Elhamma Walker (Lepidoptera: Hepialidae) revisited: adult morphology, assessment of recently proposed synonyms and descriptions of two species

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Abstract

I revise the Australian-New Guinean ghost moth genus Elhamma. Two recent synonymies are assessed, and two new species from New Guinea, E. grehani sp. nov. and E. viettei sp. nov., are described. I provide an updated diagnosis for the genus and conclude that the presence of only 2 M-veins in the hind wing in both sexes (when females are known) and a strongly cup-shape juxta in the male genitalia are unique diagnostic characters among Hepialidae. I give a detailed description of the adult morphology based on male E. australasiae, and provide a key to all known species based on adult male characters.

Key words: Exoporia, adult morphology, taxonomy, Australia, New Guinea

Introduction

The genus Elhamma Walker (Figs 1–12) was originally erected to accommodate five species of Hepialidae from Australia and New Zealand, all of which were subsequently transferred to other genera, either by Walker himself in the same publication (Walker 1856), or by Butler (1877) and Meyrick (1890). Meyrick (1890) also recognised that E. inconcluso Walker was the male, and junior synonym, of Hepialus australasiae Walker as the two names represented male and female of the same species (although Meyrick listed the author of the latter as 'Donovan'), and placed the species in the new genus Perissectis, recognised by Tindale (1935) to be a synonym of Elhamma. Kirby (1892) upheld Elhamma as a good genus and designated E. inconcluso as the type species. Tindale (1935) provided the first detailed descriptions and illustrations of Elhamma as well as an overview of the past taxonomy and synonymy of the genus, and treated the genus as part of the Oxycanus Walker genera group in his revision of Australian Hepialidae.

Nielsen (1996) in the Checklist of Australian Lepidoptera (Nielsen et al. 1996) synonymised the two New Guinea genera Zauxieus Viette and Theaxieus Viette with Elhamma, synonymies that were later upheld in a world catalogue on Exoporia (Nielsen et al. 2000). Likely as a consequence of the catalogue format of these publications, no justification was given for the synonymies, and sadly E. S. Nielsen died before such justifications could be published. Zauxieus and Theaxieus were both described based on material in the National Dutch Museum of Natural History, Naturalis (RMNH): Zauxieus comprised only a single species, Z. toxopeusi; Theaxieus comprised the two superficially very similar species T. diakonoffi and T. roebkei (Viette 1952).

During my ongoing systematic studies on Australian Hepialidae (T. J. Simonsen unpublished) it became clear that it would be desirable to justify these synonymies, especially as there has been a recent increase in studies of Australian Hepialidae (Edwards & Green 2011, Moore & Edwards 2014, Moore 2014) which is likely to continue in the future (T. J. Simonsen unpublished, M. D. Moore pers. comm.). Here I re-examine all known Elhamma species, describe two new species, E. viette sp. n. and E. grehani sp. n. from New Guinea, and provide a detailed account of the adult skeletal morphology of E. australasiae. The synonymies proposed by Nielsen (1996) are evaluated based on the results, and a key to all species is provided. The morphological account presented here is more detailed than previous systematic treatments of Hepialidae, except Nielsen & Kristensen’s (1989) highly
detailed account of the primitive genus *Fraus*. It is, however, in line with what will be presented in an upcoming revision of the so-called ‘hepialine’ hepialids in Australia. As *Elhamma* represents the other major lineage of Australo-Papuan-New Zealand hepialids, the so-called ‘oxycanine’ Hepialidae (e.g. Grehan 2012), these two contributions will form a detailed baseline for studies into Hepialidae morphology in the future. Furthermore, the Australian region is one of the diversity hotspots for Hepialidae, and the ‘oxycanine’ hepialids in Australia and New Guinea (in particular the genus *Oxycanus*) are poorly known and should be a priority for future studies. I further hope that the accounts given here can assist such studies in the future.

**FIGURES 1–12.** Exemplars of all *Elhamma* species: 1–4, *E. australasiae*; 1—female, 2–4—males (2 is *E. inconcluso* Holotype); 5, *E. diakonoffi* male (Holotype); 6, *E. roebkei* male (Holotype); 7–8, *E. grehani* males (7 is Holotype, 8 is paratype RMNH INS 910279); 9–10, *E. viettei* males (9 is Holotype, 10 is paratype RMNH INS 910276); 11–12, *E. toxopeusi* males (11 is Holotype, 12 is the non-type RMNH INS 910272).
Material and methods

An account of the specimens examined is given under each species in the Taxonomy section. Specimens of *E. australasiae* are from the collections of the Natural History Museum, London (BMNH), Australian National Insect Collection, Canberra (ANIC), Naturalis Biodiversity Centre, Leiden (RMNH), South Australian Museum, Adelaide (SAM), Australian Museum, Sydney (AM), Museum Victoria, Melbourne (MV), Queensland Museum, Brisbane (QM) and Muséum National d'Histoire Naturelle, Paris (MNHN). Additional information on distribution in Victoria in particular was from Kallies A., Marriott, P. Hewish M., Williams S. (pers. comm.: from records gathered for the Moths of Victoria Project (Book 6)).

Genitalia dissections of *E. australasiae* were carried out by macerating abdomens in hot, 10% aqueous KOH solutions for 15–45 minutes. The dissections were subsequently cleaned in distilled H$_2$O and stained in Chlorazol Black in an aqueous solution. Preparations were either mounted immediately on euparal microscope slides or transferred to 70% ethanol for long term storage. Genomic DNA was extracted from the abdomens of *E. toxopeusi*, *E. viettei* and *E. grehani* prior to maceration by soaking them in 360 µl Qiagen Lysis Buffer ATL and 40 µl Proteinase K at 37°C for 18h before the abdomens were macerated. DNA extractions were simultaneously completed following the manufacturer’s manual (see Krush & Cranston (2012) for details). The male *E. australasiae* used for whole-body examinations and illustrations first had the wings removed and it was subsequently softened in a relaxing jar until the pin could be removed. After removal of the pin the specimen was macerated and stained as described above. Wing venation was examined using two methods: wings from one female *E. australasiae* as well as from the male selected for whole body dissection were cut off the specimen as close to the body as possible, scales were removed in absolute ethanol, and the wings were embedded in euparal on a microscope slide. Wing venation was then directly examined under a stereo microscope as described below. For all other specimens venation was examined by placing the specimen upside down under a stereo microscope and placing a droplet of absolute ethanol on the underside of the wing. Whole specimens and all preparations were examined under stereo microscopes (Zeiss SV 6 and SV 11, and Nikon SMZ800). Photographs to aide illustrations were made with a Canon EOS 450D in conjunction with a Zeiss SV 11 stereo microscope. Scanning electron microscopy preparations of wing scales, legs and antennae were prepared following Simonsen (2001, 2008).

Body and genitalia terminology follows Nielsen & Kristensen (1989), Dugdale (1994) and Kristensen (2003), antennal sensilla morphology follows Hallberg *et al.* (2003), wing venation terminology follows Kristensen (1998), and wing vestiture terminology follows Simonsen (2001) and Kristensen & Simonsen (2003). Distribution maps were constructed in ESRI ArcMap version 10.2.2.

Morphology

(Based on *E. australasiae*, male).

Head (Figs 13–18, 55–59). The head capsule is dominated by the very large compound eyes which are higher than the non-ocular head. The eyes lack interommatidial setae, and there is no subgenal process. 

Intercocular index (Davis 1975); vertical eye diameter/distance between the eyes immediately above the antennae: 1.5

Supraocular index (Kristensen & Nielsen 1979); height of the head capsule above the compound eye/total height of head capsule: 0.08

The eyes are most widely separated dorsally. The antennal sockets are close to the eye margin in a shallow, well defined emargination. Both dorsal and ventral cranial condyles are present and well-developed. The outer margin of the socket is particularly well reinforced. The serrat antenna is relatively small, less than twice the total width of the head. The scape is unmodified, sub-globular with a slightly extended inner distal corner. The pedicel is almost globular, slightly longer than the first flagellum segment and twice the width. The intercaleraly sclerite is a typical elongate hepialoid sclerite. The flagellum is comprised of less than 40 unmodified, laterally flattened, slightly keeled segments tapering towards the tip. The surface of each segment is covered in dense microtrichia. The most numerous types of sensilla are sensilla trichodea, but several sensilla chaetica are also present on the terminal segment. Sensilla auricillica are found near the distal margin of some of the subsequent segments, and the tip of the antenna holds what appears to be a pair of such sensilla, but they appear slightly atypical. No sensilla
coelocinica or sensilla stiloconica were observed. The epicranial sulcus is very weakly developed with no internal crest. Two flat sulci run from the anterior end of the epicranial sulcus to the margin of the compound eyes above the base of the antennae, forming a flat inverse "Y". It is possible that the "arms" of the Y are homologous to the postintercancellar sulcus, despite ocelli being absent as in all exoporians (Kristensen 1998). Below these lines the head capsule is produced into a flat ridge which protrudes over the antennal base. The ridge is flatly triangular with paired latero-dorsal bumps. The front of the head below the antennal sockets to the labrum is densely scaled with piliform scales. There is no frontoclypeal sulcus, but it is conceivable that this entire area comprises the frontocyclus. The labrum is a well-defined, flat ridge. A minute, central lobe just below the labrum may be a vestige of the proboscis. The labium is well developed as a small, roundish base for the labial palps. The palps are relatively long and two segmented with the terminal segment being ca. 50% longer than the basal segment. Vom Rath's organ is present, but small, less than 20% of the length of the terminal segment. The maxillary palps are not discernible, but the mandibles are recognisable as minute, triangular lobes. Posteriorly, a narrow ellipse of scale-covered, unsclerotised cuticle is present along the hind margin of the compound eyes. Despite being unsclerotised, this ellipse, which is only incomplete most ventrally, likely represent the occipital sulcus. The occipital foramen is large. Dorsally and laterally it is framed by a sclerotised ridge which is produced dorsally into the occipital foramen as a small, pointed ridge. Laterally the ridge is unsclerotised with the occipital condyles, and (just below the occipital condyles) with the base of the corporotentorium. Ventrally (beyond the corporotentorium), it continues around the postlabial wart (sensu Nielsen & Kristensen 1989). The occipital condyles are prominent with a well-defined sclerotised base. The postlabial wart is large and square. The postero-median tentorial process is very small. The anterior tentorial arm is narrow basally, but broadened posteriorly with a long, thin dorsal crest, a small secondary dorsal crest, and a smaller, tooth-like ventral crest. There are no anterior tentorial pits on the frontoclypeus.

**Prothorax** (Figs 13–14, 19–20). The laterocervicale is narrow and arched, apically joined to the occipital condyle by a small, but well-defined, thick membranous ligament. Laterally, it is articulated to the dorsal corner of the episternum via a broad, thick membranous ligament. Ventrally it terminates in a third thick membranous ligament, almost joining it to the dorso-anterior corner of prosternal lamella. The propleural rim and anterior dorsal plate are fully synsclerotised and cannot be separated. The combined structure is divided in the dorsal midline, and only broader dorsally than laterally. The scaled patagia are very large and meet dorsally for most of their length. They are separated from the broad, membranous edge of the pronotum by a distinct sulcus which tapers laterally. Pronotum continues posteriorly over mesonotum as a thin membranous ridge. The episternum (propleural wart of Neilsen & Kristensen 1989) is relatively well defined and scaled, with the anterior edge ventrally produced into a long, narrow downwards pointed episternal tooth. The basal margin of katepisternum is smooth and strongly sclerotised, whereas the majority of katepisternum is a weakly sclerotised, densely scaled area dorsal to coxa. Prosternum is anteriorly invaginated and forms a medial ridge leading to the furcal bridge. Postero-dorsally prosternum is proceeded into a thick, membranous lamella which continues to the base of the furcal bridge. The bridge in anterior view is broad and smoothly curved. The profurcal arms arise from the inner dorsal corners of the bridge into the body cavity. Centro-ventrally the prospina extends from the bridge. The spina has a long, thick, unsclerotised central articulation: ventrally the articulation carries a weakly sclerotised triangular lamella; dorsally it has two membranous muscle articulations just before the arched, terminal section of the spina.

**Pterothorax** (Figs 13–14, 21–22). As is the case in all winged insects, the meso- and metathorax are greatly modified to accommodate the flight apparatus. Although the two pterothoracic segments are overall similar in their basic plan they also have fundamental differences with several potentially important characters. They will therefore be treated separately. The ratio between the length of the mesothoracic and metathoracic alinota is approximately 3.

**Mesothorax** (Figs 13–14, 21). **Mesonotum**: The anterior metascutal margin has a well-developed, bi-lobed phragma 1. The metascutal longitudinal sulcus is well developed and continued through the length of the phragma; internally with a well developed ridge which is deepest anteriorly and tapers towards the mesoscutellum. The scutum is narrowed anteriorly (in dorsal view). The tegula is membranous, triangular and slightly projected posteriorly over the wing base. Subtegula is well developed, elongate and upside-down hook-shape (the tip of the hook pointing backwards). The prealar arm is well developed and terminates ventrally in a broad, outwards pointing flap. The scutellum is broad and anteriorly rounded in dorsal view and only sclerotised laterally.
FIGURES 13–14. Overview of head and thorax skeletal morphology of *E. australasiae* (BMNH Micro-33263). 13: dorsal view; 14: lateral view. Abbreviations: Ac, antecoxale; As, anepisternum; As-S, anterolateral scutal sulcus; Awp, anterior notal wing process; Ba, basalare; Bs, basisternum; Ca, chorda axillaris; Cx, coxa; Ec, eucoxa; Em, epimeral margin; Eps, epicranial sulcus; Me, meron; Mp, median notal wing process; Ms-S, mesoscutal sulcus; Pep, preepisternum; Pl, pleural sulcus; Plw, pleural wing process; Pom, post medial notal wing process; Pr, precoxal sulcus; Pwp, posterior notal wing process; Sa, subalare; Sct, scutum; Sctl, scutellum; Stg, subtegula; Su, sualare; T1, 1st abdominal tergum; Tp, tergopleural apodeme. Numbers after an abbreviation refer to: 1 = prothorax; 2 = mesothorax; 3 = metathorax.
FIGURES 15–18. Details of head morphology of *E. australasiae* (BMNH Micro-33263). 15: frontal view, flagellum of right antenna removed except two segments, entire left antenna removed; 16: ventral view, eyes not drawn completely; 17: posterior view; 18: tentorial arm, lateral view. Abbreviations not previously used: Ata; anterior tentorial arm; Ct, corporotentorium; Dc, dorsal cranial condyle; Dt, dorsal tentorial arm; Fc, frontoclypeus; Lfp, sclerotised lateral process of the occipital foramen; Md, mandible, Oc, occipital condyle; Of, occipital foramen; Or, organ of vom Rath; Os, occipital sulcus; P, labial palp; Po, postlabial "wart"; Prb, proboscis vestige; Prl, prelabium, Rf, sclerotised rim of occipital foramen; Tp; tergopleural apodeme Vc, ventral cranial condyle; Vt, ventral tentorial tooth.

*Mesopleurosternum*: The pleural sulcus and associated structures and sulci are complex and not easy to interpret. The pleural sulcus is strongly sclerotised ventrally and clearly folded longitudinally, it appears to originate on the reinforced dorsal margin of the meron. The tergopleural apodeme is elongate with a downwards pointing base and a spatulate apex. Basisternum is an elongate, tongue-shape plate with a basal mediolongitudinal sulcus which terminates approximately halfway from the anterior margin. The preepisternum is a well-defined, trapezoid-triangular sclerite with a well-developed preepisternal sulcus along the dorsal margin bordering the anapleural cleft. The anapleural cleft is narrow. The anepisternum is a large sclerite with an reinforced ventral margin, and a vertical sulcus separating the inward bent distal tip from the rest of the sclerite. Dorso-basally the anepisternum is separated from basalarare by a weak, horizontal sulcus. The basalarare is low and elongate. The precoxal and marginopleural sulci run sub-parallel from the preepisternum/pleural sulcus to the ventral base of the basisternum and enclose a small, elongate and setose sclerite, here interpreted (in agreement with Dugdale 1994) to represent the posterior katepisternum. The antecoxale is elongate and membranous with a weakly sclerotised
dorso-posterior corner. The trochantin is an elongate, free sclerite. The paracoxal sulcus is only a narrow line on the outside, but has a large, free internal discrimen. Eucoxa is sclerotised with a sigmoid anterior margin and a basal sulcus at the base of the trochantin. The coxal sulcus separating the eucoxa and the large, sclerotised meron is enforced dorsally.

FIGURES 19–20. Details of prothorax morphology of *E. australasiae* (BMNH Micro-33263). 19: Prothorax frontal view. 20: Proendosternum, lateral view. Abbreviations not previously used: Adp, anterior dorsal plate; Br, prosternal bridge; Es, episternum; Est; episternal tooth; Ks,Katepisternum; Lc, laterocervicale; Pa, patagium, Pf, profurcal arm; Ps, Prosternum; Psp, prospina; Sl, prosternal lamella.

**Metafurca** (Fig. 22). The furca stem rises from the anterior inner base of the meron. The basisternal discrimen is short and low, and connects basally to the sclerotised furca-basisternal lamella. The furca stem is more or less vertical. Dorsally the furca-basisternal lamella bears a pair of backwardly curved, primary furcal arms which basally bear a small outer lamella which is clearly visible in posterior view. Dorsally the primary furcal arms continue as a long, thin tendon-like apodeme. The secondary furcal arms are thick and terminate in a long, thick, non-sclerotised articulation to the relatively short, dorsal sclerotised epimeral margin.

**Wings** (Figs 23, 29, 33, 39, 42, 47, 60–75). The following descriptions of the wing venation are based on all species for the males (five specimens of *E. australasiae* and all available specimens for all other species), and five *E. australasiae* specimens for the female.

**Forewing, male:** Overall shape short, broad triangular with apex being almost a right angle; a smoothly rounded distal margin and tornus; a more or less straight posterior margin; and a small jugum. H well developed. H and the base of Sc+R inflated. Sc and R near parallel, but well separated for most of their length. Stems of R and Rs close together before the Rs1–2 fork. Rs1–3 share common stem beyond the cell as in all oxycanine hepialids. Rs1–2 fork longer than the combined Rs1-2-3 stem. Rs4 originating from cell. Cross vein Rs4-M1 slightly curved towards base of the wing by M1. M1-M3 well developed and free. Cross vein M1-M2 longer than cross vein Rs4-M1; cross vein M2-M3 well developed, curved slightly towards the base. M stem continuous with M2 through the cell to the anterior base of the CuA1-1A cross vein. CuA1 and CuA2 well developed; CuA cross vein and with it the basal CuA cell variably developed. CuA1-1A cross vein well developed, but incomplete centrally. CuP weak, passing through the gap in the CuA2-1A cross vein, but terminating well before the wing margin. 1A well developed, basally with a sigmoid curve towards CuP. 2A absent: 3A weak and non-tubular, present only apically.
Notes: Tindale (1935) reported that the stems of the R and Rs veins were partly anatomosed between the cell and the Rs1-2 and Rs3 fork to form a small cell. This character is highly variable and I have seen it in only one of the E. australasiae specimens I examined. It was not present in the specimen used for the illustrations. The curve at the base of vein 1A is here interpreted as being homologous to the anterior branch of the 1A-2A "Y-configuration" found in some females, to which the anal veins are otherwise found to be identical (see below). As a consequence, I interpret the 2A vein to be absent here, and the minute vein close to the jugum is interpreted as a vestige of 3A.

Hindwing, male: Shorter and more rounded than forewing. H well developed. H and the base of Sc+R inflated. Sc and R closely adjacent for almost their entire length. R and Rs sharing a long stem with R branching of the stem just before the Rs1-2 fork. The Rs1-2 fork is almost twice the length of the Rs stem beyond the cell. Rs3 branches of the Rs stem halfway between the cell and the Rs1-2 fork. Rs4 originates from cell. Cross vein Rs4-M1 well developed with a curvature that varies between species. Only two M veins present, here interpreted as M1 and M3. M stem reaches M3 at the branching point for CuA2. M1-M3 cross vein present or absent. M3-CuA1 and CuA1-CuA2 cross veins may be present and forming a distinct CuA-cell from which CuA1 originates. Or these cross veins may be absent and both CuA1 and CuA2 branch off M3. CuA2-1A cross vein absent. CuP very weak and only discernable basally. 1A well developed. 2A and 3A absent.

Notes: Tindale (1935) considered M1 and M2 to be fused, or M1 to be absent. When comparing the forewing and hind wing, the positions of M1 and M3 appear to have shifted only marginally in the latter, whereas there are no traces of M2 and cross vein M2-M3. I therefore interpret the hind wing venation as explained above.

Wing vestiture, male: The scale covering can be either single layer or type-2 bilayer (Simonsen 2001), although in the latter case, the main differences between the cover scales and ground scales are that the former are more than twice the length of the latter. Both types are narrow and elongate without apical teeth. On the abwing surface, they have very large windows (some obscured by cuticle), cross-ribs, and both primary and secondary longitudinal ridges. On the adwing surface both types have longitudinal ridges, cross-ribs and numerous well-developed windows.

Notes: Simonsen (2002) considered single-layer scale covering to be the widespread type of scale covering in Hepialidae, whereas type-2 bilayer was suggested as a potential synapomorphy for the two South American genera Dalaca and Callipielus. As will be shown elsewhere in a study focused on the higher-level classification of Hepialoidea (TJ Simonsen and NP Kristensen in prep), many of the Hepialidae genera not examined by Simonsen (2002) actually have a type-2 bilayer scale covering, and this type of scale covering is not necessarily phylogenetically informative within Hepialidae.

Forewing, female: Overall shape longer and narrower than in the male, with less obvious tornus. H well developed. H and the base of Sc+R inflated. Sc and R near parallel, but well separated for most of their length. Stems of R and Rs close together before the Rs1-2 fork. In the illustrated specimen, the two veins are anatomosed shortly just beyond the Rs3-Rs1-2 fork forming a long, but narrow cell. Rs1-3 share a common stem as in all oxycanine hepialids. Rs1-2 fork not as long as the combined Rs1-2-3 stem. Rs4 originating from cell. Cross vein Rs4-M1 slightly curved towards base of the wing by M1. M1-M3 well developed and free. Cross vein M1-M2 longer than Rs4-M1; cross vein M2-M3 well developed. M stem continuous with M2 through the cell to the minute M3-CuA2 cross vein. CuA1 and CuA2 well developed, and CuA cross vein well developed. Both cross veins M3-CuA1 and CuA1-CuA2 oriented towards the merging of the wing, and CuA1 consequently short. CuA2-1A cross vein well developed. CuP weak, passing through the CuA2-1A cross vein, but terminating soon after. 1A well developed, basally with a sigmoid curve towards CuP. 2A may be present basally before anastomosing with 1A to form a "Y-configuration": 3A weak and non-tubular, present only apically.

Notes: Tindale (1935) only reported that the stems of the R and Rs formed a small cell in males, but I observed this condition in some females as well, including the specimen illustrated. The 1A-2A "Y-configuration" is not always present, but when it is, it illustrates that the small vein found adjacent to the jugum cannot be 2A and thus must be 3A.

Hindwing, female: Shorter and more rounded than forewing. H well developed. H and the base of Sc+R inflated. Sc and R closely adjacent for almost their entire length. R and Rs sharing a long stem with R branching off the stem halfway between the branching of Rs3 and the Rs1-2 fork. The Rs1-2 fork is shorter than the length of the
Rs stem beyond the cell. Rs3 branches off the Rs stem halfway between the cell and the Rs1-2 fork. Rs4 originates from cell. Cross vein Rs4-M1 slightly curved towards base of the wing by Rs4. Only two M veins present, here interpreted as M1 and M3. But the original M2-M3 cross vein appears to be present. M stem reaches M3 at the minute M3-CuA2 cross vein. CuA1 and CuA2 well developed, and the M3-CuA1-2 branching patterns and cross veins are similar to the forewing. No CuA2-1A cross vein present. CuP is weak, but long and reaches the margin of the wing. 1A and 2A are both well developed; in some specimens (including the one illustrated) they anastomose briefly before the wing margin. 3A is very small, but present.

**FIGURES 21–22.** Details of meso- and metathorax morphology of *E. australasiae* (BMNH Micro-33263). 21: mesothorax, anterior view; 22: metafurca, lateral view. Abbreviations not previously used: Ar, prealar arm; Cs, coxal sulcus; Dast, dorsal tooth of anepisternum; Fs, furcal stem; Mb-S, mesolongitudinal basisternal sulcus; Pfa, primary furcal arms; Ph1, first phragma; Pcs, paracoxal sulcus; Pks2, posterior section of katepisternum; Sfa, secondary furcal arms; Tn, trochantin; Vast, ventral tooth of anepisternum.

**Notes:** Tindale (1935) considered the hind wing venation of the female to be identical to *Oxycanus* except for the absence of 2A (the vein here interpreted to be the minute 3A). One can only assume that the presence of two well-developed Anal veins along with a fully (albeit weakly) developed CuP convinced Tindale that the most anterior of these was CuA2. This would lead to CuA2 being interpreted as CuA1, and CuA1 as M3. However, when the venation, and especially the cross veins are compared to the forewing as well as to other hepialids, it is clear that there are indeed only two M veins present also in the female. As in the male, I interpret M2 to be either absent or fully fused with M1. But intriguingly, an M2-M3 cross vein still appears to be present running from the M-stem to M3.

**Legs** (Figs 52–54). **Foreleg:** Tibia with flap-like, flat epiphysis, free only most distally. Epiphysis totally 0.3 the length of tibia and arises approximately one third from the base. Basal tarsus segment 2.5x as long as the second, which is twice as long as either of the two following segments, but the same length as the terminal segment.

**Mid leg:** Basal tarsus segment 2.5x as long as the second, which is twice as long as either of the two following segments, but the same length as the terminal segment.

**Hind leg:** Basal tarsus segment 2.5x as long as the second, which is twice as long as either of the two following segments, but the same length as the terminal segment.
The arolium is rectangular U-shape and well-sclerotised in all species except *E. toxopeusi* where it is comprised of a narrow, membranous flap. The pulvilli are reduced to small, microtrichiated lobes at the base of the tarsal claws in all species.

**Taxonomy**

*Elhamma* Walker, 1856


Type species: *Elhamma inconcluso* Walker, 1856 by subsequent designation.


Type species: *Hepialus australasiae* Walker, 1856 by monotypy.


Type species: *Theaxieus diakonoffi* Viette, 1952 by original designation.


Type species: *Zauxieus toxopeusi* Viette, 1952 by original designation.

**Diagnosis.** Among Hepialidae *Elhamma* species are readily recognised by the unique hind-wing venation where only two M-veins are present. Males are furthermore recognised by the deeply cup-shaped juxta which at least in part appears to accommodate the prominent posterior projection of S8.

*Elhamma australasiae* (Walker, 1856)

(Figs 1–4, 23–32, 76)


Type data: Lectotype Male, BMNH (designated by Tindale (1935)—see ABRS (2009)).


Type locality: Sydney, NSW.


Type data: Holotype Female, BMNH.

Type locality: Sydney, NSW.


Type data: Holotype Male, SMF.

Type locality: Parramatta, NSW.

**Material examined.** Holotype, female, not dissected (FW: 30.7mm); Lectotype (*E. inconcluso*), male, not dissected (FW: 19.4mm).

**Dissected.** Males (BMNH Micro 33263–whole body dissection; BMNH Micro33831; BMNH Micro 33832; BMNH Micro 33833), Females (BMNH Micro 33264; BMNH Micro 33835). Other material examined: males (415); females (267).

**Distribution and localities (Fig. 76).** Found only in Australia, widespread throughout much of Victoria, eastern New South Wales and south eastern Queensland. Two further populations apparently occur in north eastern Queensland: one around Eungella National Park, and one in Tully between Townsville and Cairns.
New South Wales: Albion Park; Allowrie, Killara; Allyn River, Upper Allyn; Barren Grounds fauna res; Batemans Bay; Bawley Point; Border Ranges NP (Antarctic Beech Lkt); Border Ranges NP (Forest Tops); Bowral; Boyd River; Broulee; Bulli; Bundanoon; 5 miles N of Bungwahl; Burrawoo; Buxton; Cabramatta; Cambewarra Mt; 5 km NE of Cambewarra Mt; Caparra; Clyde Mt; Coneid Tops SF; Depot Beach; Dingo SF; Dorrigo; Durras; Ebenezer; George Basin; 5km SW of Gerringong; Gibraltar Ranges NP; Gosford; Greenwith; Jarvis Bay; Kanagra NP; Kiama; Killara; Lisarow; Manly; Medlow Bath; Menangle Park; Minnamurra Falls; Mittagong; Mt Kaputar; Mt Keira; Mt Tomah; Myall Lakes; Narara; 4 km NE Nerriga; Newnes Plateau; North Sydney; Nowra; Otford; Ourimbah SF; 3 miles S of Port Macquarie; 2.7km NE of Queanbeyan; Roseville; Royal (Sydney) NP; Springwood; Sydney; Toolum Scrub; Ulladulla; Washpool; Wedderburn; Wingham; 9 miles NE of Windsor; Wilton (CSIRO Exp. Farm); Wollongong; .

Queensland: Brisbane; Camira; Cougal Creek, Eungella NP; Dalrymple Hts Road, near Eungella; Lamington National Park (sometimes as " National Park Queensland"—including Binna Burra;); Manly; Mary Cairncross; Stanthorpe; Tallebudgera Vly falls area; Tambourine Mt; Toowoomba; Tully; Upper Tallabudgera; .

Victoria: Anglesea; Aspendale; Ballarat; Balwyn; Banksia Peninsula; Beaconsfield; Bentleigh; Black Rock; Black Snake Range; Blackburn; Camberwell; Cann River; Cape Conron; Carlisle River; Coburg; Condah; Crib Point; Dromana; Ferntree Gully; Flowerdale; Forrest; Frankston; Garfield; Gembrook; Glen Waverley; Gruyere; Hastings; Heyfield; Holey Plains SP; Kallista; Lake Entrance; Little Desert; Longford; Melbourne; Mallacoota; Mitcham; Moe; Moorabbin; Mordialloc; Morwell NP; Mt Angus Creek; Mt Cannibal East; Mt Martha; Nar Nar Goon; Nowa Nowa; Nunawading; Nyora; Ocean Grove; Park Orchards; Providence Ponds; Red Hill; Riddells Creek; Stoney Creek; Tanjil River; Traralgon Creek; Tyers River; Valencia Creek; Warrandyte; Warrangul; Wensleydale; Windsor; Wingan; Wonnangatta; Yarra Junction

Notes to distribution: Tindale (1935) listed a single Western Australian female labelled "K.S.G" and two associated, unlabelled males in the Australian Museum, Sydney. He noted they were slightly different in appearance (paler and more ochreous) than eastern specimens, but suggested that this may be due to their "state of preservation" (Tindale 1935, p. 278). I have not been able to locate these specimens, and have not seen any other specimens from Western Australia; hence I have not included these records in the distribution data. Furthermore, some specimens in MNHN were simply labelled "Verraux, Tasmania". These specimens were likely collected by the botanist and ornithologist Jules P. Verraux who collected in Australia for the MNHM in the 1840s (e.g. https://www.anbg.gov.au/biography/verreaux-jules.html). Since I have seen no other specimens from Tasmania, I consider the locality records dubious and have not included them in the distribution data.

Flight period: Specimens have been collected from early January to early May (2/1-5/5) with most records being from February and March.

Diagnosis. Small to medium size. Both sexes can readily be recognized by the small, but sharp, tuft of piliform scales protruding horizontally over the eye from the ventral base of the scape. Males can be recognised by the following combination of characters: hind wings uniformly golden-beige, at most with greyish dusting centrally. Females can also be recognized by the long, narrow wings; the uniform golden-beige ground colour of both wing pars; and the numerous, small, darker spots each comprised by few scales, studded across the forewing.

Redescription male. Small (FW: 12.7–20.8mm). Forewing posteriorly dark greyish-brown; anteriorly golden-brown. HW with CuA1 and CuA2 originating on M3 and the M-stem respectively, with no M3-CuA1 or CuA1-CuA2 cross veins present. Wings otherwise as in diagnosis. Wing vestiture type-2 bilayer, both ground and cover scales elongate without a dentate apical margin; both scale types with primary and secondary ridges and large windows on abwing surfaces; adwing surfaces of both types with well-developed primary ridges, windows and cross-ridges. Head with golden-brown, short, semi-rough vestiture dorsally, and protruding, rough vestiture frontally; antennae with scape scaled, otherwise naked. Pro- and mesothorax golden-brown; metathorax paler golden-yellow; legs all with normal, dense grey-brown and golden-brown vestiture; legs with tarsal claws short and stout with a clear basal point; arolium melanised and U-shape. Abdomen basally and ventrally golden yellow; darker greyish-brown disto-dorsally. S3–6 without dark spots; posterior edge of S3–6 smooth.

Genitalia. Sternum 8 (Figs 27–28) short with rounded lateral and anterior sides, and a sharply inwardly bent, sclerotised, posterior ridge with a broad pointed central projection. Tergal lobe clearly bilobed and setose. Pseudoteguminal lobes high and broad with a pointed latero-basal corner; pseudoteguminal arms strongly sclerotised, originating low on the lobes, both dorsal and ventral arms present; dorsal arms long and slender, recurved towards the tergal lobe; ventral arms long, basally slender and sharply bent towards trulleum, arms below...
trulleum broader, terminating in a strongly melanised tip just above juxta. Intermediate plate small and narrow, synclerotised with dorso-basal corner of the pseudoteguminal lobe. Valva long and narrow, sacculus long and setose basally; a very large, curved tooth present disto-ventrally on sacculus; valva proper narrow, club-shape and setose. Trulleum bilobed, attached basally to the base of juxta by a narrow, membranous connection; attached high on the ventral pseudoteguminal arms by a very narrow membranous connection. Juxta deeply cup-shaped with an anterior ridge and a centro-ventral lamella. Phallus approximately twice as long as height of genitalia. Vinculum and saccus broadly U-shaped with a dorsal cross-ridge and a U-shaped sulcus separating vinculum proper and the apodemal vinculum (sensu Nielsen & Kristensen 1989).

FIGURES 23–28. *E. australasiae*, male wings and genitalia morphology. 23: Wings; 24: Genitalia, 'classic' slide preparation; 25: Genitalia, ethanol preparation, posterior view; 26: Genitalia, ethanol preparation, lateral view with valva removed; 27: Sternum 8, posterior view; 28: Sternum 8, dorsal view. Abbreviations not previously used: Dpa, dorsal pseudoteguminal arm; Ip, intermediate plate; Ju, juxta; Pt, pseudotegumen; Scu, sacculus; Sus, saccus; Tru, trulleum; Va, valva; Vh, valva hook; Vi, vinculum; Vpa, ventral pseudoteguminal arm.
Redescription female. Medium size (FW: 18.9–38.8mm). Wings as in diagnosis. Head with golden-yellow, short, semi-rough vestiture dorsally, and upturned, short vestiture frontally; antennae with scape and pedicel scaled, otherwise naked; pedicel with ventral point; frontoclypeus scaled; labial palpus short, either two-segmented or terminal segment very short; with ventral scale tuft from palpus base; eyes almost at high as head, but far from meeting. Pro- and mesothorax golden-yellow; metathorax paler beige-yellow; legs all with normal, dense golden-yellow vestiture; hind legs without tibial pecten. Abdomen basally and ventrally golden yellow; darker greyish-brown disto-dorsally.
Genitalia: Dorsal plate large and bi-lobed with a small central incision dorsal to the anus. Subanal plates very large and taking up almost the entire area between the dorsal plate and the ostium with the sclerotisation surrounding the anus: subanal plates divided centrally by a narrow, vertical groove running from the anus to the ostium; horizontal, transverse grooves present on both plates lateral to the vertical groove. Antevaginal lamella trilobed, with the individual lobes widely separate: ventral lobe small, narrow and pointed with a setose tip; lateral lobes positioned just below the lateral corner of the dorsal plate, each lobe narrow, triangular and setose. Ductus bursae long, membranous and unmodified; corpus bursa an ellipsoid broadening of the terminal section of the bursa, similar in structure to the ductus. Spermatheca typically hepialoid (see Kristensen 1978), with a few concentric rings around the terminal end.

**Biology.** Nothing is known about the biology of this species, but Common (1990, p. 149) states that "adults fly in grassy areas, and the larvae probably feed on grass".

**Elhamma diakonoffi** (Viette, 1952)
(Figs 5, 33–35, 77)

**Theaxieus diakonoffi** Viette 1952
Type data: Holotype Male, Naturalis.
Type locality: Iebele Camp, New Guinea


Distribution (Fig. 77). Known only from the type locality. The locality is in the Baliem Valley in the central highlands at 138°46'E and 3°58'S (de Vos 2013).

Diagnosis: A medium sized, pale species that is most similar to *E. roepkei*. It can be recognized from the former by a smaller sized, paler ground colour and uniformly pale, yellow-beige hind wings with no pattern near the apex.

Redescription male. Medium sized (FW: 19.4 mm). Head with semi rough, golden-orange vestiture dorsally and pronounced, rough coffee-brown vestiture on frontoclypeus; with golden-orange antenna scale tufts, and a broad circle of coffee-brown scales around the base of the antenna; scape scaled, antennae otherwise naked; length more than half the width of the thorax, not serrate, each flagellomere keel-shaped; eyes as in genus; labial palpus just discernible. FW with a golden beige ground colour and a mottled dark-brown scale pattern; FW with “inflated” area on forewing basis caudal to the Sc stem. HW uniformly pale beige-yellow. Wing venation: Generally similar to *E. australasiae*, but HW with M1-M3, M3-CuA1 and CuA1-CuA2 cross veins present. Wing vestiture single layer; wing scales droplet shaped with a slightly pointed apical margin; abwing surface with stout primary ridges, windows and cross-ribs; adwing surface with primary ridges, smaller and less numerous windows and cross-ribs. Pro- and mesothorax uniformly golden-orange; metathorax yellow-beige; legs normally developed, hind legs without tibial scale tuft; claws short and thick with pronounced basal corner; arolium short U-shape. Abdomen uniformly yellow-beige without large, anterior ventro-lateral paired dark spots.

Genitalia: Sternum 8 (Fig. 35) slightly higher than broad with a rounded lateral and anterior sides, posterior margin strongly sclerotised with a broad central projection and a strong (presumably inwards pointed) hook. Tergal lobe clearly bilobed and setose. Pseudoteguminal lobes and rounded, relatively narrow; pseudoteguminal arms strongly sclerotised, both dorsal and ventral arms present; dorsal arms long and broad at base, tip pointed inwards; ventral arms long and slender with a well-defined outer margin, arms syncerotised ventrally terminating in two small, sclerotised tips. Valva long, slightly upwards curved, relatively broad; sacculus short; a short, sclerotised, outwards curved tooth present disto-dorsally on sacculus. Juxta deeply cup-shape.

Vinculum and saccus broad U-shape with a dorsal 'flat-M' shape cross-ridge and a U-shaped sulcus separating vinculum proper and the apodermal vinculum (sensu Nielsen & Kristensen 1989).

**Female:** Unknown.

**Biology.** Unknown.
Elhamma roepkei (Viette, 1952)
(Figs 6, 36–38, 77)

Theaxieus roebkei Viette, 1952
Type data: Holotype Male, Naturalis,
Type locality: Mist Camp, New Guinea

**Material examined.** Holotype, male (RMNH INS 910273, Viette genital slide no. 2491, FW: 26.6 mm), Mist Camp, 1800 m, New Guinea Exp., Neth. Ind.-Amer., 11939, L. J. Toxopeus leg.

**Distribution (Fig. 77):** Known only from the type locality. The locality is in the Rouffaer Area at the northern edge of the central highlands at 139°05'E and 3°30'S (de Vos 2013).

**Diagnosis.** Similar to *E. diakonoffi*, but larger, darker and an indistinct pattern of darker spots along the HW Rs veins.

**Redescription male.** Medium size (FW: 26.6 mm); Head with a rough vestiture of golden-orange scales dorsally and pronounced, rough grey-brown vestiture on fronsoclypeus; with dark-golden antenna scale tufts, and a broad circle of coffee-brown scales around the base of the antenna; scape scaled, antennae otherwise naked; more than half the width of the thorax, not serrate, each flagellomere keel-shape; eyes as in genus; labial palpus large; maxillary palpus just discernible. FW cinnamon beige ground colour with a mottled pattern of dark coffee-brown
scales, and a series of well-defined dark spots along the costal margin. Wing venation: Generally similar to *E. australasiae*, but HW with M1-M3, M3-CuA1 and CuA1-CuA2 cross veins present. Wing vestiture similar to *E. diakonoffi*. Pro- and mesothorax golden-orange dorsally; prothorax coffee-brown ventrally; mesothorax golden-orange ventrally; metathorax yellow-beige; legs normally developed, hind legs without tibial scale tuft; claws short and thick with pronounced basal corner; pulvilli short U-shape. Abdomen uniformly yellow-beige without large, anterior ventro-lateral paired dark spots. Posterior edge of S3-6 smooth.

**Genitalia**: Sternum 8 (Fig. 38) slightly higher than broad, with strongly sclerotised posterior margin; overall similar to *E. diakonoffi*, but central projection broader and flatter; central hook apparently missing, but preparation appears damaged, so the structure may well be present. Tergal lobe clearly bilobed and setose. Pseudoteguminal lobes very broad, not as high as in *E. diakonoffi*; pseudoteguminal arms strongly sclerotised, both dorsal and ventral arms present; dorsal arms very long and broad at base, curved strongly outwards (likely recurved towards the tergal lobe in non-mounted specimens); ventral arms overall similar to *E. diakonoffi*, long and slender with a well-defined outer margin, arms synclerotised ventrally terminating in two small, sclerotised tips. Valva long, relatively broad; sacculus short; a strong, sclerotised, outwards-downwards curved tooth present disto-dorsally on sacculus. Juxta deeply cup-shaped. Vinculum and saccus broad U-shape with a dorsal V-shaped cross-ridge and a U-shaped sulcus separating vinculum proper from the apodemal vinculum (sensu Nielsen & Kristensen 1989).

**Female**: Unknown.

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Elhamma grehani, sp. n.
(Figs 7–8, 39–41, 77)

Type data: Holotype Male, Naturalis
Type locality: Abmisibil, Star Mountains, Papua, Indonesia

Etymology. The species is named in honour of the New Zealand/USA Hepialidae specialist John Grehan. The name is a noun in the genitive case.

Paratype, male, (RMNH INS 910279—dissected, FW: 19.5mm) Abmisibil, Star Mountains, Papua, Indonesia, 4˚40’S–140˚34’E, 1970m, 29/1–9/2 2005, at light. Paratype, male, (RMNH INS 910280, FW: 20.8mm) Abmisibil, Star Mountains, Irian Jaya, 1850m, 11/3/1988, on light. Paratype, male (RMNH INS 910281, FW: 20.9mm) (abdomen missing, left FW damaged), Ok Sibil, Sterren Gebergte, Nieuw Guinea, 1260m, Ned. Exp. 1959, 1-31-V.

Distribution (Fig. 77): Found in the Abmisibil/River Sibil Area in the Star Mountains in the central highlands close to the border between Indonesia and Papua New Guinea (de Vos 2013).

Diagnosis. A rather variable species, but males can be recognised by the uniform olive brown-green FW (holotype and second paratype) sometimes with (first paratype) a broad pale-beige band running centrally from the base to the termen, in either case with a distinct, large blackish-brown dark spot basally in the cubital cell.

Description. Medium size (FW: HT 21.6mm; PT 19.5–20.8mm), the smallest known New Guinean Elhamma. Head with dark beige-brown, short, semi-rough vestiture dorsally, and protruding, rough grey-brown vestiture frontally (the aberrant paratype has yellow-beige vestiture on head and thorax); with dark-golden antennal scale tufts, and a broad circle of coffee-brown scales around the base of the antenna; scape scaled, antenna otherwise naked, length more than half the width of the thorax and slightly serrate, each flagellomere keel-shape; labial palpus short and pointed; eyes as described for genus; palps short with dark golden vestiture. Wing venation: Generally similar to E. australasiae, but HW with M3-CuA1 and CuA1-CuA2 cross veins present, and M1-M3 cross vein present in one specimen (not illustrated). Wing venature type-2 bi-layered; both scale types with parallel sides and rounded apical margin, but cover scales twice the size of ground scales; both types with stout primary ridges, large windows and cross-ribs on abwing surface, but windows on cover scales larger than on ground scales; adwing surface with primary ridges, windows and cross-ribs. Dorsal thorax and head either olive brown-green or pale-beige depending on wing pattern (essentially same colour as FW base). Basal antenna scale tufts dark. Ventral thorax and legs pale yellow-beige, but prothorax anteriorly dark grey. Legs normal; tarsal hooks short and stout with a clear basal point; arolium melanised and U-shape. Ventral abdomen and T2-6 pale yellow beige without dark spots; T7-8 dark-grey. Posterior edge of S3-6 smooth.

Genitalia: Sternum 8 (Fig. 41) small and rounded with a broadly protruded anterior margin; posterior margin with a strongly sclerotised trapezoid central projection, margin less sclerotised laterally; central hook present and similar to E. diakonoffi. Tergal lobe clearly bilobed and setose. Pseudoteguminal lobes broad and rounded, not very high; pseudoteguminal arms strongly sclerotised, both dorsal and ventral arms present; dorsal arms long and slender with a blunt tip, curved outwards (slightly recurved towards the tergal lobe in non-mounted specimens); ventral arms overall similar to E. diakonoffi, long and slender, but without with a well-defined outer margin, arms synclerotised ventrally terminating in two small, sclerotised tips. Intermediate plate small and narrow, synclerotised with dorso-basal corner of the pseudoteguminal lobe. Valva broad and rounded rectangular; sacculus short; a strong, sclerotised, inwards-downwards curved tooth present disto-dorsally on sacculus. Trulleum marginally bilobed at base, attached basally to the base of juxta by a very narrow, membranous connection; attached high on the ventral pseudoteguminal arms by a narrow membranous connection. Juxta deeply cup-shaped with a basal ridge. Phallos very long, approximately 4x the height of the genitalia (note: the phallus of the HT is damaged and appears shorter). Vinculum and saccus broad squarish U-shape with a dorsal flat cross-ridge and a U-shaped sulcus separating vinculum proper and the apodemal vinculum (sensu Nielsen & Kristensen 1989).

Female: Unknown.

Remarks. Females are unknown, and nothing is known about the biology of the species. But an additional label on the Holotype and the paratype with the same collecting data reads: “cultivated area/disturbed montane forest UNCEN-ZMA Expedition Papua Indonesia 2005".
**Elhamma viettei**, sp. n.
(Figs 9–10, 42–46, 77)

Type data: Holotype Male, Naturalis.
Type locality: Walmak, Kecamatan Nipsan, Papua, Indonesia

**Etymology.** The species is named in honour of the late French Hepialidae expert Pierre Viette (1921–2011). The name is a noun in the genitive case.

**Material examined.** HOLOTYPE male, (RMNH INS 910275—dissected, FW: 23.9mm) Indonesia, Papua, Kecamatan Nipsan, Walmak, 1710m, 4°07’S–138°38’E, 31/1–16/2 2005, at light.


**Distribution (Fig. 77):** The species is apparently widespread as the three specimens are from three different and quite distant localities. The holotype from Walmak in the Jayawijaya Mountains (139°38’E 4°41’S) and one paratype from the Star Mountains (Bivak 39, 140°46’E 4°51’S) are both from the central highlands. Whereas the last paratype is from the island of Biak (135°49’E 0°41’S) to the north east of the New Guinea mainland (exact localities from de Vos 2013).

**Diagnosis.** Most similar to *E. diakonoffi* and *E. roepkei*, but can be distinguished from both species by the much darker overall habitus including dark brown forewings, dorsal thorax, head, antennae and almost black basal antenna scale tufts.

**Description.** Medium size (FW: HT 23.9mm; PT 23.5–25.8mm). Head with dark golden-brown, short, semi-rough vestiture dorsally, and protruding, rough blackish-brown vestiture frontally; antennae short, with scape scaled, otherwise naked, length more than half the width of the thorax, not serrate, each flagellomere keel-shaped; labial palpus short and pointed; with blackish-brown antennal scale tufts, and a broad circle of blackish-brown scales around the base of the antenna; eyes as described for genus; palps short with dark golden-brown vestiture. Wing pattern as in species diagnosis; wing vestiture type-2 bi-layered; both scale types droplet shaped with a rounded apical margin, but cover scales twice the size as ground scales; both types with stout primary ridges, large...
windows and cross-ribs on abwing surface; secondary ridges on cover scales only; adwing surface with primary ridges, windows and cross-ribs, but windows more numerous on cover scales. FW overall dark olive brown with a mottled pattern of paler dark-beige scales; costal region and remaining margins with a row of dark spots (along latter margins restricted to the ‘cilia’); cubital cells basally with a large, diffuse dark spot of blackish-brown scales. HW uniform pale yellow-beige; margin darker, with ‘cilia’ at the veins being black. Wing venation generally similar to *E. australasiae*, but HW with M3-CuA1 and CuA1-CuA2 cross veins present. Thorax ventrally with a mixture of dark brown and yellow beige scales; legs yellow-golden; tarsal hooks short and stout with a clear basal point; arolium melanised and U-shaped. Abdomen generally yellow beige except of T6-8 which are dark grey. S3-6 without dark spots; posterior edge of S3-6 smooth.

**Genitalia**: Sternum 8 (Figs 45–46) larger than in *E. grehani*, lateral and anterior margins U-shape, posterior margin with a strongly sclerotised trapezoid central projection, margin more sclerotised laterally than in *E. grehani*; central hook present and similar to *E. grehani*. Tergal lobe clearly bilobed and setose. Pseudoteguminal lobes broad and rounded, not very high, similar to *E. grehani*; pseudoteguminal arms strongly sclerotised, both dorsal and ventral arms present; dorsal arms short and broad with a pointed tip, curved outwards (pointed straight up in unmounted specimens); ventral arms overall similar to *E. grehani*, long and slender, with a well-defined outer margin, arms synclerotised ventrally terminating in two small, sclerotised tips. Intermediate plate small and narrow, sclerotised with dorso-basal corner of the pseudoteguminal lobe. Valva slightly upwards curved, relatively broad; sacculus short; a strong, sclerotised, inwards-downwards curved tooth present disto-dorsally on sacculus.

Trulleum overall similar to *E. grehani*: bilobed at base, attached basally to the base of juxta by a narrow, membranous connection; attached high on the ventral pseudoteguminal arms by a narrow membranous connection. Juxta similar to *E. grehani*; deeply cup shaped with a basal ridge. Phallus very long, approximately 6x height of the genitalia. Vinculum and saccus broad U-shape with a flat dorsal cross-ridge and a U-shaped sulcus separating vinculum proper and the apodemal vinculum (sensi Nielsen & Kristensen 1989).

**Female**: Unknown.

**Remarks**: Females are unknown, and nothing is known about the biology of the species. But an additional label on the Holotype reads: “cultivated area/disturbed montane forest UNCEN-ZMA Expedition Papua Indonesia 2005”.

*Elhamma toxopeusi* (Viette, 1952)  
(Figs 11–12, 47–51, 77)

*Zauxieus toxopeusi* Viette 1952  
Type data: Holotype Male, Naturalis  
Type locality: Scree Valley Camp, New Guinea

**Material examined**. Holotype (Viette genital slide no. 2492, FW: 23.3 mm), Scree Valley Camp, 3800m, New Guinea Exp., Neth. Ind.-Amer., ix 1938, L. J. Toxopeus leg.; Paratype (Viette genitalia slide no. 2436, FW: 25.2 mm); one additional male, same label data (RMNH INS 910272—dissected FW: 24.4mm).

**Distribution** (Fig. 77). Known only from the type locality. The locality is in the Baliem Valley in the central highlands at 138°40'E and 4°20'S (de Vos 2013).

**Diagnosis**. A medium sized, robust and very dark species that can easily be recognized from other *Elhamma* by the dark, coffee-brown ground colour of the forewing and the uniformly dark, coffee-brown hind wing.

**Redescription male**. Medium sized (FW: 23.3–25.2 mm). Head with golden-brown, short, semi-rough vestiture dorsally, and protruding, rough golden-brown vestiture frontally; antennae with scape scaled, otherwise naked, length more than half the width of the thorax, not serrate, each flagellomere keel-shaped; labial palpus short and pointed; with dark beige-brown antennal scale tufts, and a broad circle of coffee-brown scales around the base of the antenna; eyes as described for genus; palps short with dark golden vestiture. FW with a mottled pattern of dark-beige scales. Eing venation generally as in genus, but FW with CuA2 curved towards CuA1 at base, and HW with M3-CuA1 and CuA1-CuA2 cross veins present. Wing vestiture type-2 bilayer, both cover and ground scales broad spindle shaped to droplet shaped, but cover scales much broader and twice the length of ground scales; both types with primary and secondary ridges, small windows and cross-ribs on abwing surface; abwing surface with primary ridges, small pores and cross ribs; abwing ridges on cover scales apparently of composite nature.
Thorax overall dark brown (types) to dark golden-orange; legs normal; hind leg without tibial tuft; tarsal claws long and slender, without prominent basal corner; arolium strongly reduced. Abdomen unmodified, dark coffee-brown dorsally, golden brown ventrally. S3-6 with large, anterior ventro-lateral paired dark spots, most prominent on S3 (fenestrae?); S3-6 with small point centrally on posterior ridge.


**Genitalia:** Sternum 8 (Figs. 50–51) U-shaped with a straight, strongly sclerotised posterior margin, sclerotisation strongest and broadest at corners; posterior margin centrally with a broad, flap-like internal projection. Tergal lobe setose, with two latero-dorsal corners, but not distinctly bilobed. Pseudoteguminal lobes high and relatively narrow, in lateral view with a broad, rectangular, central projection; dorsal arms absent; ventral arms relatively short and stout, with a well-defined outer margin, arms synclerotised ventrally terminating in two prominent, sclerotised tips. Intermediate plate small and very narrow, separated from the pseudoteguminal lobe by a membranous band. Valva long, slightly upwards curved, relatively broad; sacculus short with small, sclerotised bump, but no well-developed tooth. Trulleum marginally bilobed at base, attached basally to the base of juxta by a membranous connection; marginally bilobed posteriorly, attached high on the ventral pseudoteguminal arms by a narrow membranous connection. Juxta deeply cup-shaped with a basal ridge. Phallus less than 2x the height of...
genitalia. Vinculum and saccus broad U-shaped with a flat dorsal cross-ridge and a U-shaped to V-shaped sulcus separating vinculum proper and the apodemal vinculum (sensu Nielsen & Kristensen 1989).

**Female**: Unknown.

**FIGURES 52–59.** SEM micrographs of tarsus and antenna morphology. 52: tarsus of *E. australasiae*; 53–54: tarsus of *E. toxopeusi*; 55–59: antennae of *E. australasiae*. 55: terminal segment showing several sensilla chaetica (Sc); 56: tip of terminal segment showing two potential sensilla auricillica (Sau); 57: detail of terminal segment showing sensilla chaetica and sensilla trichodea (St); 58: ordinary flagellum segments, arrows are indicating positions of sensilla auricillica; 59: detail of 58 showing sensilla auricillica. Abbreviations not previously used: Au, arolium; Pu, pulvillus; TC, tarsal claw. Scale bars: 52–53: 100 µm; 54, 58: 20 µm; 55: 10 µm; 56: 1 µm; 57, 59: 2 µm.
FIGURES 60–67. SEM micrographs of wing vestiture. 60–62: *E. australasiae*; 60: overview showing cover scales (CoS) and ground scales (GS); 61: detail of cover scale, adwing surface; 62: scales, abwing surface; 63–65: *E. diakonoffi*; 63: overview showing undifferentiated scales; 64: detail of scale, abwing surface; 65: detail of scale, adwing surface; 66–67: *E. roebkei*; 66: overview showing undifferentiated scales; 67: detail of scale, abwing surface. Abbreviations not previously used: Cr, cross ribs; Prd, primary ridges; Sr, secondary ridges; W, windows. Scale bars: 60, 63, 66: 20 µm; 62: 5 µm; 64–65, 67: 1 µm.
FIGURES 68–75. SEM micrographs of wing vestiture. 68–70: *E. grehani*; 68: overview showing cover scales and ground scales; 69: detail of cover scale, abwing surface; 70: detail of cover scale adwing surface; 71–72: *E. viettei*; 71: overview showing cover scales and ground scales; 72: detail of cover scale, abwing surface; 73–75: *E. toxopeusi*. 73: overview showing cover scales and ground scales; 74: detail of cover scale, abwing surface; 75: detail of cover scale adwing surface. Abbreviation not previously used: P, pore. Scale bars: 68, 73: 10 µm; 71: 20 µm; 69–70, 72, 74–75: 1 µm.
FIGURE 76. Distribution of *Elhamma australasiae* based on specimen records.

**Keys to species (males only)**

**External characters**

1. Fore- and hind wings with similar dark brown ground colour; ampulla small and narrow .......................... *E. toxopeusi*
   - Forewings darker than hind wings; ampulla large and broadly U-shaped ...................................................... 2
2. Hind wing with both CuA veins originating on M3 with no CuA cross vein or basal CuA-cell .................. *E. australasiae*
   - Hind wing with a distinct, basal CuA-cell formed by M3-CuA1 and CuA1-CuA2 cross veins ......................... 3
3. Forewing with a dark spot caudally between M2 and CuA2 ................................................................. 4
   - Forewing without a dark spot between M2 and CuA2 .................................................................
4. Forewing spot very distinct, clearly darker than the surrounding wing surface; FW < 22mm ................. *E. grehani* sp.n.
   - Forewing spot discernable, but not distinct, marginally darker than the surrounding wing surface, FW > 22mm ................................................................. *E. viettei* sp.n.
5. Forewing > 23mm; hind wing apex between Rs1 and Rs2 dark-beige with small back dots ...................... *E. roepkei*
   - Forewing < 23mm; hind wing apex between Rs1 and Rs2 pale-beige without dots .......................... *E. diakonoffi*

**Genitalia characters**

1. Long and narrow dorsal pseudoteguminal arms absent ................................................................. *E. toxopeusi*
   - Long and narrow dorsal pseudoteguminal arms present ........................................................................ 2
2. Valva narrow with long sacculus; basal hook very long, originating on ventral margin of valvav .................. *E. australasiae*
   - Valva broad with short sacculus; basal hook short, originating centrally on valva ................................. 3
3. Basal hook curved upwards ................................................................. *E. diakonoffi*

**Discussion**

**Morphology of Elhamma compared to literature accounts of other Hepialids.** *Head:* Compared to *Fraus* (Nielsen & Kristensen 1989) the sclerotised rim of the occipital foramen is remarkably well-developed and encircles not only the occipital foramen, but also the scaled postlabial "wart". This configuration is illustrated for some New Zealand "oxycanine" genera such as *Dioxycanus* and *Dumbletonius*, and the hepialine *Aoraia* (Dugdale 1994 figs 92, 95 and 100). The antennae are positioned very low (centrally) on the head compared to other Hepialidae except *Aenetus* and *Aoraia* (Dugdale figs 81, 90), and *Afrotheora* (Nielsen & Scoble 1986). The apparent absence of anterior tentorial pits has not been reported from other Hepialidae.

*Prothorax:* The broad episternum with a long, narrow episternal tooth widely separated from the ventral base of the laterocervicale resembles the conditions found in *Dioxycanus* and *Dumbletonius*, and the narrow laterocervicale with long dorsal and ventral arms resembles the condition found in the former (Dugdale 1994 figs 114, 115). The full synsclerotisation of the propleural rim and anterior dorsal plate differs from *Fraus* (Nielsen & Kristensen 1989 fig. 55), but is similar to all species illustrated by Dugdale (1994). The absence of pronotal "nipples" is apparently unique among the examined Hepialidae (Nielsen & Kristensen 1989, Dugdale 1994, Simonsen unpublished). The profurca has not been studied in detail in Hepialidae except *Fraus* (Nielsen & Kristensen 1989), but comparisons between that genus and *Elhamma* indicate that the structure may hold phylogenetically important characters for Hepialoidea phylogeny.

*Pterothorax:* In the mesothorax, both the first (anterior) phragma and the prealar arm are more developed than reported in *Fraus* (Kristensen & Nielsen 1989). The second (posterior) phragma is much more bipartite distally.
with a more developed longitudinal sulcus than reported in *Fraus* (Kristensen & Nielsen 1989). The anapleural cleft is narrowed as reported by Dugdale (1994) for all New Zealand genera except *Aenetus*. Unlike the condition in *Fraus* (Nielsen & Kristensen 1989), the mesolongitudinal basisternal sulcus does not continue to the edge of meso-basisternum, but stops abruptly at approximately the centre of the basisternum.

The metascutum is very short dorsally which resembles the condition reported in New Zealand genera with 'oxycanine' wing venation (Dugdale 1994). The median lamella of the acrotergite is much more developed than in *Fraus* (Kristensen & Nielsen 1989), and resembles the transphragma in higher Lepidoptera (Kristensen 2003).

**Thoraco-abdominal junction:** The tergosternal bar is elongate and evenly broad. The structure thus resembles the condition in *Aenetus* more than the condition in other New Zealand hepialids (Dugdale 1994). As reported by Grehan (2010), *Elhamma* possesses neither an anterior broken margin nor a posterior 'knob' on the tergal brace.

*Theaxieus* and *Zauxieus* as synonyms of *Elhamma*. Nielsen's (1996) treatment of *Theaxieus* and *Zauxieus* as subjective junior synonyms of *Elhamma* had not been previously tested. The unique hind wing venation where only two M-veins are present, and the specialised three-dimensional, cup-shaped juxta (which to my knowledge is not found elsewhere in Hepialidae) allows for easy and unequivocal identification of the genus as here defined, and provide full justification for Nielsen's proposed synonymy.

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**References**


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