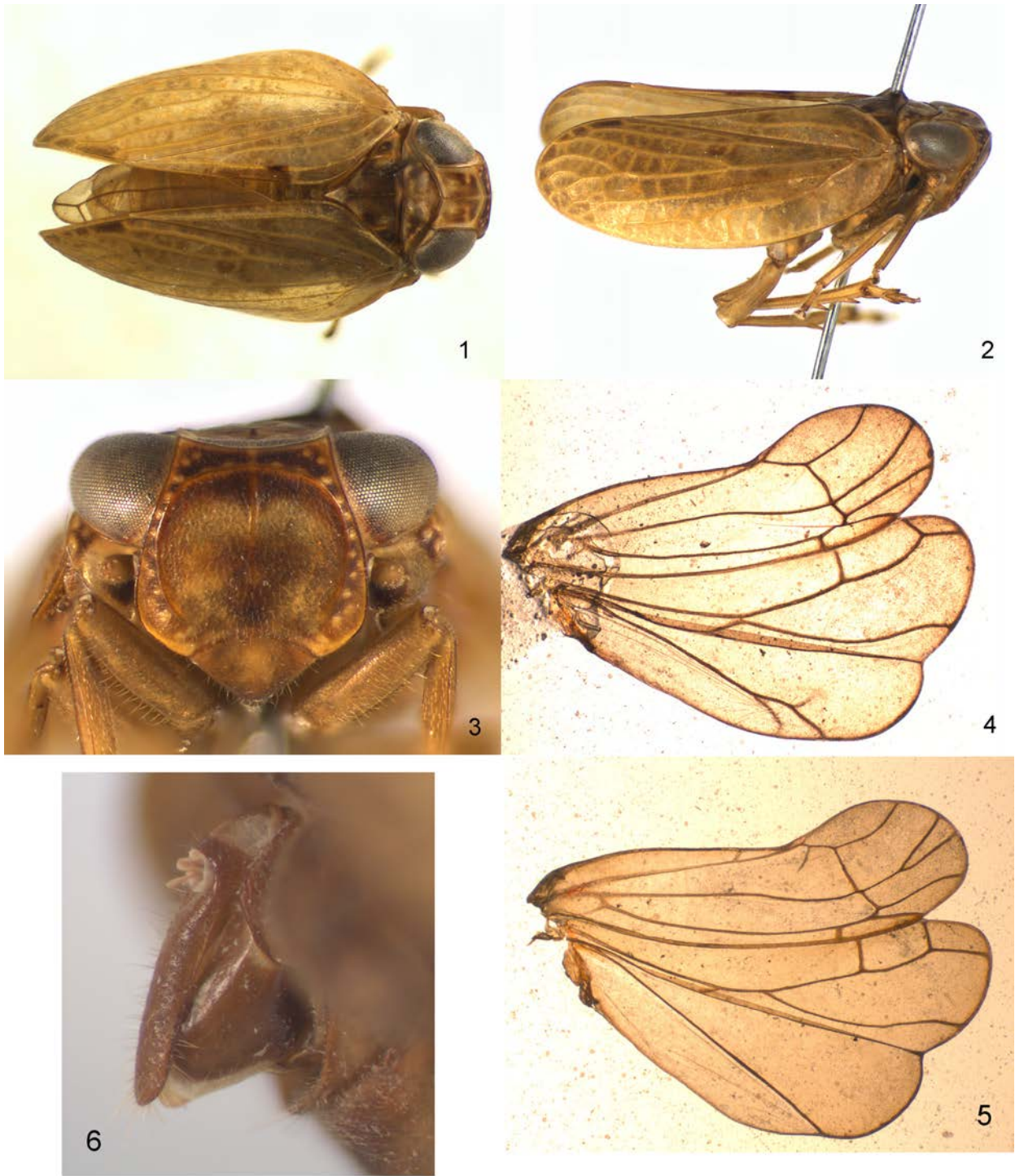
males, “Coll. I.R.Sc.N.B. / Canopy Mission Papua / New Guinea (Madang / prov.): Baiteta 1995 / Fogging AR 34 / Leg. Olivier Missa” (RBINS: 3 males, 1 female; ZIN: 1 male, 1 female).

**Description.** Structure as mentioned for the genus. General coloration light yellowish brown (Figs 1–3). Metope brown to dark brown, with horse-shoe-shaped light yellow band inside of sublateral carinae. Lower angles of metope and traces of larval sensory pits pale. Median and sublateral carinae of metope pale to black. Postclypeus light yellowish brown to dark brown laterally. Anteclypeus dark brown. Coryphe brown to dark brown, with pale anterior and lateral margins. Pronotum with dark brown spots laterally. Paranotal lobes of pronotum each with large round black spot. Mesonotum with dark brown to black (medially) spots. Scutellum pale. Forewings with dark brown apical cells. Sometimes *R*, *Pcu*, *A*<sub>1</sub>, and some transverse veins red. Hind wings matte, with brown veins. Apices of leg spines black. Abdominal sternites light brown to dark brown (medially). Gonoplacs and female anal tube brown to dark brown.

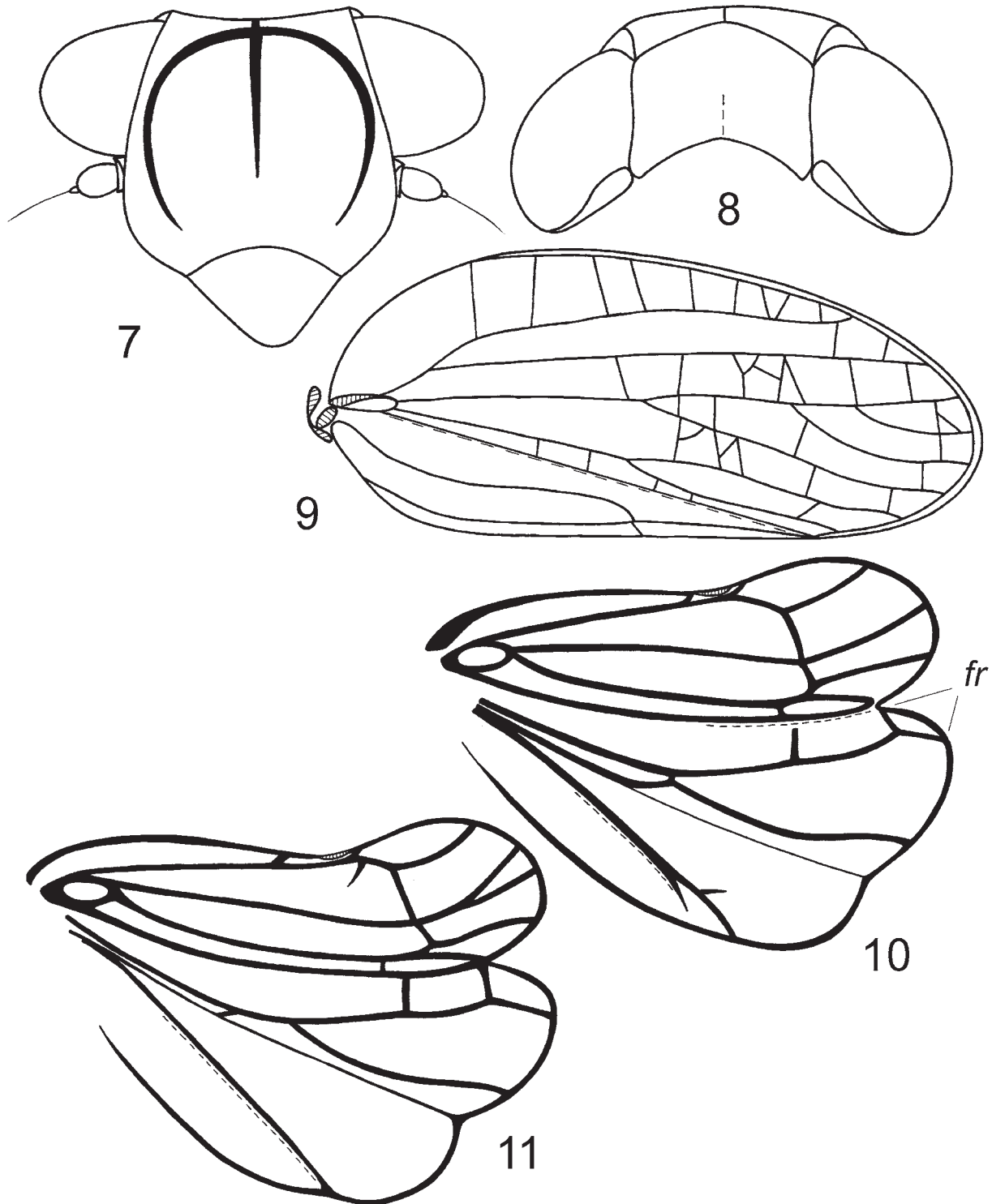
**Male genitalia** (Figs 12–17). Pygofer wide (in lateral view), with convex hind margins (Fig. 15). Anal tube elongate, twice as long as wide medially, slightly narrowing apically (in dorsal view) (Fig. 14). Anal column (paraproct) short. Phallobase strongly curved (in lateral view), with dorso-lateral lobes narrowing apically and fused dorso-apically forming finger-shaped process (Figs 12, 13, *fp*), without subapical processes. Ventral phallobase lobe long and wide, widely rounded apically, with a small apical notch and with two lateral combs. Apical aedeagal processes long, well visible above phallobase margin, wide, not narrowing apically, truncated, each with large hook-shaped subapical process (Fig. 12, *sp*). Ventral aedeagal hooks long, arising subapically, each with two long braches directed downwards and back (Figs 12, 13). Connective with wide cup. Style with wide plate and widely rounded caudo-dorsal angle (Fig. 17). Capitulum on long and wide neck, with small lateral tooth. Capitulum wide, truncate apically (in dorsal view) (Fig. 16).

**Female genitalia** (Figs 6, 18). Hind margin of VII sternite widely concave (Fig. 18). Gonoplacs elongately triangular (Fig. 6). Anal tube very narrow and long, 5 times as long as wide basally. Anal column (paraproct) short.

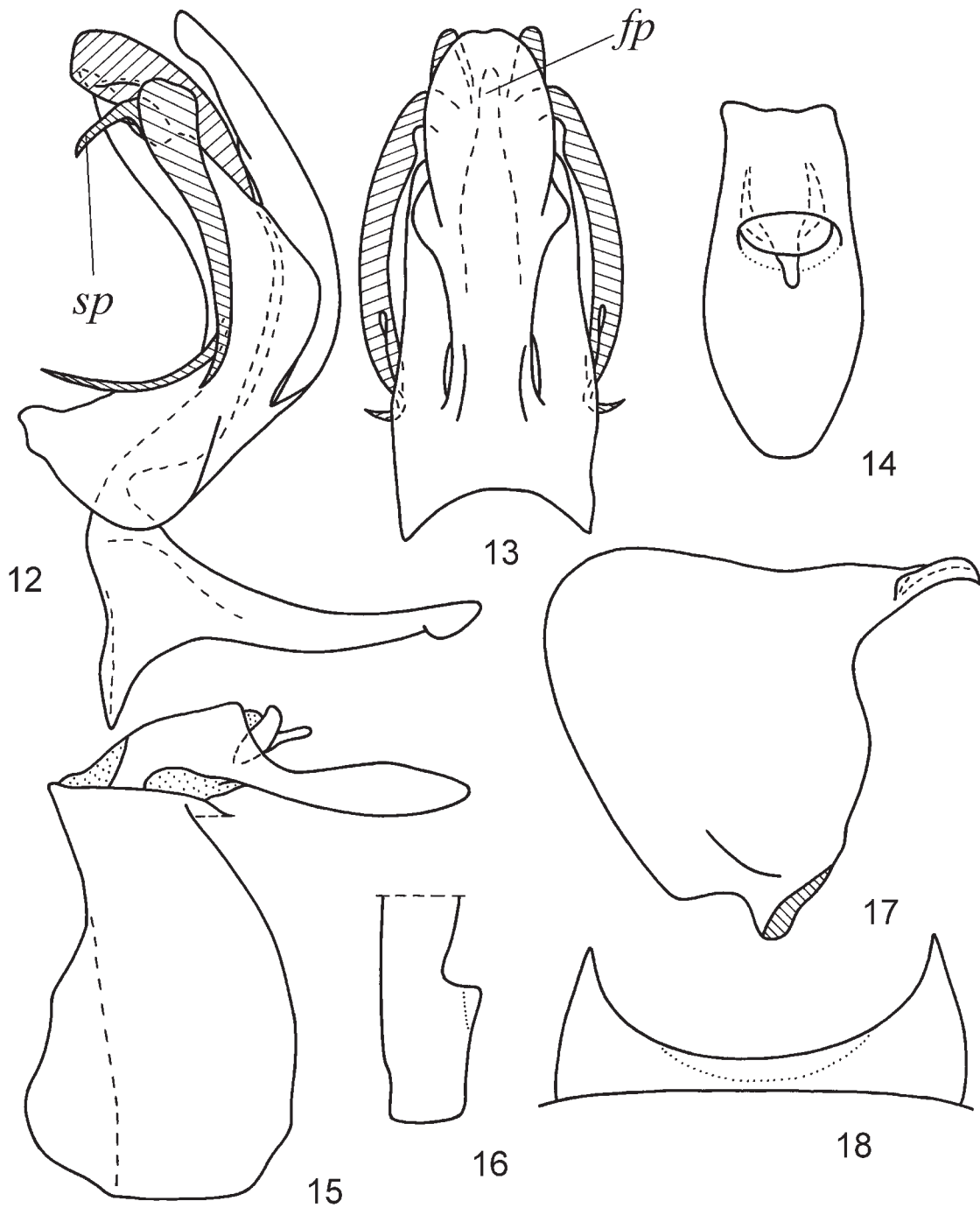
**Total length.** Males – 5.0–6.0 mm. Females – 5.5–6.0 mm.



**Figs 1–6.** *Paguinella ramosa* gen. et sp. nov. 1 – male, holotype, dorsal view; 2 – male, holotype, lateral view; 3 – male, holotype, frontal view; 4 – male, holotype, hind wing; 5 – male, paratype, hind wing; 6 – female, paratype, ovipositor, lateral view. Total length of male specimen is 6.0 mm.



**Figs 7–11.** *Paguinella ramosa* gen. et sp. nov. 7 – male, holotype, face; 8 – male, holotype, head, dorsal view; 9 – male, holotype, forewing; 10 – male, holotype, hind wing; 11 – male, paratype, hind wing. Abbreviation: *fr* – apical furcation of hind wing *Pcu*. Total length of male specimen is 6.0 mm.



**Figs 12–18.** *Paginella ramosa* gen. et sp. nov., 12–17 – male, holotype, 18 – female, paratype. 12 – penis and connective, lateral view; 13 – penis, ventral view; 14 – anal tube, dorsal view; 15 – pygofer and anal tube, lateral view; 16 – capitulum of style, dorsal view; 17 – style, lateral view; 18 – hind margin of sternite VII, ventral view. Abbreviations: *fp* – finger-shaped process of dorsal side of phallobase; *sp* – hook-shaped subapical process of apical aedeagal processes.

**Tribe Eupilisini trib. nov.**

**Type genus:** *Eupilis* Walker, 1857.

**Diagnosis.** Externally long and narrow (body with forewings) in dorsal and lateral views. Ocelli present. Forewings well developed, far surpassing abdominal apex, sometimes transparent, never overlapping. Hindwings well developed, with remigial, remigio-vannal, and anal lobes wide and nearly equal in width and with weak cubital and vannal clefts of lateral margins; *CuA* and *CuP* fused apically, but not flattened; *Pcu* and  $A_{1,1}$  fused medially;  $A_1$  2;  $A_2$  1. Male anal tube long, nearly as long as pygofer vertically, and narrow. Ovipositor rounded (gonoplacs conex and rounded) or beak-shaped (anal tube and gonoplacs narrow and curved).

**Composition.** In addition to the type genus also the genera *Gabaloecca* Walker, 1870, *Syrgis* Stål, 1870, and *Bornepilis* gen. nov.

**Distribution.** Malaysia, Indonesia, Philippines, Papua New Guinea.

**Comparison.** It is similar to the members of the American subtribe Oronoquina Gnezdilov of the tribe Issini Spinola by transparent forewings in some members of the tribe and by weak clefts of lateral margins of hindwings.

**Genus *Eupilis* Walker, 1857**

*Eupilis* Walker, 1857: 93.

**Type species:** *Eupilis albilineola* Walker, 1857, by original designation and monotypy.

**Diagnosis.** Metope with large hemispherical bulge, without carinae (Figs 20, 24, 33, 44, 47). Lateral margins of metope sharply diverging below the eyes. Pronotum with sharply convex anterior margin. Forewings elongate, without hypocostal plate, transparent, with dark brown veins;  $R$  2  $M$  3 *CuA* 2 (Figs 60, 61). Hindwings well developed, 3-lobed (Figs 19, 110). Style enlarged from the basement, with large lateral tooth turned backwards (Figs 30, 40, 49, 58). Female anal tube and gonoplacs forming beak-shaped ovipositor; apex of anal tube shortly surpassing apices of gonoplacs (Figs 34, 35). Female pygofer with strongly convex hind margins.

**Composition.** Four species.

**Distribution.** Borneo Island.

**Comparison.** Well differs from other genera of the tribe by metope with hemispherical bulge.

***Eupilis albilineola* Walker, 1857**

(Figs 19–31)

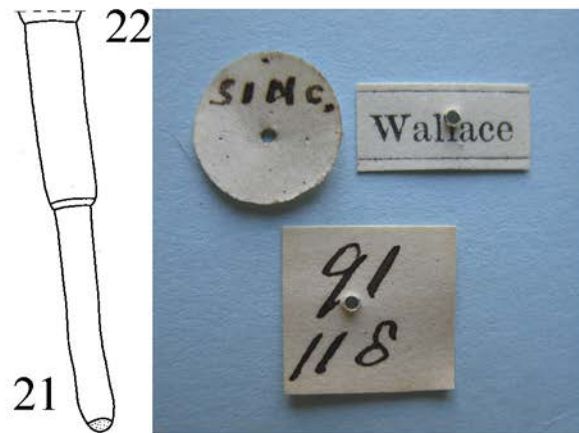
*Eupilis albilineola* Walker, 1857a: 93, Pl. 3, figs 1, 1a, 1b, 1c.  
*Eupilis albilineola*: Walker, 1858: 122.

**Type material examined.** Female, holotype, “SING.” [hand written in ink on white circle] // “Wallace” [white rectangular, printed] / “91/116” [hand written in ink on white square] (BMNH).

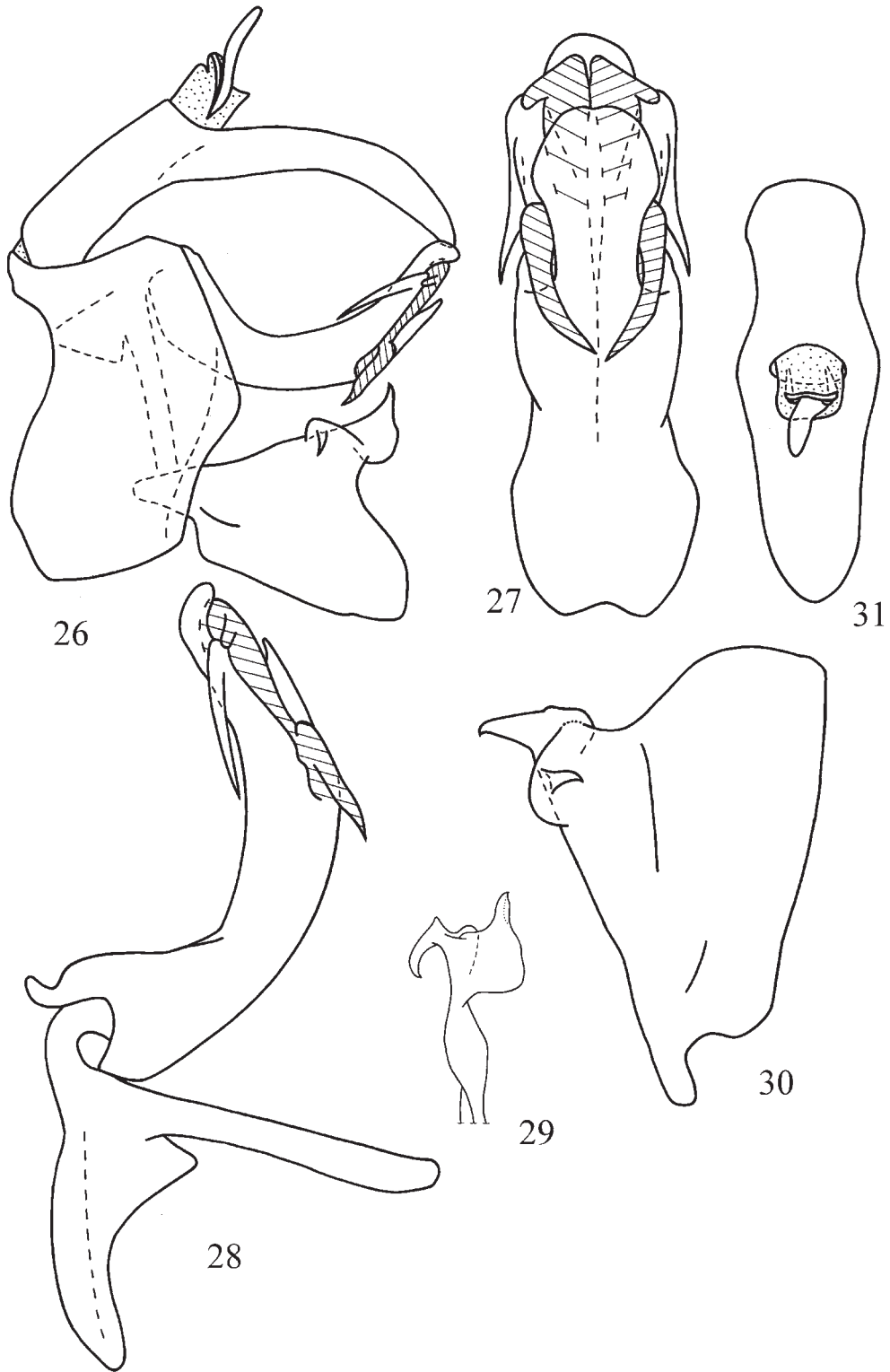
**Other material examined.** 2 males, 4 females, “Singapore / Coll. Baker” // “Loan from / USNMNH / 2040603” (USNM and ZIN).

**Supplementary description (holotype)** (Figs 19–21). Metope with large hemispherical matte shiny bulge in its upper half between the eyes, without intermediate carinae. Upper margin of metope weakly concave, almost straight. Lateral margins of metope sharply diverging below the eyes, hanging over the pedicels. Metopoclypeal suture distinct, almost straight. Postclypeus large, as long as 2/3 of metopial length, without carinae. Pedicels elongately cylindrical. Ocelli present. Coryphe almost square, anterior margin straight, lateral margins diverging posteriorly; posterior margin strongly angularly concave. Rostrum long, reaching hind coxae; 2nd and 3rd segments are equal in length; 3rd segment weakly narrowing apically. Pronotum slightly longer than coryphe, depressed at midline; anterior margin strongly angularly convex, carinated below the eyes; posterior margin weakly concave medially. Paradiscal fields of pronotum very narrow. Paranotal lobes of pronotum wide. Mesonotum 2.5 times as long as pronotum, with lateral carinae. Tegulae large, covered by setae. Forewings long and narrow, truncate apically, without hypocostal plate. Clavus long, 4/5 of wing length. Basal cell long, narrowly oval. Forewing vein sequence:  $R$  2, furcating closely to basal cell, anterior branch ( $R_1$ ) running closely to costal margin;  $ir$  3–5;  $M$  3, firstly furcating near to wing middle, anterior branch ( $M_1$ ) furcating also in apical fifth of wing;  $r-m$  4;  $im$  4; *CuA* 2, furcating after wing middle; *icua* 1; *cup-pcu* 3–4. *Pcu* joined  $A_1$  near to middle of clavus. Hindwings with smoothly concave costal margin and with coupling lobe. Lateral margin of the wings with three weak clefts. Basal cell large, oval. Hindwing vein sequence:  $R$  2, furcating after coupling lobe;  $r-m$  1;  $M$  1;  $m-cua$  1; *CuA* 3, anterior branch also furcating apically; *CuP* 1; *cup-pcu* 1; *Pcu* 1;  $A_1$  2;  $A_2$  1. *CuA* fused with *CuP* in its apical half, but separated apically.  $A_{1,1}$  fused with *Pcu* medially. Hind





**Figs 19–25.** *Eupilis albilineola* Walker, 1857, 19–22 – holotype, 23–25 – non type female from Singapore. 19, 23 – dorsal view; 20, 24 – frontal view; 21 – rostrum, lateral view; 22 – labels; 25 – lateral view.



**Figs 26–31.** *Eupilis albilineola* Walker, 1857, male genitalia. 26 – genital block, lateral view; 27 – penis, ventral view; 28 – penis and connective, lateral view; 29 – capitulum of style, dorsal view; 30 – style, lateral view; 31 – anal tube, dorsal view.

tibia with two lateral spines in its distal half and with 6 apical spines. First and second metatarsomeres are equal in length. First metatarsomere with two latero-apical and 6 intermediate spines arranged in arc. Second metatarsomere with only two latero-apical spines. Each claw with three long setae.

**Coloration (holotype).** General coloration light yellow. Metopial bulge black, with brown median line. Metope with wide dark brown laterally and black medially band below the bulge and with black narrower band above metopoclypeal suture. Postclypeus with three dark brown to black large spots below metopoclypeal suture – in each lower angle and medially. Pronotum with large black spot behind each eye. Mesonotum black between lateral carinae and with black spots outside of carinae. Scutellum light yellow. Middle epimerae and episternae each with large dark brown spot. Hind coxae dark brown. Hind femora brown along its outer margins. Apices of leg spines black. Abdominal tergites yellow, with brown hind margins. Abdominal sternites III–VI yellow, with brown hind margins. Sternite VII and pygofer with black hind margin. Anal tube dark brown. Gonopods brown yellowish.

**Male genitalia** (Figs 26–31). Pygofer long and wide, twice as long vertically as wide medially (in lateral view), with strongly convex medially hind margins (Fig. 26). Anal tube long and narrow, curved (in lateral view), narrowing apically (in dorsal view) (Fig. 31). Anal column short. Phallobase long and narrow, curved (in lateral view), with long (longer than ventral aedeagal hook) and narrow spine-shaped subapical process directed downwards on each side (Figs 26, 28). Dorso-lateral phallobase lobes fused dorsally. Ventral phallobase lobe long and wide, enlarged subapically (Fig. 27). Aedeagus with pair of short ventral hooks, 0.25 as long as phallobase, gradually narrowed and pitted apically, directed downwards and to the midline. Apical aedeagal processes long and wide, each with short elongate subapical process (Figs 27, 28). Connective with large cup. Style enlarged from the basement, with strongly convex hind margin and obtuse caudo-dorsal angle; apical tooth large; lateral tooth large, turned backwards (Fig. 30). Capitulum of style without neck (in lateral view), wide, almost square (in dorsal view) (Fig. 29).

**Female genitalia.** Sternite VII convex medially.

**Total length.** Males – 9.5 mm. Females – 10.5–11.0 mm.

**Note.** The species was described after the female collected in Singapore by A.R. Wallis (Walker

1857a) and soon after recorded from Sarawak in Borneo (Walker 1858). Walker (1857a) gave the drawings of the holotype – a female with opened fore and hind wings and apart legs (Walker 1857a, Pl. 3, figs 1, 1a, 1b, 1c) which correspond (except for fore legs are missed) to the specimen deposited in the Natural History Museum (London, UK) and listed above as the holotype (Figs 19–22). Gnezdilov (2016c) illustrated male genitalia of *Eupilis* species from Sarawak under the name *Eupilis albilineola* (Gnezdilov 2016c, fig. 17) which in fact represents a new species described below as *Eupilis walkeri* sp. nov. which is well different from *E. albilineola* Walker in details of male genitalia structure.

### *Eupilis hebes* Walker, 1857

(Figs 32, 33, 36–41)

*Eupilis hebes* Walker, 1857b: 162.

*Eupilis hebes*: Walker, 1858: 123.

**Type material examined.** Male, lectotype (here designated), “Sar.” // “Wallace” (BMNH); female, paralectotype, “Sar.” // “Wallace” // “*hebes*” [hand-writing] (BMNH).

**Supplementary description.** Pronotum with weak median carina. Mesonotum with weak lateral carinae. Hind tibia with 6 apical spines. First metatarsomere with two latero-apical and 8–9 intermediate spines apically.

**Coloration** (Figs 32, 33). General coloration light brown yellowish. Metopial bulge with horse-shoe-shaped dark brown to black spot. Metope with brown area below the bulge and with fuzzy wide median dark brown stripe running from above metopoclypeal suture throughout postclypeus. Rostrum with dark brown apex. Pronotum and mesonotum with brown spots. Forewings transparent with dark brown veins. Hindwings transparent with brown veins.

**Male genitalia** (Figs 36–41). Pygofer short and wide (in lateral view), with strongly convex hind margins (Fig. 36). Anal tube long, longer than pygofer vertically, curved (in lateral view), narrow, narrowing apically (in dorsal view) (Fig. 37). Anal column short and wide, narrowing apically. Phallobase long and narrow, slightly curved (in lateral view) (Fig. 38). Dorso-lateral phallobase lobes without processes, narrowing apically (in lateral view). Ventral margins of dorso-lateral phallobase lobes strongly convex under ventral aedeagal hooks. Ventral phallobase lobe long and wide, weakly enlarged subapically (Fig. 39).



**Figs 32–35.** *Eupilis* spp. 32 – *E. hebes* Walker, 1857, female, paralectotype, lateral view; 33 – same, frontal view; 34 – *E.* sp., ovipositor, dorsal view; 35 – same, lateral view.

Apical aedeagal processes narrowing apically, without processes. Connective very narrow. Aedeagus with a pair of short, rounded apically, ventral hooks appearing in its apical third. Style with convex hind margin, caudo-dorsal angle acute (Fig. 40). Capitulum of style sharply narrowing apically (in dorsal view) (Fig. 41).

**Total length.** Male – 9.8 mm. Female – 11.0 mm.

**Note.** The species was described after male and female, collected in Sarawak by A.R. Walles (Walker 1857b). The lectotype is designated here to stabilize the species concept (ICZN 1999: Art. 74).

***Eupilis borneoensis* sp. nov.**

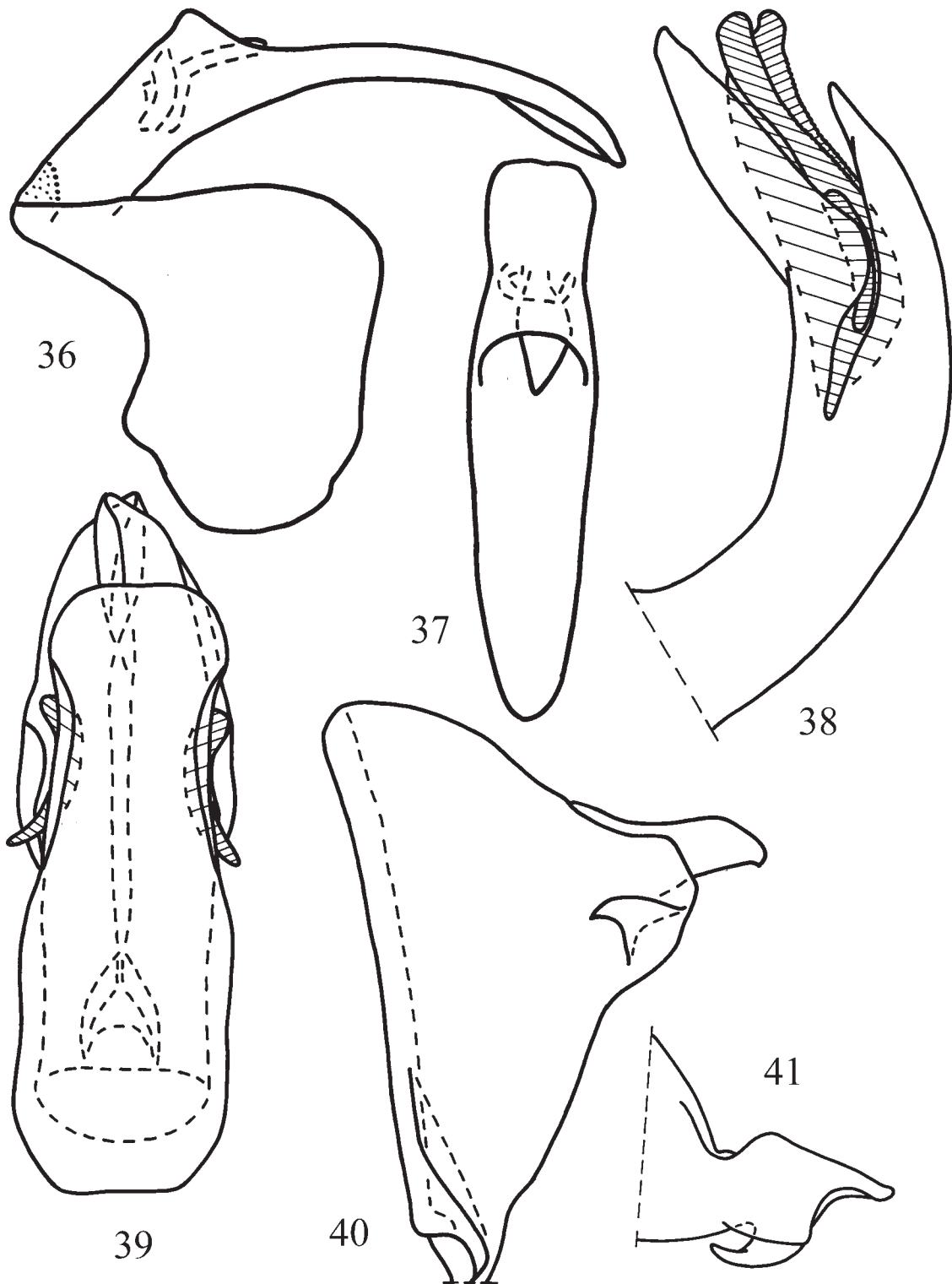
(Figs 42–45, 48–53)

**Type material.** Holotype, male, “N.W. BORNEO, / Kuching. / Capt. Oct. 2.99 / by Dyak coll. /

Pres. 1900 by / R. Shelford.” // “1900 / 10285 [hand written by ink]” (BMNH).

**Etymology.** The species is named after Borneo Island.

**Description** (Figs 42–44). Coryphe transverse, twice as broad as long at midline, anterior margin straight, posterior margin acutely angulate (Fig. 42). Ocelli present. Pronotum concave medially, with sharply convex anterior margin, posterior margin nearly straight. Paranotal lobes of pronotum wide. Mesonotum long, twice as long as pronotum, with lateral carinae. Forewings long and narrow, with truncate askew apices.  $R\ 2\ M\ 3\ Cu\ A\ 2$  (Fig. 43). Hind tibia with two lateral spines distally and 6 apical spines. First and second metatarsomeres are equal in length. First metatarsomere with two latero-apical and 6 intermediate spines in straight row.



**Figs 36–41.** *Eupilis hebes* Walker, 1857, lectotype, male genitalia. 36 – pygofer and anal tube, lateral view; 37 – anal tube, dorsal view; 38 – penis, lateral view; 39 – penis, ventral view; 40 – style, lateral view; 41 – capitulum of style, dorsal view.



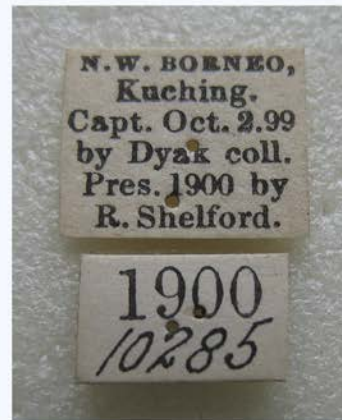
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43



44



45

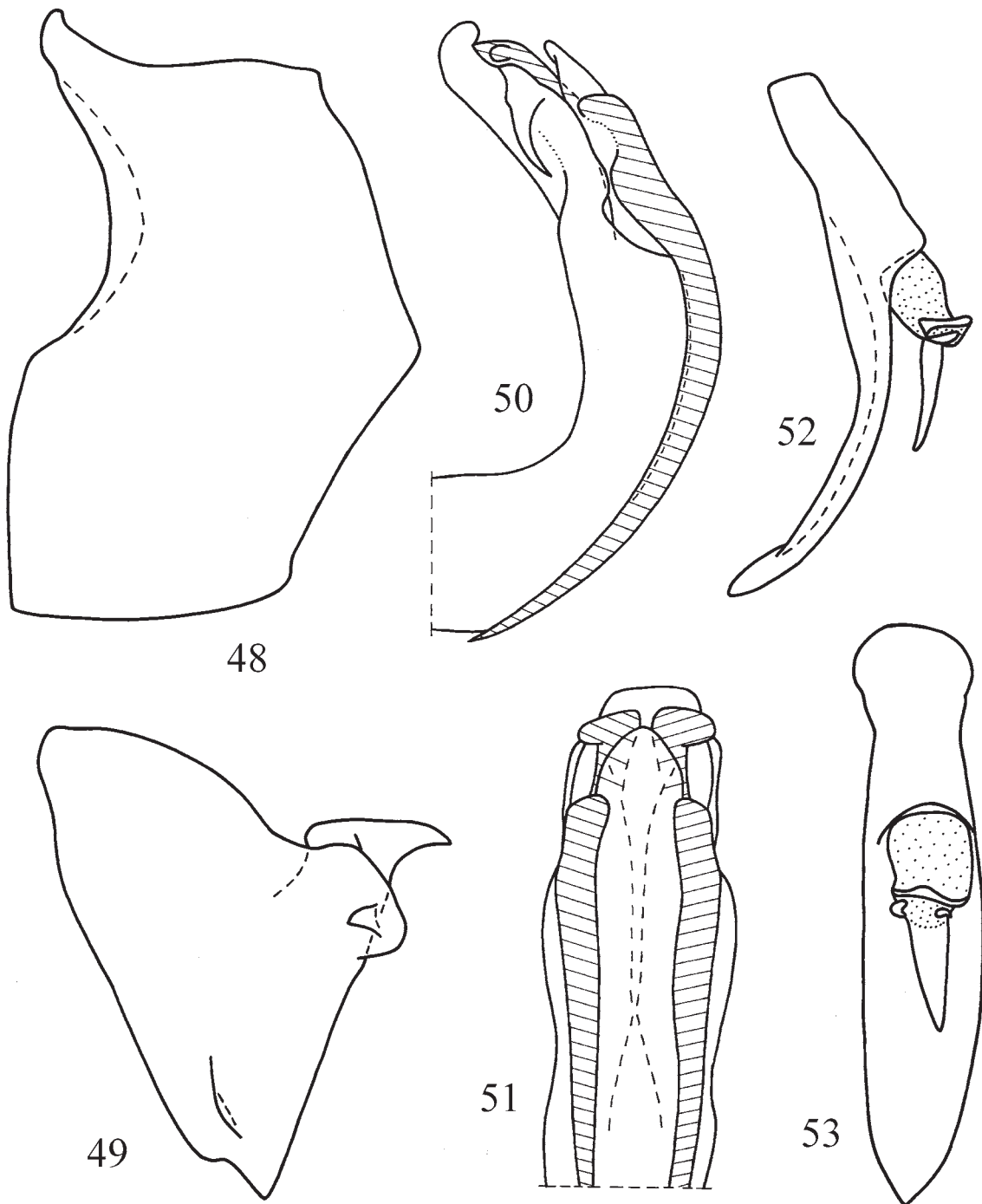


46



47

**Figs 42–47.** *Eupilis* spp. 42–45 – *Eupilis borneoensis* sp. nov., holotype, 46, 47 – *Eupilis walkeri* sp. nov., paratype. 42 – dorsal view; 43, 46 – lateral view; 44, 47 – frontal view; 45 – labels.



**Figs 48–53.** *Eupilis borneoensis* sp. nov., holotype, male genitalia. 48 – pygofer, lateral view; 49 – style, lateral view; 50 – penis, lateral view; 51 – penis, ventral view; 52 – anal tube, lateral view; 53 – anal tube, dorsal view.

**Coloration** (Figs 42–44). General coloration of head, thorax, and abdomen light yellow brownish, with brown spots on episternae, epimerae, and hind coxae. Coryphe light yellow greenish, with pair of elongately oval light brown spots near its posterior margin. Pedicels light brown. Metopial bulge dark-brown, with yellow brownish large spot in the middle. Metope with whitish band below the bulge and with dark brown margins above metopoclypeal suture. Postclypeus light yellow, except brown medially, with pair of triangular dark brown spots laterally below metopoclypeal suture. Anteclypeus light yellow. Pronotum light yellow greenish. Paranal lobes of pronotum light brown marginally. Mesonotum with pair of large round dark brown spots and pair of small dark brown spots outside of lateral carinae and with pair of wide longitudinal dark brown stripes inside of the carinae. Scutellum yellow greenish. Forewings with brown yellowish veins; costal margin dark brown in front of furcation of radius. Cells between  $R_{1,1}$  and  $R_{1,2}$  dark brown. Hindwings matte, with dark brown veins. Fore femora and tibiae light yellow, with wide brown bands. Fore tarsi dark brown. Claws dark brown. Apices of leg spines black.

**Male genitalia** (Figs 48–53). Pygofer long and wide, nearly twice as long vertically as wide medially (in lateral view), with sharply convex medially hind margins (Fig. 48). Anal tube long, as long as pygofer vertically, and narrow, curved (in lateral view) (Fig. 52), narrowing to pointed apex (in dorsal view) (Fig. 53). Anal column short, less than  $\frac{1}{4}$  of anal tube length. Phallobase long and narrow, curved (in lateral view), each dorso-lateral lobe with rather short tooth-shaped, wide basally and narrowed apically, subapical process directed downwards (Fig. 50). Dorso-lateral phallobase lobes fused dorsally. Ventral margins of dorso-lateral phallobase lobes weakly convex under ventral aedeagal hooks. Ventral phallobase lobe long and wide, narrowing apically (Fig. 51). Apical aedeagal processes long and wide, each with short rounded subapical process (Figs 50, 51). Aedeagus with pair of very long ventral hooks, nearly as long as phallobase, arising in its apical fifth, gradually narrowed and pointed apically, directed downwards. Style with convex hind margin, caudo-dorsal angle acute (Fig. 49). Capitulum of style narrowing apically.

**Total length.** 11.0 mm.

***Eupilis walkeri* sp. nov.**

(Figs 46, 47, 54–59)

*Eupilis albilineola*: Gnezdilov, 2016c: 182, fig. 17.

**Type material examined.** Holotype, male, “SAR.” // “Borneo” (BMNH). Paratype: female, “SAR.” // “Wallace” // “*Eupilis albilineola*” [hand-written] (OXUM).

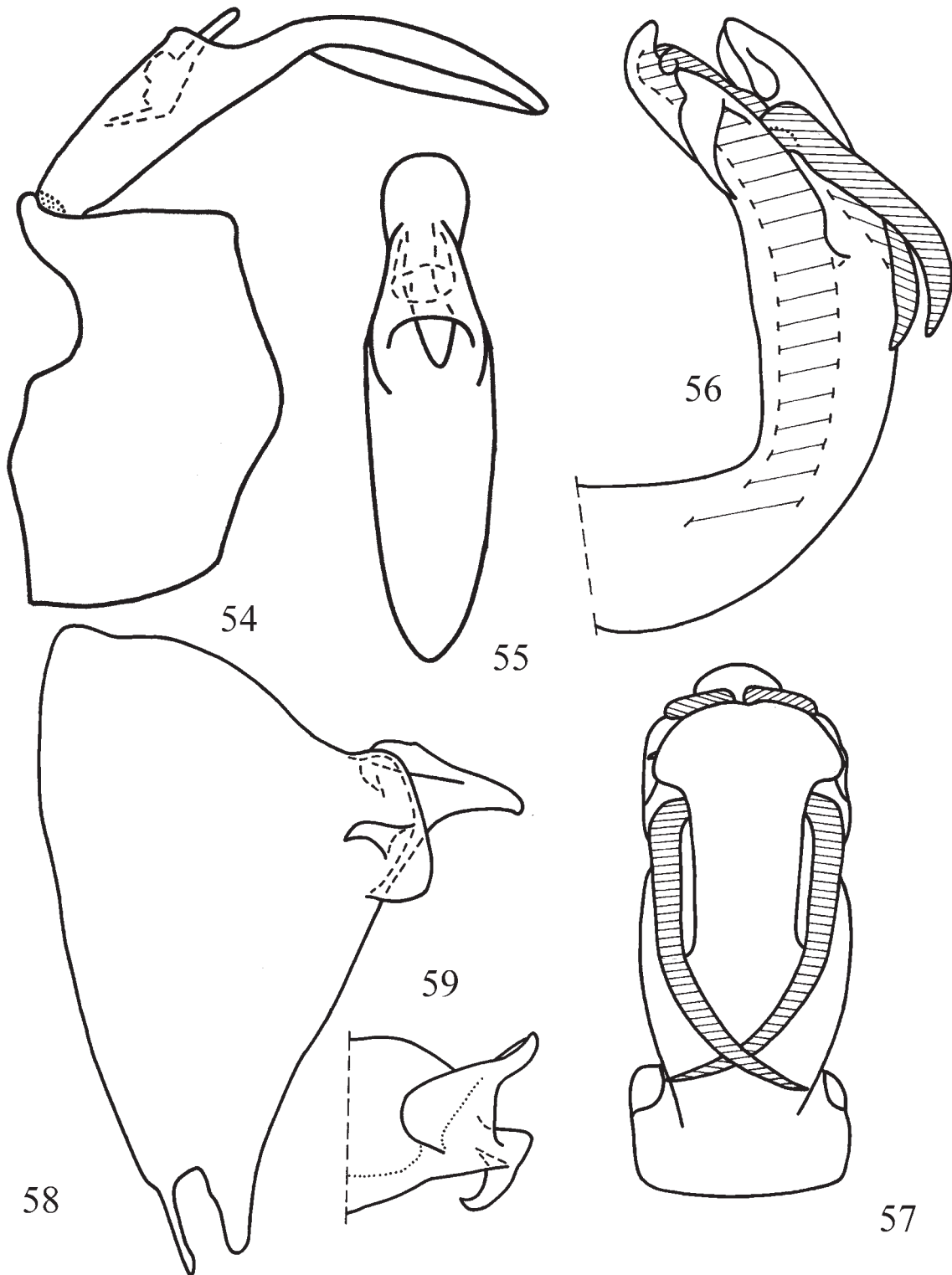
**Etymology.** The species is named in honor of famous British entomologist Francis Walker (1809–1874) who described the genus *Eupilis*.

**Description (holotype)** (Figs 46, 47). Base of clypeus weakly convex. Pronotum with acutely angulate anterior margin. Hind tibia with 6 spines apically. First metatarsomere with two latero-apical and 6 intermediate spines apically.

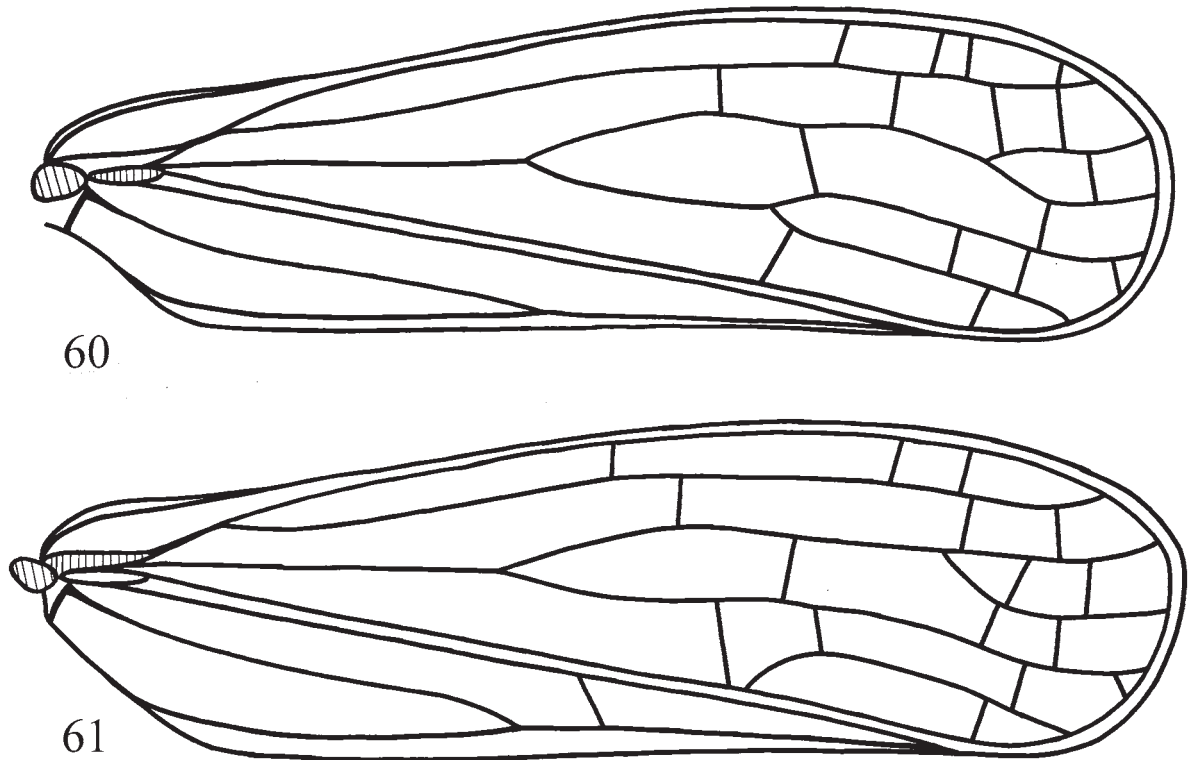
**Coloration.** General coloration yellowish light brown. Metopial bulge black in its upper  $\frac{2}{3}$ , bearing brown spot in the middle, and whitish in its lower third. Metope with dark brown to black band below the bulge and black lower margin above metopoclypeal suture. Postclypeus dark brown medially, with two large black spots laterally. Mesonotum with dark brown spots. Forewings with dark brown longitudinal and light yellow transverse veins, costal margin black in front of stem of radius, apical cells dark brown between furcation of  $M_r$ . Hindwings transparent. Fore coxae, and fore and middle femora and tibiae with dark brown to black areas. Apices of leg spines dark brown to black.

**Male genitalia** (Figs 54–59). Pygofer long and wide, nearly twice as long vertically as wide medially (in lateral view), with strongly convex medially hind margins (Fig. 54). Anal tube long and narrow, curved (in lateral view) (Fig. 54), narrowing apically (in dorsal view) (Fig. 55). Anal column short. Phallobase long and narrow, curved (in lateral view), each dorso-lateral lobe with rather short tooth-shaped, wide basally and narrowed apically, subapical process directed downwards (Fig. 56). Dorso-lateral phallobase lobes fused dorsally. Ventral phallobase lobe long and wide, sharply enlarged subapically – mushroom-shaped, with weak apical concavity (Fig. 57). Aedeagus with pair of rather long ventral hooks, half as long as the phallobase, gradually narrowed and pointed apically, directed downwards and to the midline. Apical aedeagal processes long and wide, each with short rounded subapical process (Fig. 56). Style enlarged from the basement, with strongly





**Figs 54–59.** *Eupilis walkeri* sp. nov., holotype, male genitalia. 54 – pygofer and anal tube, lateral view; 55 – anal tube, dorsal view; 56 – penis, lateral view; 57 – penis, ventral view; 58 – style, lateral view; 59 – capitulum of style, dorsal view.



Figs 60–61. *Eupilis* sp., male (Kuala Lumpur), forewings. 60 – left wing; 61 – right wing.

convex hind margin and straight caudo-dorsal angle; lateral tooth large, turned backwards (Fig. 58). Capitulum of style without neck (in lateral view), wide, narrowing apically (in dorsal view) (Fig. 59).

**Total length.** Male – 10 mm. Female – 11.0 mm.

### Genus *Bornepilis* gen. nov.

**Type species:** *Bornepilis longipennis* sp. nov., by original designation.

**Etymology.** Generic name is combination of the words “Borneo” and “Eupilis”.

**Description.** Metope elongate, flat, with distinct median carina and short or weak sublateral carinae. Coryphe 1.5–2.0 times as wide as long medially. Pronotum with obtuse- or acute-angled anterior margin. Mesonotum large, more than twice as long as pronotum. Forewings long and narrow, narrowing apically, surpassing abdominal apex, without hypocostal plate. Forewing vein sequence: *R* 2 *M* 3–4 *CuA* 1. Hind wings well developed, 3-lobed, with *Pcu* furcating apically, five veins between *CuP* and *Pcu* and two

veins between *Pcu* and  $A_{1,1}$  (Figs 66, 120). Hind tibia with two lateral spines. Male pygofer with straight or weakly convex hind margins. Male anal tube as long as pygofer vertically or longer, slightly curved (in lateral view), narrow (in dorsal view). Each dorso-lateral lobe of phallobase with large ear-shaped lobe apically and with large angular lobe of its margin under aedeagal ventral hook. Ventral phallobase lobe long and wide, concave laterally. Aedeagus with pair of long ventral hooks arising in its apical third, slightly curved and directed downwards. Style with straight hind margin and obtuse caudo-dorsal angle. Capitulum of style on short and wide neck or without neck. Hind margin of female sternite VII concave. Gonoplasts convex, rounded (Figs 65, 80). Female anal tube long and narrow.

**Composition.** In addition to the type species also *Eupilis hyalinocosta* Melichar, 1914 and *E. rubrovenosa* Melichar, 1914 belong to this genus.

**Distribution.** Borneo, Philippines.

**Differential diagnosis.** The new genus well differs from other genera of the tribe by hindwing venation.

tion, with *Pcu* furcating apically, five veins between *CuP* and *Pcu* and two veins between *Pcu* and  $A_{1,1}$ , and by the phallobase with large ear-shaped lobes apically.

***Bornepilis longipennis* sp. nov.**

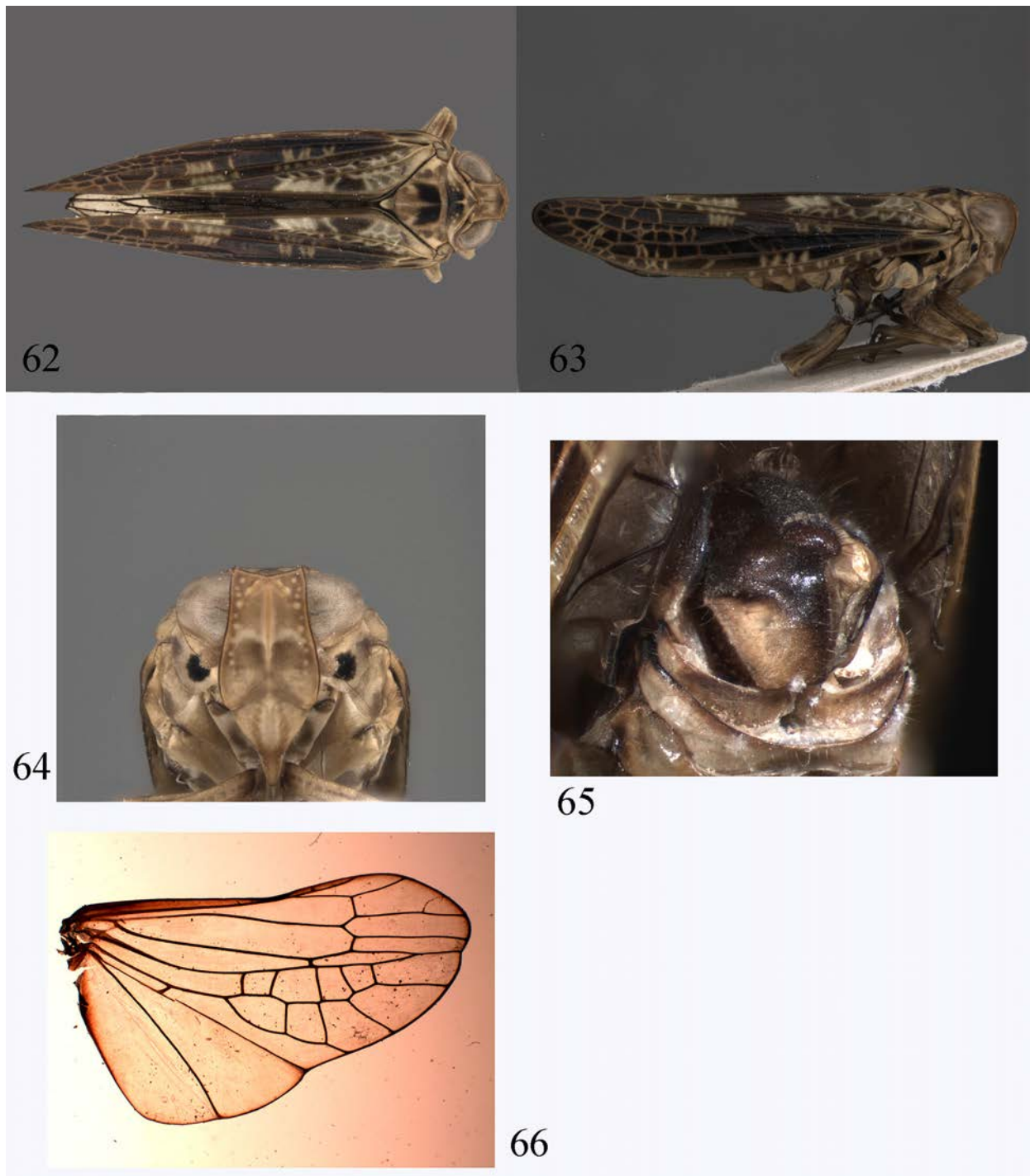
(Figs 62–76)

**Type material.** Holotype, male, “Fog A 71 / F 1 / 21.III.1993 / A. Floren” [white, with ochre yellow stripe on left margin, printed] // “SABAH: Poring Spring. / Aporusa sp., Lower Montane > 650 m / Mixed dipterocarp. Fst.” [white, printed] (SNSD). The specimen is glued on paper rectangular. Paratypes: 2 males, 1 female, “Fog A 71 / F 1 / 21.III.1993 / A. Floren” [white, with ochre yellow stripe on left margin, printed] // “SABAH: Poring Spring. / Aporusa sp., Lower Montane > 650 m / Mixed dipterocarp. Fst.” [white, printed] (SNSD – 1 male 1 female; ZIN – 1 male); 1 female, “Fog A 73 / F 3 / 22.III.1993 / A. Floren 3” [white, with pink stripe on left margin, print and hand written] // “SABAH: Poring Spring. / Aporusa sp., Lower Montane > 650 m / Mixed dipterocarp. Fst.” [white, printed] (ZIN).

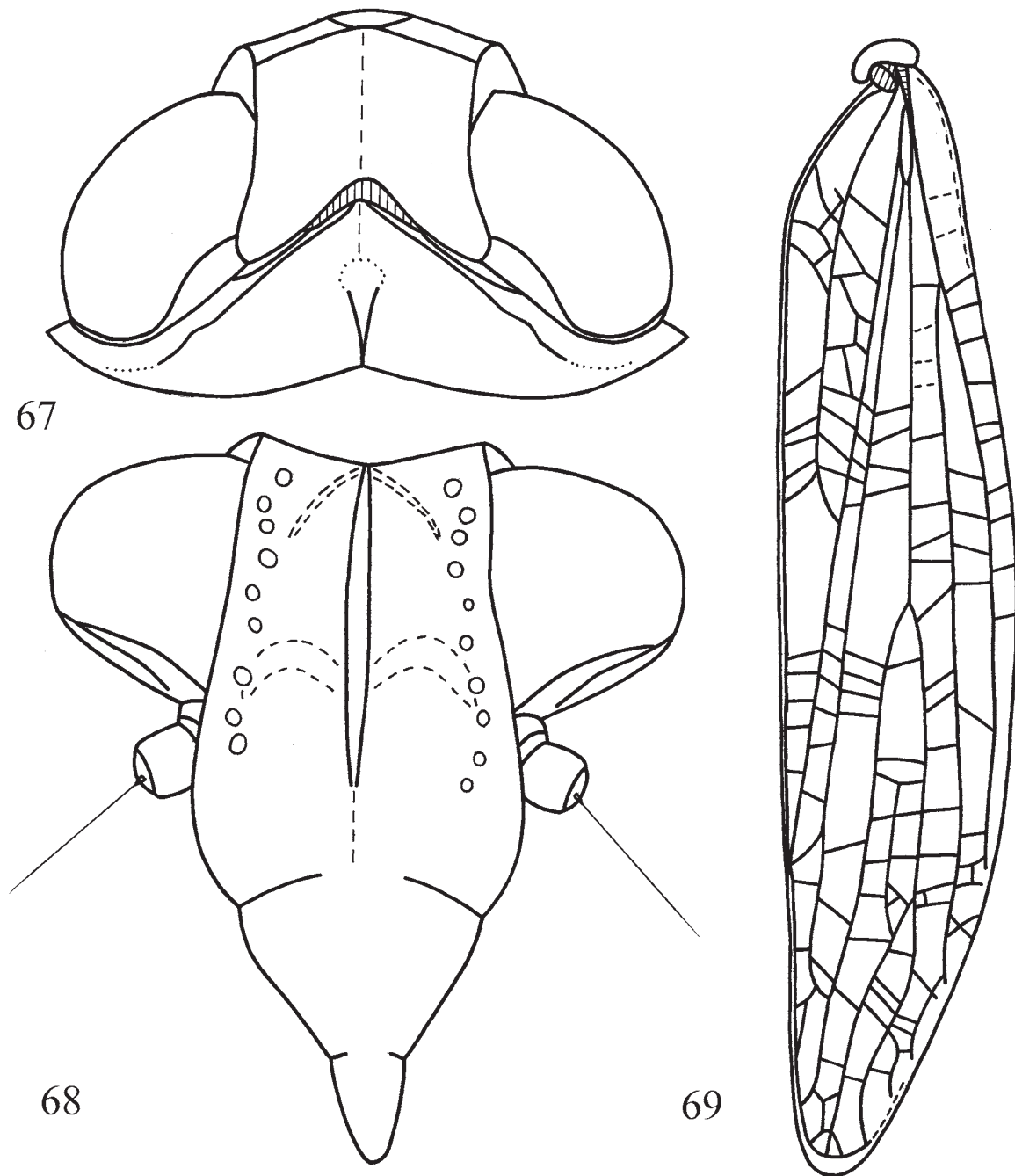
**Description** (Figs 62–69). Metope elongate, enlarged from below the eyes to clypeus, with distinct median carina, running from its upper margin, but not reaching metopoclypeal suture, and short sublateral carinae in its upper part (Figs 64, 68). Metope with row of tubercles between its lateral margins and sublateral carinae on each side. Upper margin of metope obtuse-angled. Lateral margins of metope hang over pedicels. Metopoclypeal suture distinct, weakly convex. Ocelli rudimentary. Pedicels cylindrical. Postclypeus flattened dorso-ventrally, without carinae. Rostrum not reaching hind coxae; 2nd and 3rd segment are almost equal in length, 3rd segment not narrowing apically. Coryphe 1.5 times as wide as long medially, with lateral margins diverging posteriorly; anterior margin convex, posterior margin acute-angled (Figs 62, 67). Pronotum almost as long as coryphe at midline, with acute-angled and keel-shaped anterior margin and weakly notched medially posterior margin. Pronotum with median carina running from its posterior margin, but not reaching anterior margin. Paradiscal fields of pronotum not narrow. Paranotal lobes of pronotum wide, without carinae. Tegulae large. Mesonotum large, more than twice as long as pronotum, with median and lateral

carinae; scutellum well separated. Forewings narrow and long, 5 times as long as wide at the middle, narrowing apically, without hypocostal plate (Fig. 63). Forewings surpassing abdominal apex at 1/3 of its length. Basal cell very long, narrowly oval. Fore wing vein sequence (Fig. 69): *R* 2, furcating closely to basal cell; *M* 3, firstly furcating at wing middle,  $M_1$  also furcating after claval apex; *CuA* 1. *Pcu* joint  $A_1$  at claval middle. Clavus long,  $\frac{3}{4}$  of wing length. Many transverse veins, distributed by series on wing area. Hind wings 3-lobed, with costal margin concave and weak cubital and vannal clefts of lateral margin (Fig. 66). Basal cell large, widely oval. Hind wing vein sequence: *R* 2, furcating after coupling lobe; *r-m* 1; *M* 2–3, firstly furcating in apical wing third; *m-cua* 1; *CuA* 1; *cua-cup* 1; *CuP* 1; *cup-pcu* 5; *Pcu* 2, furcating in apical wing third; *pcu-a*<sub>1,1</sub> 2;  $A_1$  2;  $A_2$  1. *CuA* and *CuP* fused apically. *Pcu* and  $A_{1,1}$  fused medially. Hind tibia with two lateral spines in its distal third and with 6 apical spines. First metatarsomere slightly longer than second one, with two latero-apical and 6 intermediate spines in a row. Second metatarsomere with only two latero-apical spines. Ventral surface of first and second metatarsomeres covered by long hair-shaped seta. Arolium of pretarsus with convex hind margin, reaching claw apices (in dorsal view). Each claw with two long setae.

**Coloration** (Figs 62–66). Metope light brown yellowish, with whitish curved stripe medially. A red spot is below each ocellus. Postclypeus whitish. Pronotum dark brown from the middle to posterior margin. Paranotal lobes whitish, each with large round dark brown spot. Mesonotum dark brown in its upper half between lateral carinae. Forewings from brown to dark brown, with brown and whitish transverse veins. Hindwings semitransparent, with brown to dark brown veins. Fore and middle tibiae with pair of brown bands. Apices of 3rd tarsomeres of fore and middle legs, apices of spines, claws, and dorso-lateral plates of arolium from dark brown to black. In some specimens postclypeus laterally reddish, coryphe with a pair of red spots near to its posterior margin, mesonotum with red spots outside of lateral carinae, and fore and middle femora with reddish tint or pair of reddish bands. Abdominal sternites IV–VII dark brown medially. Abdominal tergites brown. Male pygofer light brown yellowish. Styles, except pale basal parts, and anal tube dark brown. Gonoplares pale in its lower halves and dark brown to black in upper halves. Female anal tube dark brown to black.



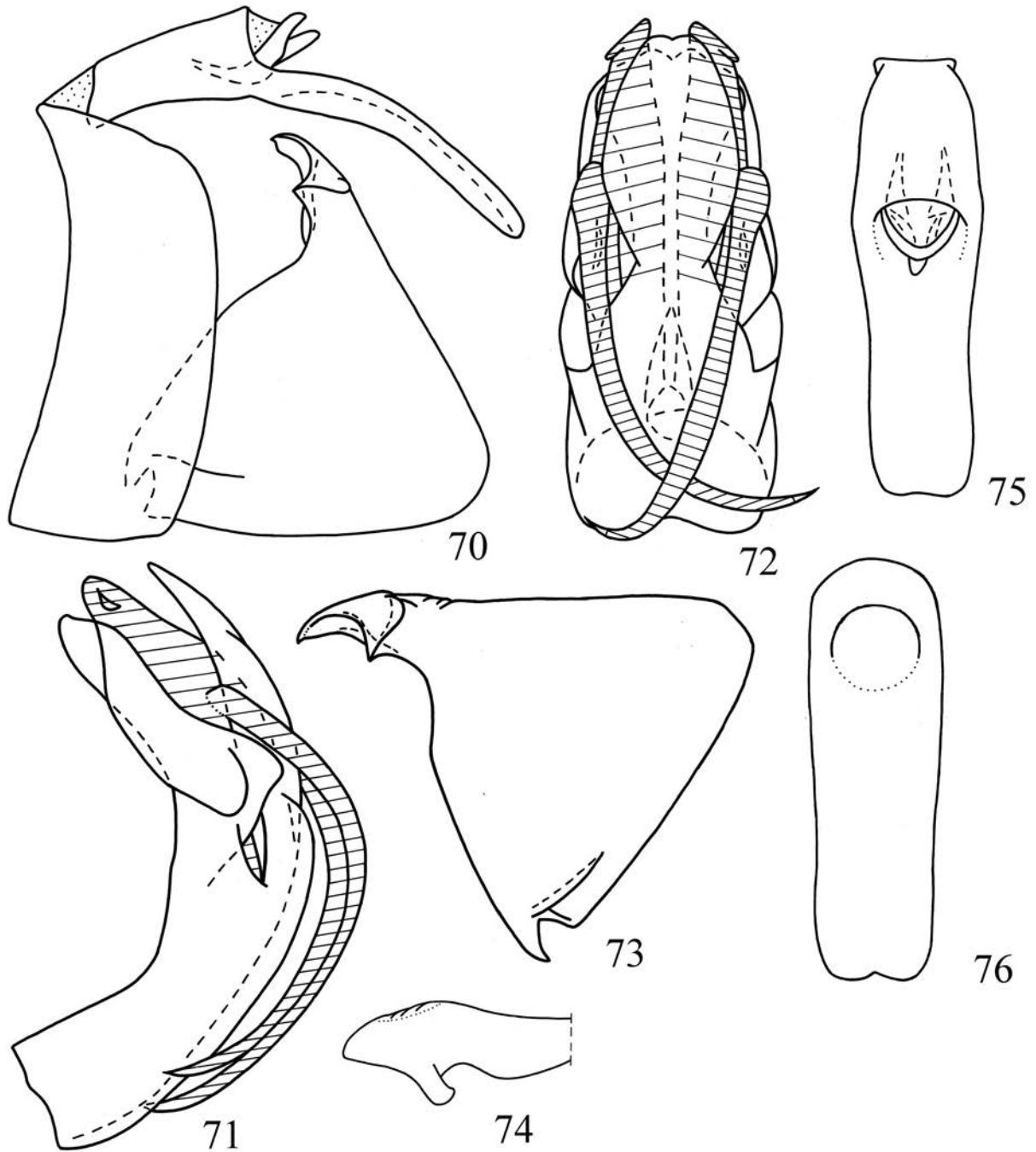
**Figs 62–66.** *Bornepilis longipennis* gen. et sp. nov. 62 – holotype, dorsal view; 63 – same, lateral view; 64 – same, frontal view; 65 – paratype, ovipositor, ventro-lateral view; 66 – male paratype, hind wing, dorsal view.



**Figs 67–69.** *Bornepilis longipennis* gen. et sp. nov. 67 – head and pronotum, dorsal view; 68 – head, frontal view; 69 – forewing, dorsal view.

**Male genitalia** (Figs 70–76). Pygofer elongate vertically, 3 times as long as wide medially, with straight hind margins (Fig. 70). Anal tube long, as long as pygofer vertically, slightly curved (in lateral view), narrow, with slightly concave lateral margins

and with weak apical concavity (in dorsal view) (Fig. 75). Anal column short. Phallobase long and narrow, curved (in lateral view), with deep incision between dorso-lateral and ventral lobes (Fig. 71); wide (in ventral view) (Fig. 72). Each dorso-lateral lobe of



**Figs 70–76.** *Bornepilis longipennis* gen. et sp. nov., genitalia, 70–75 – male, 76 – female. 70 – pygofer, anal tube, and style, lateral view; 71 – penis, lateral view; 72 – penis, ventral view; 73 – style, lateral view; 74 – capitulum of style, dorsal view; 75, 76 – anal tube, dorsal view.

phallobase with large ear-shaped lobe apically and with large angular lobe of its margin under aedeagal ventral hook. Ventral phallobase lobe long and wide, with sharply concave lateral margins and with weak apical notch (Fig. 72). Apical aedeagal processes well visible above the phallobase margins, wide, narrowing apically, each with small semicircular subapical process. Aedeagus with pair of long ventral hooks, 3/4 of phallobase length (in lateral view), arising in its apical third, slightly curved, gradually narrowed apically, pointed and directed downwards. Style large, with straight hind margin and obtuse caudo-dorsal angle (Fig. 73). Capitulum of style on short wide neck (in lateral view), with large lateral tooth. Capitulum of style spear-shaped in dorsal view (Fig. 74).

**Female genitalia** (Figs 65, 76). Hind margin of sternite VII widely concave (Fig. 65). Gonoplares convex, rounded. Anal tube long and narrow, with weak concavity apically (Fig. 76). Anal column short.

**Total length.** Males – 9.5–10.2 mm. Females – 11.0–11.5 mm.

**Note.** The species was collected in mixed *Dipterocarpus* forest on *Aporusa* sp. (Phyllanthaceae).

**Differential diagnosis.** It well differs from other species of the genus by longer and narrower forewings brown to dark brown, with whitish transverse veins.

***Bornepilis hyalinocosta* (Melichar, 1914), comb. n.**  
(Figs 77–89)

*Eupilis hyalinocosta* Melichar, 1914: 279.

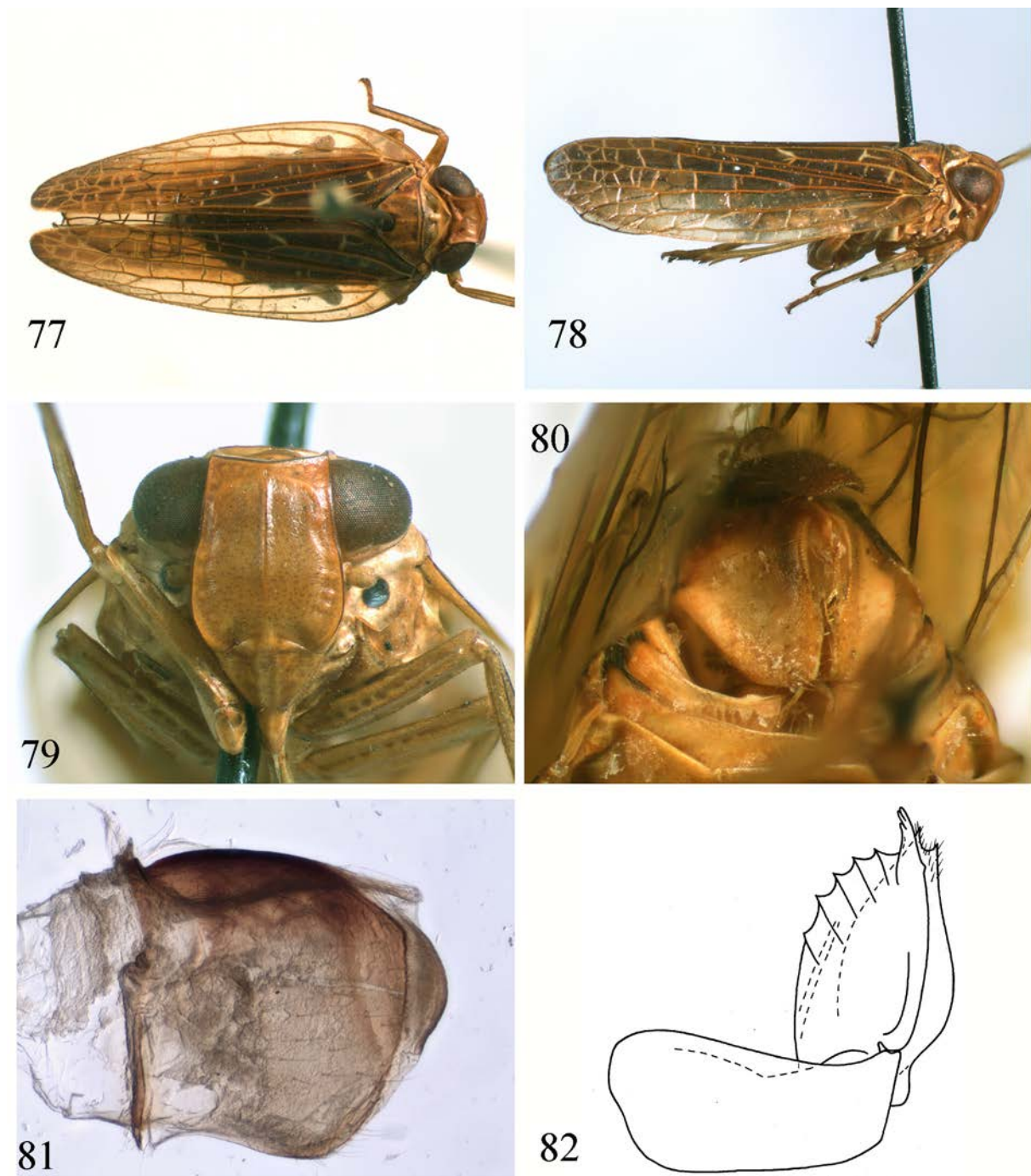
**Material examined.** Philippines: 1 female, “Mt Makiling / Luzon, Baker” // “Loan from / USNMNH / 2040603” (USNM); 1 female, “Mt. Makiling / 14°09′N 121°14′E. / 4 km. SE Los Baños / Laguna, PHILIP / 3.II.1979” // “Brit. Mus. / 1983–171” (BMNH); 2 males, 4 females, “Island / Samar / Baker” // “Loan from / USNMNH / 2040603” (USNM and ZIN); 1 female, “Davao / Mindanao / Baker” // “Loan from / USNMNH / 2040603” (USNM); 1 female, “Zamboanga / Mindanao / Baker” // “Loan from / USNMNH / 2040603” (USNM); 1 female, “Dapitan / Mindanao / Baker” // “Loan from / USNMNH / 2040603” (USNM).

**Supplementary description** (Figs 77–79, 89, 120). Metope flat, almost twice as long as wide between the eyes, slightly enlarged above the clypeus, with median carina running from its upper margin to metopoclypeal suture, but weak above the suture,

and with weak sublateral carinae joint with median carina below its upper margin (Fig. 79). Median carina running throughout post- and anteclypeus, but become smooth on postclypeus which is flattened dorso-ventrally. Metope and coryphe joint at obtuse angle (in lateral view). Rostrum short, not reaching hind coxae; 3rd segment slightly longer than 2nd one, narrowing apically. Coryphe transverse, without carinae, twice as wide as long at midline, anterior margin weakly obtusely angulate, posterior margin concave. Ocelli present. Pedicel elongately cylindrical. Pronotum with weak median carina and keel-shaped obtusely angulate anterior margin. Paradiscal fields of pronotum very narrow behind the eyes. Mesonotum 2.5 times as long as pronotum medially, with median and lateral carinae. Forewings long, narrowing to apices, without hypocostal plate, semitransparent. Clavus long, 3/4 of wing length. Basal cell long and narrow. Forewing vein sequence: *R* 2, furcating closely to basal cell; *M* 3–4, firstly furcating near to wing middle; *CuA* 1 (Fig. 89). Hind wings well developed, with 3 weak clefts – cubital, vannal, and anal. Basal cell large, oval (Fig. 120). Hind wing vein sequence: *R* 2, furcating after coupling lobe; *r-m* 1; *M* 2, furcating after *R*; *m-cua* 1; *CuA* 1; *cua-cup* 2; *CuP* 1; *cup-pcu* 5; *Pcu* 2; *pcu-a*<sub>1,1</sub> 2; *A*<sub>1</sub> 2; *A*<sub>2</sub> 1. *CuA* and *CuP* fused apically without flattening. *Pcu* fused *A*<sub>1,1</sub> medially. Hind tibia with two lateral spines in its distal half and with 6 apical spines. First and second metatarsomeres are nearly equal in length. First metatarsomere with two latero-apical and 11–13 intermediate spines arranged in two rows. Claw apices extending arolium hind margin (in dorsal view).

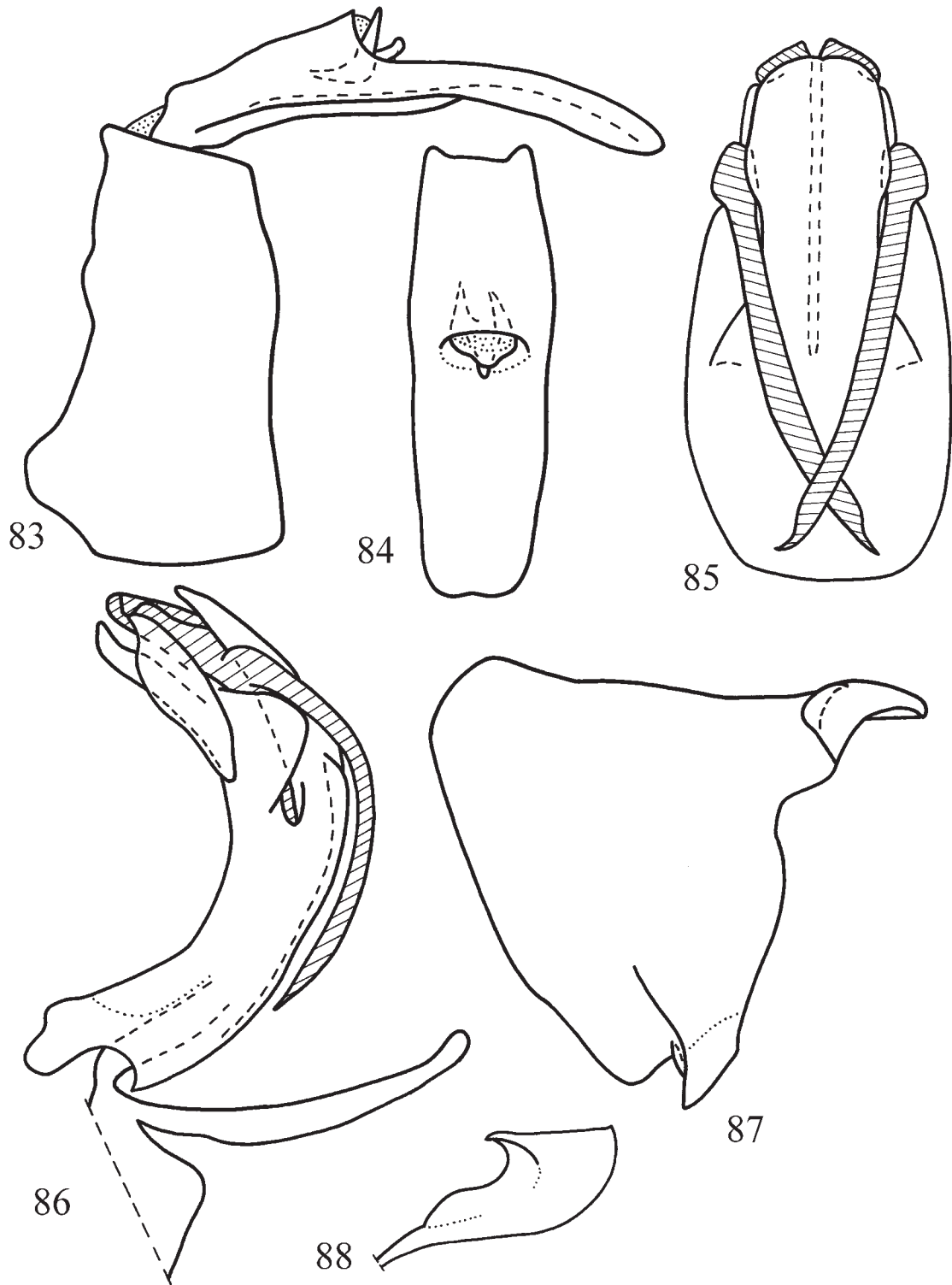
**Coloration** (Figs 77–80). General coloration brown yellowish, with green tint. Coryphe often with two brown spots at posterior margin. Apices of rostrum and spines of legs black. Forewings with whole clavus and corium below median vein brown. Paranotal lobes each with large round black spot. Apices of third tarsomeres of fore and middle legs dark brown. Claws black basally. Abdominal tergites, except laterally, dark brown. Female anal tube and gonoplares dorsally dark brown.

**Male genitalia** (Figs 83–88). Pygofer elongate vertically, three times as long as wide medially, with weakly convex hind margins in its upper halves (Fig. 83). Anal tube long, longer than pygofer vertically, slightly curved (in lateral view), narrow, slightly narrowing apically, with weak apical concavity (in dorsal view) (Fig. 84). Anal column short. Phal-

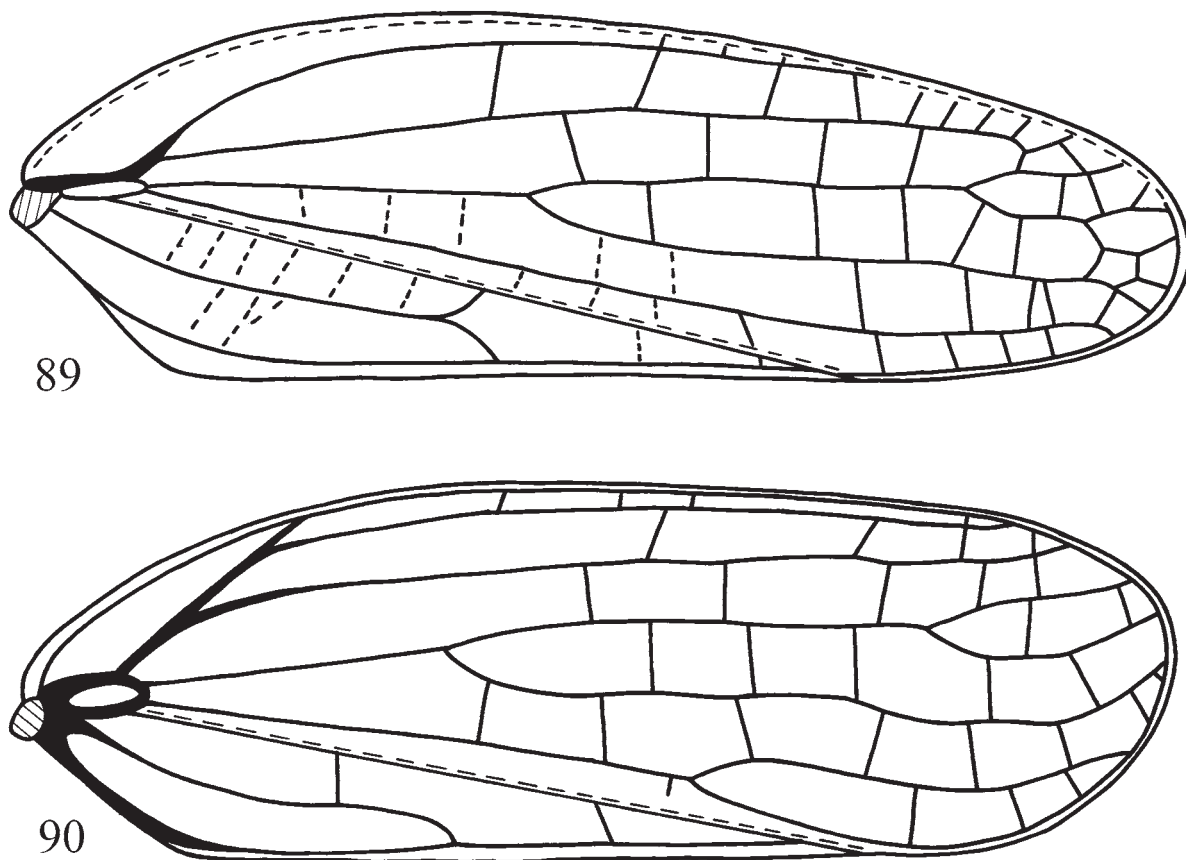


**Figs 77–82.** *Bornepilis hyalinocosta* (Melichar, 1914), female (Samar I.). 77 – dorsal view; 78 – lateral view; 79 – frontal view; 80 – ovipositor, ventral view; 81 – right gonoplac lobe, ventro-lateral view; 82 – gonocoxa VIII and anterior connective lamina of gonapophyse VIII, ventral view.





**Figs 83–88.** *Bornepilis hyalinocosta* (Melichar, 1914), male genitalia (Samar I). 83 – pygofer and anal tube, lateral view; 84 – anal tube, dorsal view; 85 – penis, ventral view; 86 – penis and connective, lateral view; 87 – style, lateral view; 88 – capitulum of style, dorsal view.



**Figs 89–90.** Eupilisini, forewing. 89 – *Bornepilis hyalinocosta* (Melichar, 1914), male (Samar I); 90 – *Gabaloeca nigrinervis* (Stål, 1870), female (not all transverse veins figured).

lobase long and narrow, curved (in lateral view), with deep incision between dorso-lateral and ventral lobes (Fig. 86); wide (in dorsal view) (Fig. 85). Dorso-lateral lobes of phallobase fused dorsally. Each dorso-lateral lobe with large ear-shaped lobe apically and with large angular lobe of its margin under aedeagal ventral hook. Ventral phallobase lobe long and wide, slightly enlarged subapically, with weak apical notch (Fig. 85). Apical aedeagal processes well visible above the phallobase margins, wide, narrowing apically, each with narrow subapical process. Aedeagus with pair of long ventral hooks, 2/3 of phallobase length (in lateral view), arising in its apical third, slightly curved, sharply narrowed apically, pointed and directed downwards and medially. Style large, with almost straight hind margin and obtuse caudo-dorsal angle (Fig. 87). Capitulum of style without neck, with large lateral tooth, spear-shaped in dorsal view (Fig. 88).

**Female genitalia** (Figs 80–82). Sternite VII with weakly concave hind margin. Anal tube long and narrow, nearly 3 times as wide as long, almost not narrowing apically, with widely rounded apex (in dorsal view). Anal tube surpassing hind margins of gonoplacs (in lateral view). Anal column short. Gonoplacs wide, square (in lateral view), flat, without carinae (Figs 80, 81). Anterior connective laminae of gonapophyses VIII with wide combs, each with three rounded teeth in apical group and five keeled teeth in lateral group (Fig. 82). Median field of posterior connective laminae of gonapophyses IX with one lobe flattened laterally in its middle part, comb-shaped (in lateral view). Lateral fields of the laminae in shape of long and wide lobes with dense setae. Gonocoxa VIII without lobe on hind margin. Endogonocoxal process bifurcate apically.

**Total length.** Males – 9.0 mm. Females – 10.5–11.0 mm.

**Note.** The specimens from Mindanao Island have forewings more narrow apically in comparison with the specimens from Samar Island and Luzon Island accordingly. Thus, apparently the specimens from Mindanao belong to another species, closely related to *B. hyalinocosta* described from “Luzon, Los Baños, Mount Maquiling (Baker)” (Melichar 1914). To solve this question the males from Mindanao Island have to be examined.

***Bornepilis rubrovenosa* (Melichar, 1914), comb. n.**

*Eupilis rubrovenosa* Melichar, 1914: 278.

**Note.** The species was described from “Luzon, Laguna, Mount Maquiling (Baker)” (Melichar 1914).

**Genus *Gabaloeca* Walker, 1870**

*Gabaloeca* Walker, 1870: 170.

**Type species:** *Gabaloeca retifera* Walker, 1870, by monotypy.

**Diagnosis.** Metope wide and long, flat, with transverse carina which is apparently upper parts of sublateral carinae, distinctly separated from its upper margin, and with median carina running from transverse carina, but not reaching metopoclypeal suture. Coryphe transverse, twice as wide as long at midline, anterior margin almost straight, posterior margin obtuse-angulated. Pronotum with strongly angularly convex anterior margin. Mesonotum large, almost twice as long as pronotum medially. Forewings long, nearly four times as long as wide medially, surpassing abdominal apex at one fifth of wing length, rounded apically, not narrowing, without hypocostal plate. Forewing vein sequence: *R* 3 *M* 3 *CuA* 2. Hindwings well developed, 3-lobed. Hind tibia with two lateral spines. Ovipositor elongate, beak-shaped.

**Composition.** In addition to the type species also *Eupilis nigrinervis* Stål, 1870 belongs to the genus.

**Distribution.** New Guinea, Philippines.

**Comparison.** Closely related to *Eupilis* by hindwing venation and beak-shaped ovipositor.

***Gabaloeca retifera* Walker, 1870**

(Figs 91–93)

*Gabaloeca retifera* Walker, 1870: 171.

**Type material examined.** Holotype, female, “N Gui / Wallace” // “67/66” // “N” (BMNH).

**Supplementary description** (Figs 91–93). Metope longer than wide between the eyes, enlarged above clypeus. Coryphe twice as wide as long at midline, anterior margin almost straight, posterior margin obtuse-angulated. Pronotum twice as long as coryphe, without carinae; anterior margin nearly acute-angled; posterior margin almost straight. Mesonotum twice as long as pronotum, with median and lateral carinae. Forewings long, not narrowing apically, without hypocostal plate, with semitransparent cells. Basal cell oval. Forewing vein sequence: *R* 3, firstly furcating near to basal cell, *R*<sub>1</sub> short; *ir* 6; *r-m* 6; *M* 3, firstly furcating closely to wing middle, *M*<sub>1</sub> furcating also apically; *im* 8; *m-cua* 7; *CuA* 2, furcating after wing middle; *icua* 3. Hind tibia with two lateral and 7 apical spines. First metatarsomere with two latero-apical and 7–9 intermediate spines.

**Coloration.** General coloration yellow brownish. Forewings semitransparent [cinereous according to Walker (1870)], with dark brown veins. Metope with two black bands on both sides of transverse carina. Anteclypeus dark brown to black.

**Total length.** 10.0 mm.

**Note.** The species was described after single female from New Guinea (Walker 1870) which is listed above as the holotype.

***Gabaloeca nigrinervis* (Stål, 1870), comb. nov.**

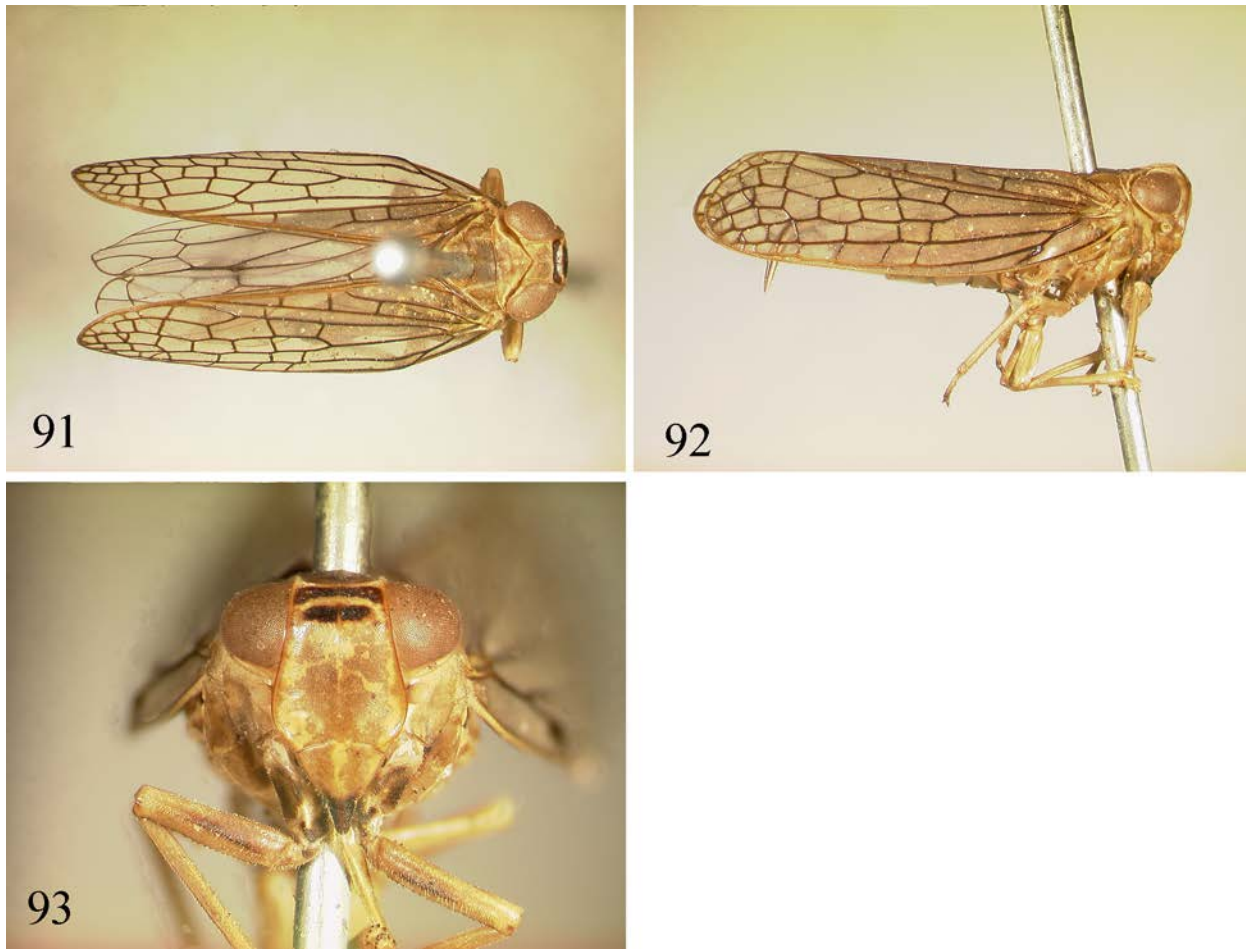
(Figs 90, 94–105, 114)

*Eupilis nigrinervis* Stål, 1870: 756.

*Euplis* [sic] *nigrinervis* Hori, 1971: 66.

**Material examined.** Philippines: 9 males, 15 females, “Island / Samar / Baker” // “Loan from / USNMNH / 2040603” (USNM and ZIN).

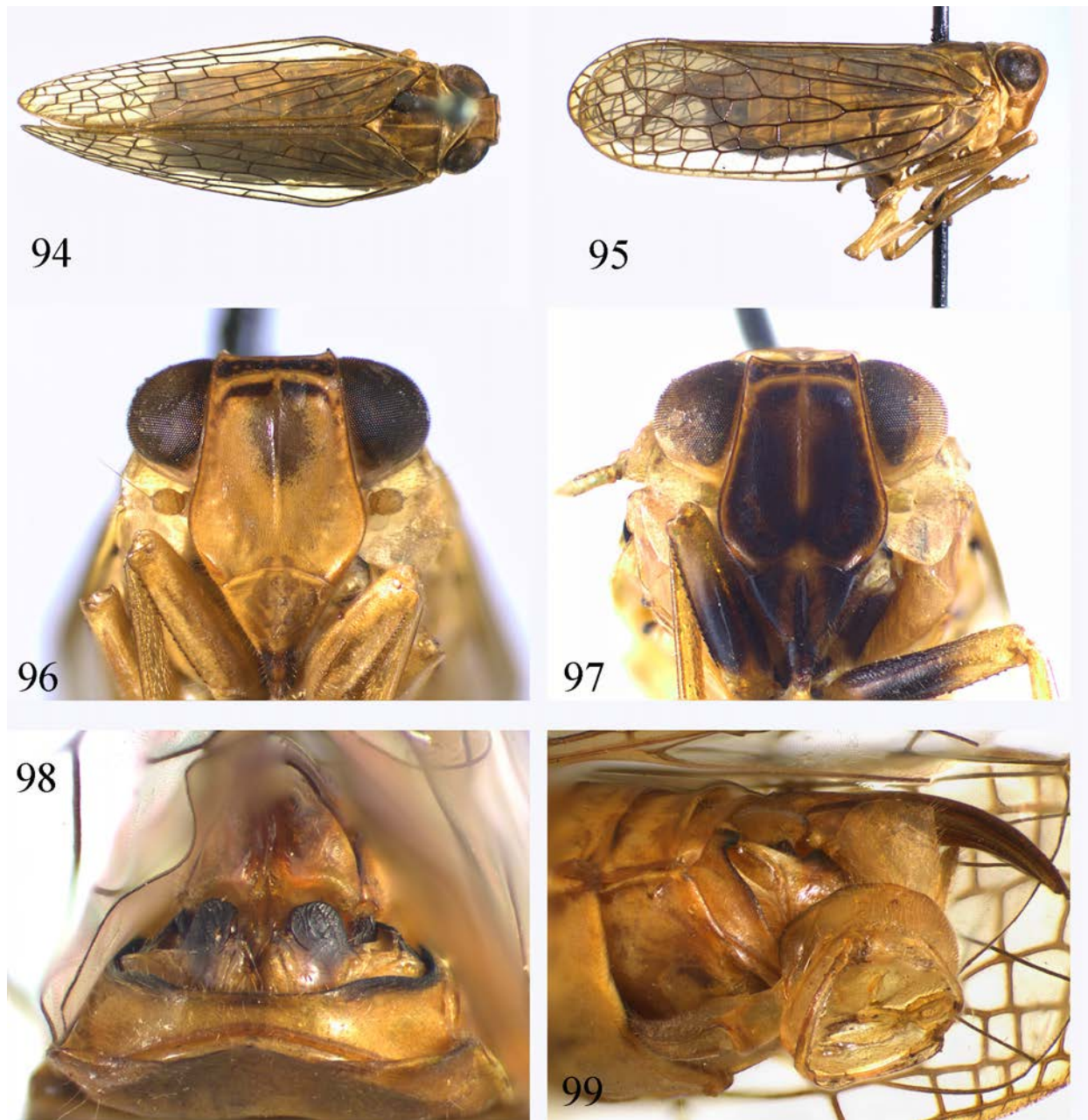
**Supplementary description** (Figs 90, 94–97, 114). Metope wide and long, twice longer at midline than wide between the eyes, with transverse carina, distinctly separated from its upper margin, and with median carina running from transverse carina, but not reaching metopoclypeal suture (Figs 96, 97). Metope flat, with lateral margins diverging from below the eyes. Metopoclypeal suture distinct, convex. Postclypeus large, flattened dorso-ventrally, without carinae. Ocelli present. Pedicel cylindrical. Rostrum reaching hind coxae. 2nd and 3rd segments of rostrum are almost equal in length; 3rd segment slightly curved and narrowed apically (in lateral view). Coryphe small, narrower than the eye, twice as wide as long medially, with keel-shaped margins, without



Figs 91–93. *Gabaloeca retifera* Walker, 1870, holotype. 91 – dorsal view; 92 – lateral view; 93 – frontal view.

carinae (Fig. 94). Anterior margin of coryphe weakly convex; posterior margin deeply angularly concave; lateral margins weakly diverging posteriorly. Pronotum 1.5 times as long as coryphe at midline; anterior margin strongly angularly convex, with pointed apex; posterior margin nearly straight. Pronotum pressed medially, without carinae. Paradiscal fields of pronotum narrow. Paranotal lobes of pronotum wide, with lower margins slightly bent. Mesonotum large, almost twice as long as pronotum medially, with median and lateral carinae. Tegulae large. Forewings long, nearly four times as long as wide medially, surpassing abdominal apex at one fifth of wing length; rounded apically, not narrowing, without hypocostal plate (Fig. 95). Clavus long,  $\frac{3}{4}$  of wing length. Basal cell large, narrowly oval. Forewing vein sequence (Fig. 90):  $R_3$ , firstly furcating closely to basal cell, anterior branch

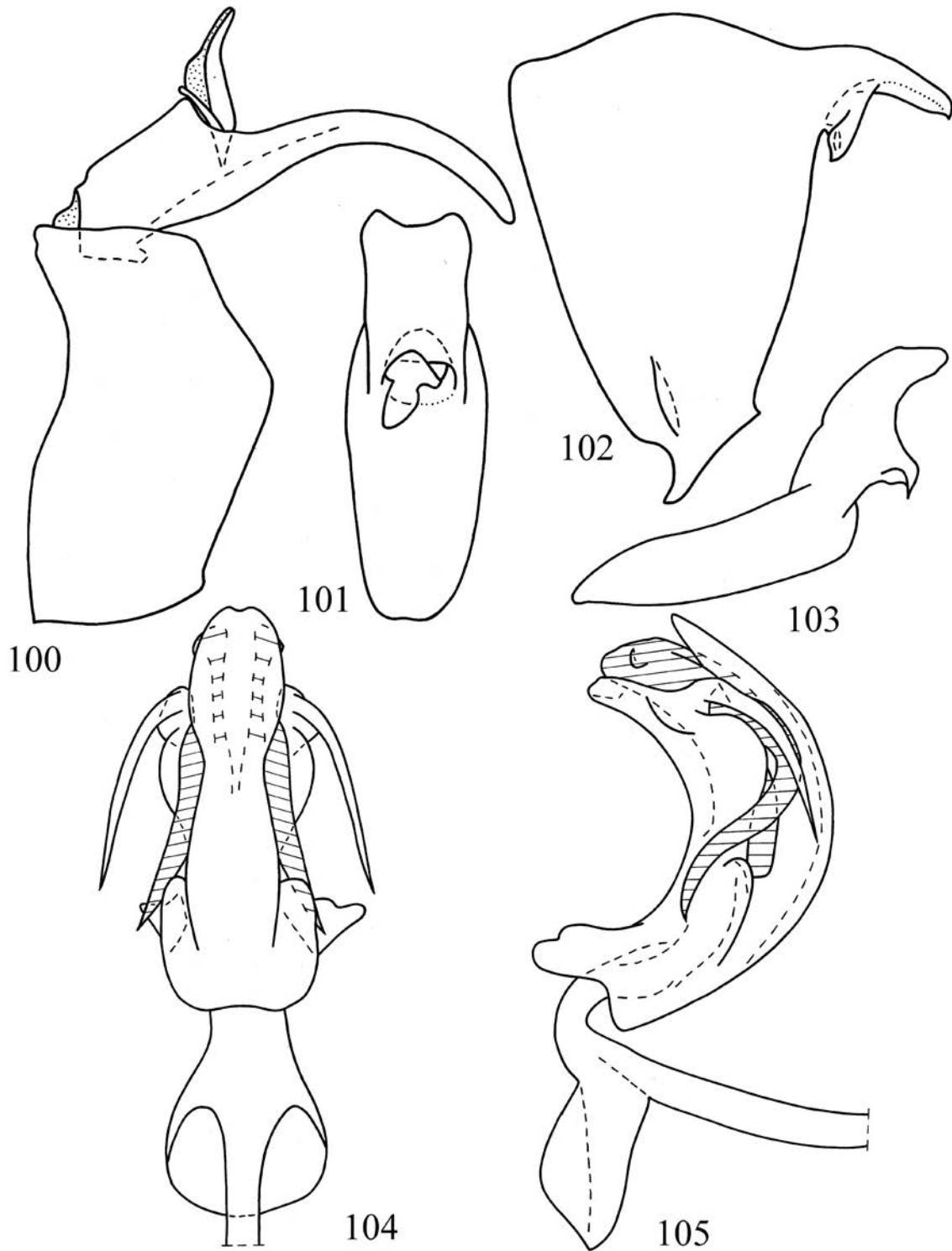
( $R_1$ ) also shortly furcating apically near to costal margin;  $ir$  6–7;  $M$  3, firstly furcating before wing middle, anterior branch ( $M_1$ ) also furcating apically;  $r-m$  6–9;  $im$  8–10;  $m-cua$  8;  $CuA$  2, furcating in apical third of wing;  $icua$  3–4;  $cua-cup$  2–3;  $cup-pcu+a_1$  4–5.  $Pcu$  joined  $A_1$  in basal third of wing. Hindwing vein sequence (Fig. 114):  $R$  2, furcating after coupling lobe;  $r-m$  1;  $M$  2;  $CuA$  1;  $CuP$  1;  $cup-pcu$  1;  $Pcu$  1;  $A_1$  2;  $A_2$  1.  $CuA$  fused with  $CuP$  in its apical half, but separated apically.  $A_{1,1}$  fused with  $Pcu$  medially. Hind tibia with two lateral spines in its distal half and 7 apical spines. First and second metatarsomeres are almost equal in length. First metatarsomere wide, with two latero-apical and 12–14 intermediate spines arranged in 2–3 rows. Arolium of pretarsus with convex hind margin, not surpassing claw apices (in dorsal view), and with pair of narrow dorso-lateral plates.



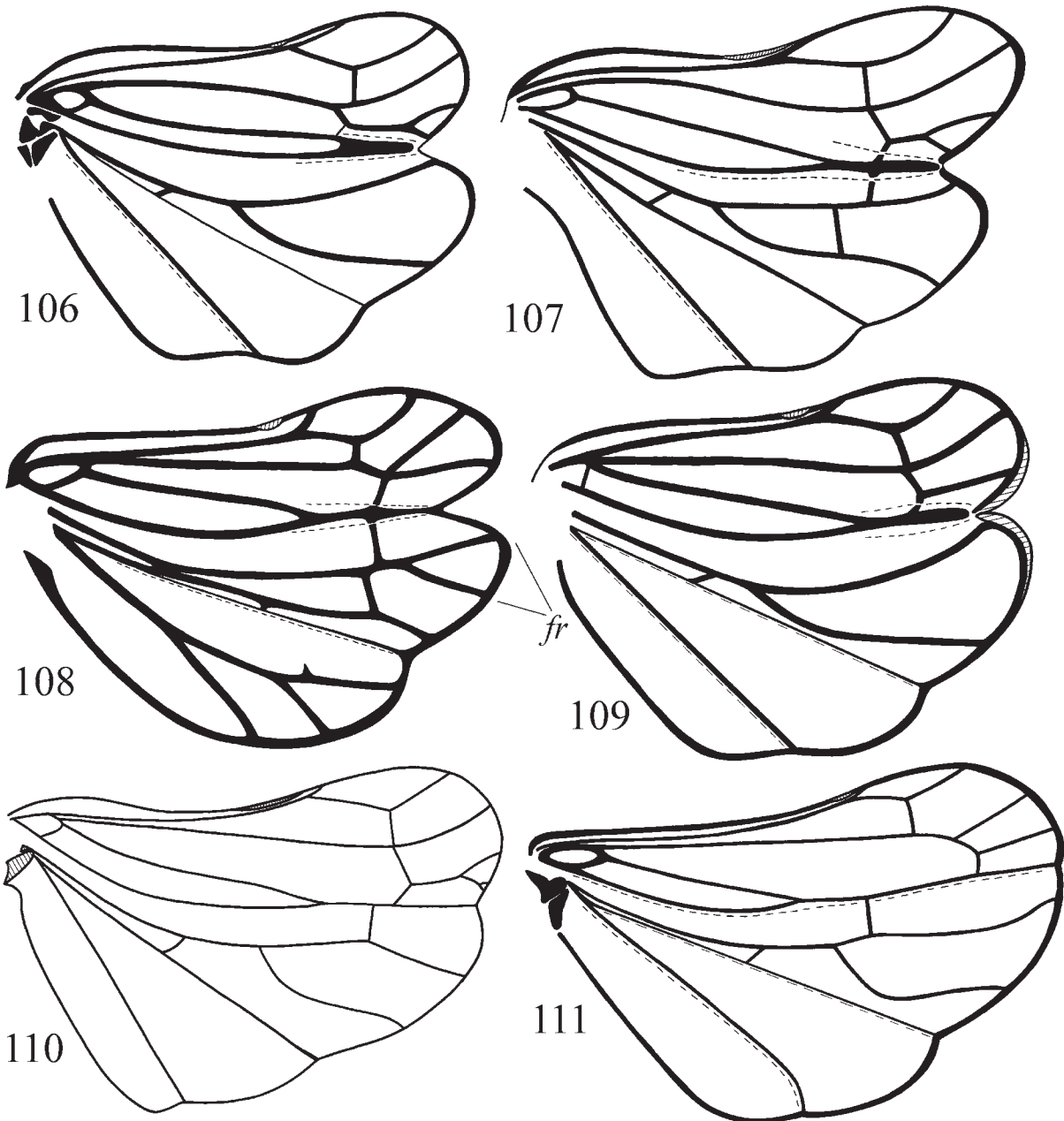
**Figs 94–99.** *Gabaloeca nigrinervis* (Stål, 1870). 94 – female, dorsal view; 95 – same, lateral view; 96, 97 – same, frontal view; 98 – ovipositor, ventral view; 99 – copula.

**Coloration** (Figs 94–99). General coloration light yellow. Metope and clypeus from brown yellowish, with dark brown spots, to almost totally black, except yellow transverse carina, lower angles of metope, and the spot on the middle of metopoclypeal suture. Lateral margins of metope dark brown. Ocelli, scapus, and pedicel light yellow. Rostrum with black apex. Fore-

wings transparent, with veins from brown yellowish to dark brown. Hindwings cinereous, with dark brown veins. Episternae and epimerae of thorax with black spots on the margins. Middle and hind femora with black areas. Hind trochanters each with large black spot on its inner side. Third tarsomeres of fore and middle legs and claws dark brown. Arolium with



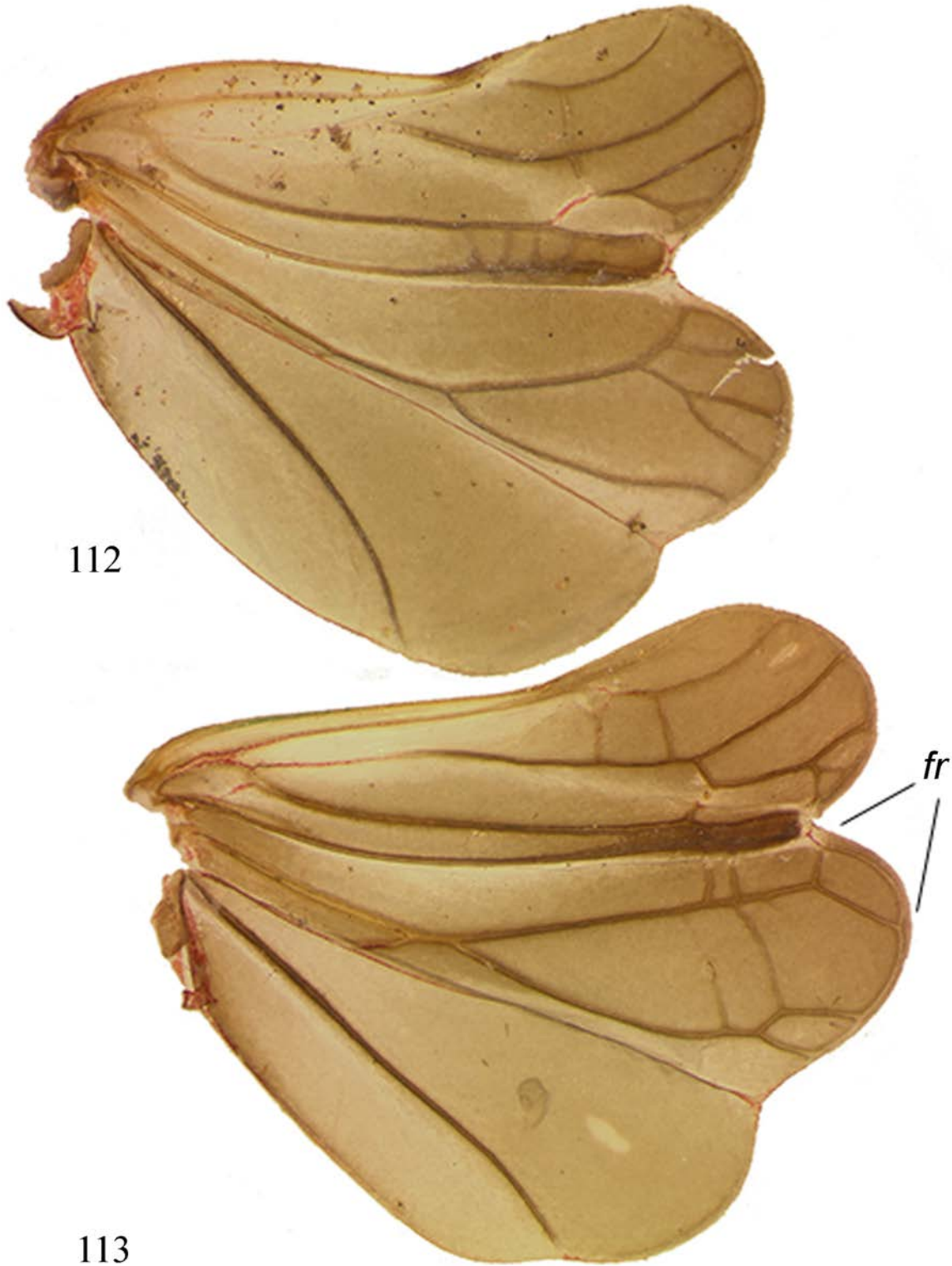
**Figs 100–105.** *Gabaloeca nigrinervis* (Stål, 1870), male genitalia. 100 – pygofer and anal tube, lateral view; 101 – anal tube, dorsal view; 102 – style, lateral view; 103 – style, dorsal view; 104 – penis and connective, ventral view; 105 – penis and connective, lateral view.



**Figs 106–111.** Issinae, hind wing (not to scale). 106 – *Sarima illibata* Melichar, 1903 (Sri Lanka); 107 – *Tempsa* sp.; 108 – *Waorania jaguarina* Gnezdilov et Bartlett, 2018; 109 – *Givaka hamptoni* Distant, 1906; 110 – *Eupilis* sp. (Kuala Lumpur); 111 – *Syrgis* cf. *acutus* (Walker, 1851) (after Gnezdilov and Bartlett 2018 and originals). Abbreviation: *fr* – apical furcation of *Pcu*.

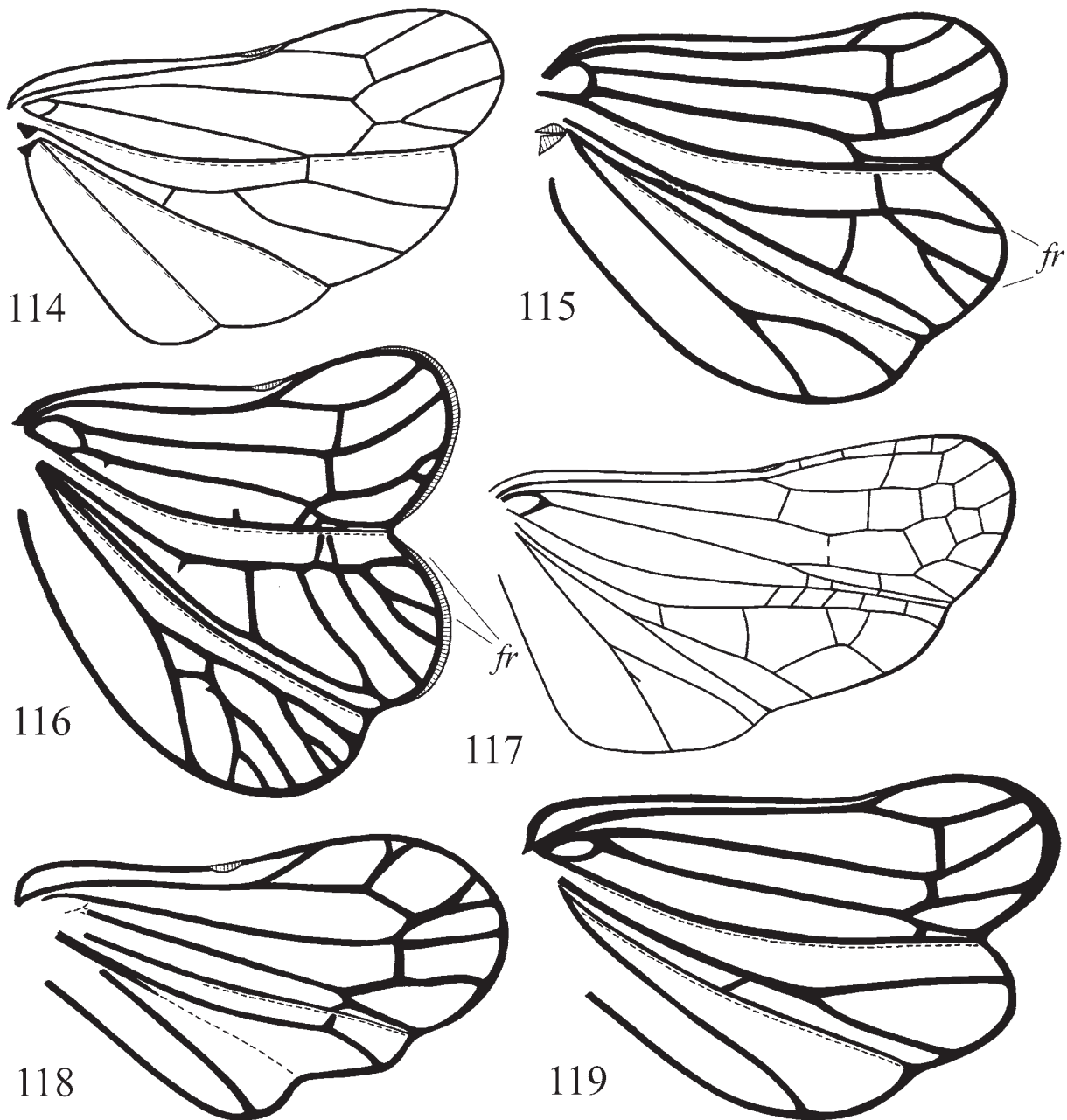
dark brown to black dorso-lateral plates. Apices of leg spines black. Apical part of male anal tube dark brown to black. Gonoplares from yellow to brown yellowish. Female anal tube from brown yellowish to dark brown.

In melanistic specimens (with black metope) (Fig. 97) genae also dark, fore coxae, trochanters and femora black, except brown yellowish apices. In pale specimens metope and postclypeus yellow, with two



**Figs 112–113.** Issinae, hind wing. 112 – *Darwallia patula* (Walker, 1857); 113 – *Nikomiklukha maklayi* Gnezdilov, 2010 (after Gnezdilov, 2010). Abbreviation: *fr* – apical furcation of *Pcu*.



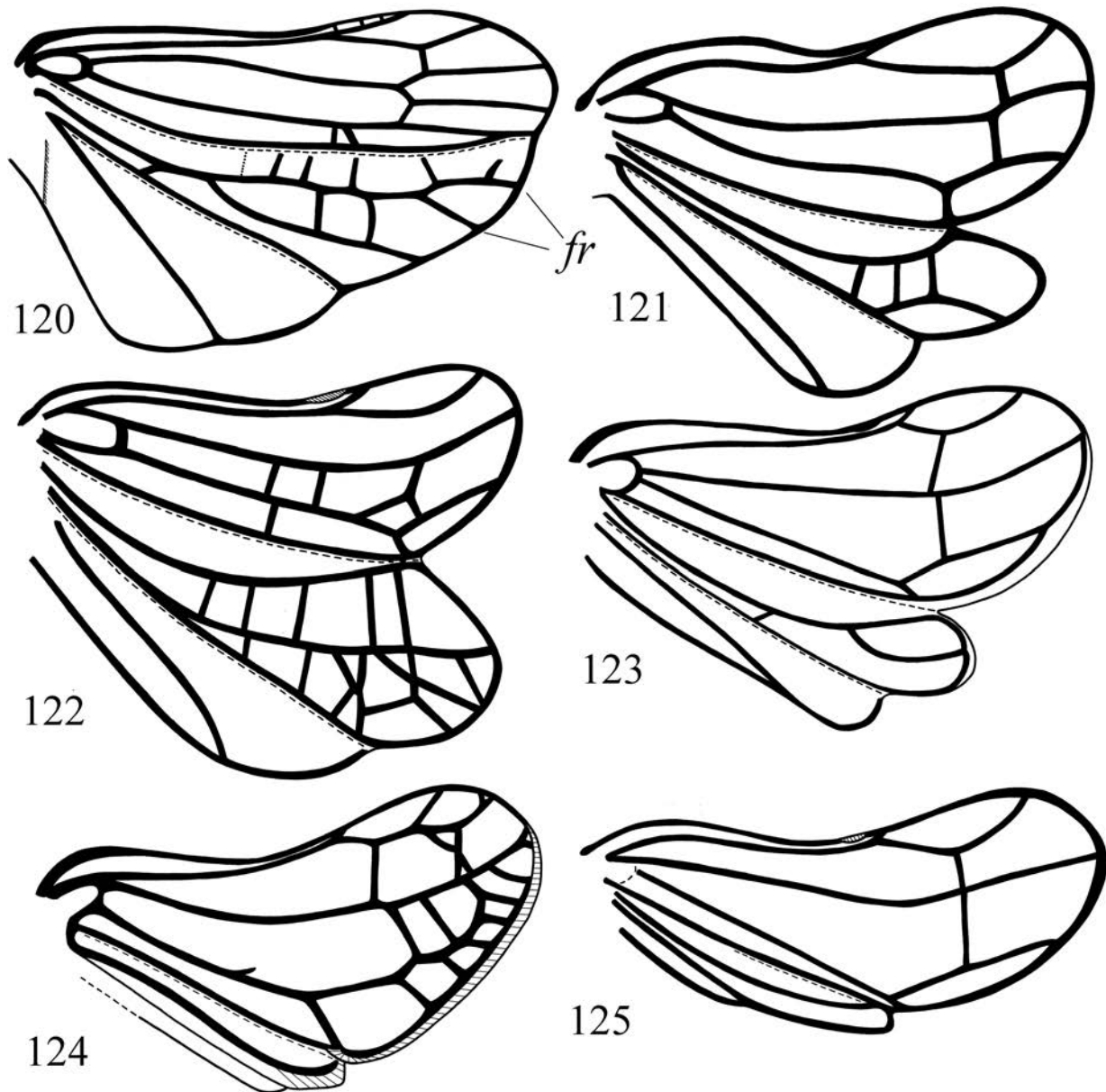


**Figs 114–119.** Issinae, hind wing. 114 – *Gabaloea nigrinervis* (Stål, 1870); 115 – *Aplos simplex* (Germar, 1830); 116 – *Dracela* sp.; 117 – *Oronoqua orellana* Gnezdilov et Bartlett, 2020; 118 – *Proteinissus punctatus* (Caldwell, 1945); 119 – *Picumna chinai* Doering, 1939 (after Gnezdilov 2018a, Gnezdilov and Bartlett 2020 and originals). Abbreviation: *fr* – apical furcation of Pcu.

black transverse stripes above and below transverse carina of metope (Fig. 96).

**Male genitalia** (Figs 99–105). Pygofer wide, twice as long as wide medially, with strongly convex hind margins (in lateral view) (Fig. 100). Anal tube large, as long as pygofer, long and narrow, curved (in

lateral view) (Fig. 99); slightly narrowing apically, with weak apical concavity (in dorsal view) (Fig. 101). Anal column (paraproct) short. Phallobase massive, wide, curved (in lateral view), with deep lateral incisions between dorso-lateral and ventral lobes (Fig. 105). Dorso-lateral phallobase lobes fused dorsally,



Figs 120–125. Issinae, hind wing. 120 – *Bornepilis hyalinocosta* (Melichar, 1914); 121 – *Cascaruna grumosa* Gnezdilov, 2017; 122 – *Chimetopon camerunensis* Schmidt, 1910; 123 – *Neokodaiana yaeyamana* Gnezdilov et Hayashi, 2015; 124 – *Narayana* sp.; 125 – *Samantiga abdominalis* Distant, 1906 (after Gnezdilov 2017, Gnezdilov and Hayashi 2015, and originals). Abbreviation: *fr* – apical furcation of *Pcu*.

each lobe with two subapical processes – narrow semicircular one and long spine-shaped one directed downwards. Basally the phallobase with pair of lobe-shaped processes below the lateral incisions. Ventral phallobase lobe long, enlarged subapically, with weak apical concavity (Fig. 104). Aedeagus large, well visible above the phallobase margins, with wide, not

narrowing apically apical process, each with small semicircular subapical process. Aedeagus with pair of long ventral hooks, 2/3 of phallobase length (in lateral view), arising in its apical third, wave-shaped, gradually narrowed apically, pointed apically and directed downwards. Connective with narrow cup (in lateral view). Style massive, with strongly convex

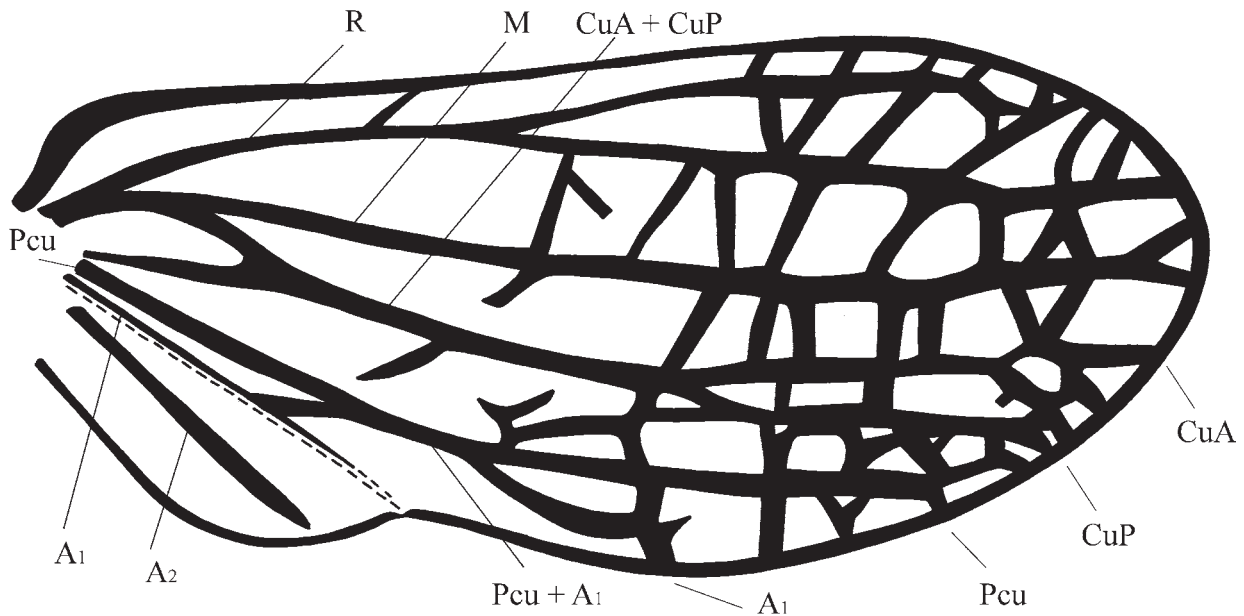


Fig. 126. *Issus pospisili* Dlabola, 1958, hind wing (after Gnezdilov 2017).

hind margin and straight caudo-dorsal angle (Fig. 102). Capitulum of style without neck, lateral tooth large. Capitulum of style narrowing apically (in dorsal view) (Fig. 103).

In copula male anal tube is fixed by its apex between V and VI female abdominal sternites and the capitulum of styles – between female pygofer lobes and the gonoplacs (Fig. 99).

**Female genitalia** (Fig. 98). Sternite VII with widely and weakly concave hind margin. Gonocoxae VIII each with large rounded lobe-shaped black process near to the base of anterior connective lamina of gonapophyses VIII (Fig. 98).

**Total length.** Males – 9.0–10.0 mm. Females – 10.0–11.5 mm.

**Note.** The species was described after a male without concrete locality in the Philippines mentioned (Stål 1870). The type labels under the specimen deposited in the Naturhistoriska riksmuseet Stockholm (Sweden) are as follows: “Insl. Philipp.” // “Semper.” // “Type” // “Typus” // “*Eupilis nigriventris* Stål” [hand written].

***Syrgis cf. acutus* (Walker, 1851)**  
(Fig. 111)

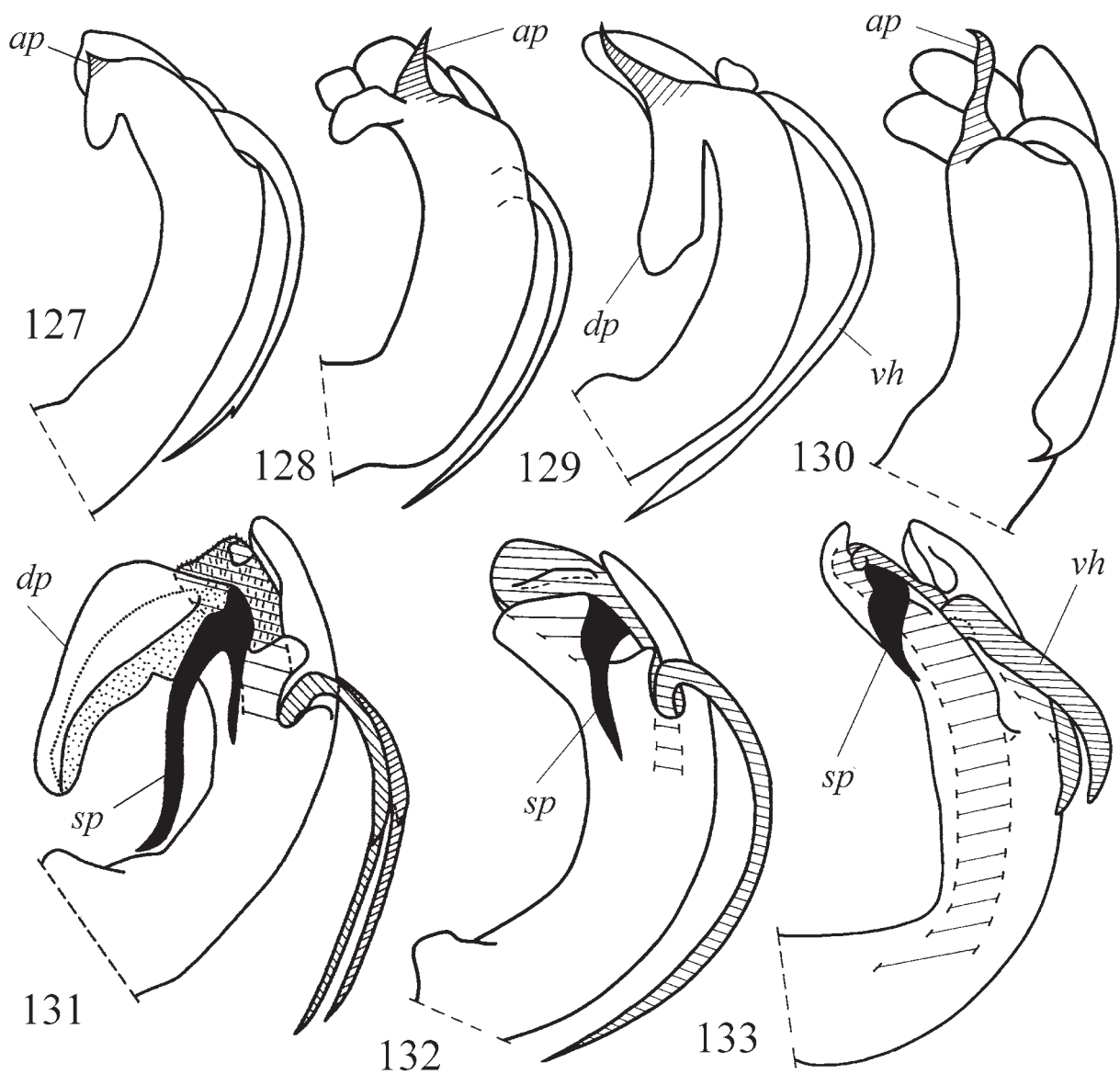
*Issus acutus* Walker, 1851: 369.

*Syrgis acutus*: Melichar, 1906: 308.

**Material examined.** Philippines: 7 males, 3 females, “Zamboanga / Mindanao / Baker” // “Loan from / USNMNH / 2040603” (USNM and ZIN); 7 males, 2 females, “Island of / Basilan / Baker” // “Loan from / USNMNH / 2040603” (USNM and ZIN).

## DISCUSSION

Two conditions of hind wing venation (*Pcu* and  $A_{1,1}$  fused medially on a long distance with simple  $A_2$  and *Pcu* and  $A_{1,1}$  fused in a point with branchy  $A_2$ ) discovered in *Paguinella ramosa* gen. et sp. nov. shows the possibility of transformation of fused on a long distance *Pcu* and  $A_{1,1}$  to shortly fused condition and even to completely free veins at one hand and most likely development of branchy  $A_2$  from the simple vein from another hand. Apparently connection (fusion) and disconnection of *Pcu* and  $A_{1,1}$  may happen independently in different groups of Issidae and even probably several times during the evolution of the group due to mechanical reasons and connected with the width of the wing lobes and development of marginal clefts (cubital and vannal ones) providing folding and turning of hind wings under forewings which is in its turn due to change of habitat, for example, from living in canopy to living in lower trees and shrubs or



**Figs. 127–133.** Issidae, penis, lateral view. 127 – *Fowlerium productum* (Van Duzee, 1908); 128 – *Aplos simplex* (Germar, 1830); 129 – *A. bullata* (Say, 1830); 130 – *Picumna maculata* (Melichar, 1906); 131 – *Aztecus montezuma* (Kirkaldy, 1913); 132 – *Proteinissus bilimeki* Fowler, 1904; 133 – *Eupilis walkeri* sp. nov. (after Doering 1938, modified, Gnezdilov and O'Brien 2008, Gnezdilov 2016c and originals). Abbreviations: *ap* – horn-shaped apical process of dorso-lateral phallobase lobes; *dp* – process of dorsal side of phallobase; *sp* – hook-shaped subapical process of dorso-lateral phallobase lobes; *vh* – ventral aedeagal hooks.

grasses when the importance and dominance of flying are changing to prevalence of jumping in living strategy of planthoppers. Analogical example of unstable condition of *Pcu* and  $A_{1,1}$  connection (disconnection) was described for two species of Neotropical genus *Waorania* Gnezdilov et Bartlett, 2018 (Gnezdilov and Bartlett 2018, figs 12, 25).

Apparently, the flattening and compaction of *CuA* and *CuP* together with deep cubital cleft of wing margin known for Oriental and American Issinae may be treated as derived conditions in comparison to apically fused without flattening or free veins, with weak cubital cleft. In particular, completely fused apically *CuA* and *CuP* with two folds by sides

and deep cubital cleft are found in the genera *Sarima* Melichar, 1903, *Tempsa* Stål, 1866, *Givaka* Distant, 1906, and *Waorania* (Figs 106–109), while *Eupilis* Walker, 1857 and *Syrgis* Stål, 1870 has these veins fused apically, but not flattened, with weak cubital cleft (Figs 110, 111). In the genus *Gabaloecca* Walker, 1870 veins are still not flattened, but cubital cleft is deeper (Fig. 114). Another cases are two Oriental species – *Darwallia patula* (Walker, 1857), with *Pcu* and  $A_{1,1}$  fused on a long distance and *CuA* and *CuP* are clearly separated apically, not flattened, but connected by several transverse veins (Fig. 112), and *Nikomiklukha maclayi* Gnezdilov, 2010, with *Pcu* and  $A_{1,1}$  fused shortly and *CuA* and *CuP* are flattened and closely situated apically (Fig. 113). The genus *Darwallia* Gnezdilov, 2010 with long fusion of *Pcu* and  $A_{1,1}$  and widely separated *CuA* and *CuP* without flattening distally have to be treated as taxon with primitive venation conditions in comparison to *Nikomiklukha* Gnezdilov, 2010 which has shortly fused *Pcu* and  $A_{1,1}$  and flattened *CuA* and *CuP*. Thus this example clearly demonstrates the direction of *Pcu* and  $A_{1,1}$  disconnection from long fusion to short one and in fact the genus *Darwallia* Gnezdilov occupying very basal position on the phylogenetic tree of Sarimini proposed by Wang and Bourgoin (2020) based on combined sequences of four generic fragments. Analogically in the subtribe Thioniina the species of the genus *Cheiloceps* Uhler, 1895 have long fusion of *Pcu* and  $A_{1,1}$  and the genera *Aplos* Gnezdilov, 2018 and *Fowlerium* Gnezdilov, 2018 have *Pcu* and  $A_{1,1}$  closely situated proximally, but still free (Gnezdilov 2018, figs 9–13) (Fig. 115). Perhaps enlarging of remigio-vannal lobe of hind wing and appearance of additional transverse veins between *Pcu* and  $A_{1,1}$  lead to separation of previously fused *Pcu* and  $A_{1,1}$ . In particular this is apparently true for *Aplos*, *Fowlerium*, and *Dracela* Signoret, 1861 (Thioniina), *Oronoqua* Fennah, 1947 (subtribe Oronoquina), *Guianaphryna* Gnezdilov, 2018 (tribe Guianaphrynini), *Scantinius* Stål, 1866 (tribe Parahiraciini), etc (Gnezdilov 2018a, 2018b, 2018c; Gnezdilov and Bartlett 2020) (Figs 115–117). The vein condition of *Cordela rubra* Gnezdilov, 2019 (tribe Cordelini) with main veins simple and separated in remigio-vannal and anal lobes (Gnezdilov 2019, figs 6, 23) is apparently due to secondary simplification.

Apical furcation of hind wing *Pcu* discovered in *Paguinella ramosa* gen. et sp. nov. (Figs 4, 5, 10, 11, *fr*) is very typical character of New World Issidae,

but this feature is also found in Oriental *Tetrica fusca* Stål, 1870, *Bornepilis hyalinocosta* (Melichar, 1914) (Fig. 120), *Darwallia patula*, *Nikomiklukha maclayi* (Figs 112, 113), and Australian *Apsadaroptyx elongatulus* (Kirkaldy, 1906) and *Tetrica tumidifrons* Jacobi, 1928 (Gnezdilov and Fletcher 2010, figs 20, 22; Gnezdilov et al. 2015, fig. 22).

American genus *Picumna* Stål, 1864 is very peculiar by its intermediate position between Oriental and American taxa in hind wing venation pattern (Fig. 119). In particular examined *Picumna chinai* Doering, 1939 has *CuA* and *CuP* closely situated, but free apically as it is in the members of the subtribes Thioniina Melichar *sensu* Gnezdilov (2018a) and Oronoquina Gnezdilov, but from another hand *P. chinai* is characterized by simple *Pcu* fused on a long distance with  $A_{1,1}$  and simple  $A_2$  which are rather typical for Oriental taxa (Gnezdilov 2012). Molecular data do not allow placing this genus in a particular tribe (Wang et al. 2016; Gnezdilov et al. 2020). However my examination of phallobase structure of *P. chinai* and *P. maculata* (Melichar, 1906) (Doering 1938, Plate LIV: figs 1, 5; Plate LV: figs 2, 8, 10) shows clearly close relationships of *Picumna* with *Aplos*, *Balduza*, and *Fowlerium* (members of Thioniina) according to the presence of horn-shaped apical process of dorso-lateral phallobase lobes directed upwards (Gnezdilov and O'Brien 2006, fig. 1) (Figs 127–130, *ap*). Possibly this horn-shaped apical process of phallobase of American taxa is homologous to those of western Palaearctic *Latilica*, *Kervillea*, and *Pseudohemisphaerius* (Gnezdilov 2003, figs 86, 87; Gnezdilov and Mazzoni 2004, figs I, 1, 2; III, 1, 2; IV, 1, 3, 4). From another hand large process of dorsal side of the phallobase of *Aplos bullata* (Say, 1830) is apparently homologous with such process of *Aztecus* Gnezdilov et O'Brien, 2008 (Gnezdilov and O'Brien 2008, figs 14, 20) (Fig. 131, *dp*). Thus perhaps *Picumna* is close to ancestral taxa spread from Asia to America via Beringian Isthmus in Eocene–Miocene (Gnezdilov 2016a) and closely related to the members of the subtribe Thioniina.

The genus *Proteinissus* Fowler, 1904, member of the subtribe Thioniina according to recently obtained molecular data (Gnezdilov et al. 2020), is characterized by hind wing with simple *Pcu*, not fused with  $A_{1,1}$  and simple  $A_2$  (Fig. 118) and by the phallobase with large hook-shaped subapical process directed downwards (Fig. 132, *sp*). The last character is also typical for Oriental genera *Tempsa* Stål and *Eupilis* Walker,

1857 and the Palaearctic genus *Phasmena* Melichar, 1902 (Gnezdilov 2016c, figs 17–19) (Fig. 133, *sp.*). Assuming that these hooks in all mentioned taxa are homologous, we can treat simple  $A_2$  of *Proteinissus bilimeki* as an “Oriental trace”. The “Oriental trace” is probably true also for the genus *Issus* Fabricius, 1803 and the subtribe Issina Spinola, 1839 accordingly, which has got sister position to American Thioniina on the tree based on molecular analysis of mitochondrial and nuclear genes (Gnezdilov et al. 2020). Thus hind wing of *Issus pospisili* Dlabola, 1958, *I. kabylicus* Dlabola, 1989, and *I. lauri* Ahrens, 1814 is characterized by general reduction of hind wing lobe size, with increasing of transverse veins number and complete fusion remigial and remigio-vannal lobe, but with fused on a long distance *Pcu* and  $A_{1,1}$ , and rudimentary anal lobe, with simple  $A_2$  (Gnezdilov 2017, fig. 22 and original data) (Fig. 126). The species of the genus *Issus* occurring on shrubs and trees, preferably on *Querus* species in the Mediterranean (Gnezdilov et al. 2019), and apparently living on low vegetation as well as in canopies where their larvae were recorded at the 8 m height (Badmin 2010).

Within the family Issidae branchy second anal vein of hind wings is a character of New World taxa (Gnezdilov 2012), however, weakly branched second anal vein was discovered in Australian *Apsadaropteryx elongatulus* (Kirkaldy, 1906) which has short projection on main branch – initial stage of branching (Gnezdilov and Fletcher 2010, fig. 20). Described above *Paguinella ramosa* gen. et sp. nov. has main branch of second anal vein with two well developed projections (Figs 4, 10). Thus we can assume that Australian issid fauna is derived from Oriental source and demonstrates independently branching of second anal vein.

African tribe Chimetopini Gnezdilov, 2017 is apparently close to ancestral Oriental Issidae as it is characterized by *CuA* and *CuP* separated, *Pcu* simple, not fused with  $A_{1,1}$ , and simple  $A_2$ , but it is specialized in having deep cubital cleft (Figs 121, 122). The genus *Chimetopon* Schmidt, 1910 is the most primitive in comparison to *Cascaruna* Gnezdilov, 2017 and *Ikonza* Hesse, 1925 as it has almost equal in width remigial and remigio-vannal lobes while two other genera are characterized by reduction of remigio-vannal lobe and *Ikonza* – by reduction also of anal lobe (Gnezdilov 2017, figs 36, 43, 64). Analogous, but apparently not homologous, reduction of remigio-vannal and anal lobes is a character of Oriental

tribe Kodaianellini Wang, Zhang et Bourgoïn, 2016 where the genera *Kodaianella* Fennah, 1956, *Neokodaiana* Yang, 1994 and *Kodaianelissus* Wang, Bourgoïn et Zhang, 2017 have remigio-vannal lobe with *Pcu* fused with  $A_{1,1}$ , and anal lobe developed, with  $A_2$  well visible, but already *Narayana* Distant, 1906 and *Samantiga* Distant, 1906 have remigio-vannal lobe reduced, with *Pcu* and  $A_{1,1}$  separated, and anal lobe rudimentary (Figs 123–125).

Further morphological and molecular studies are needed to build up the phylogeny and classification of the family Issidae and develop evolutionary scenario of this peculiar group of planthoppers.

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