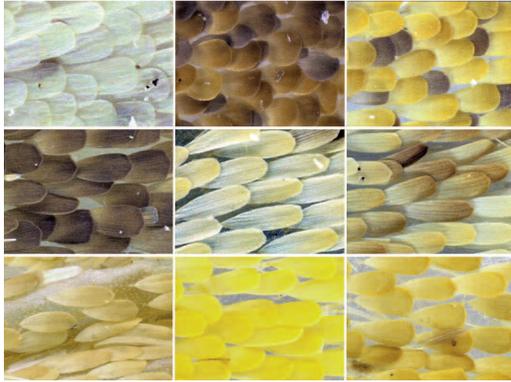

BISHOP MUSEUM OCCASIONAL PAPERS

TAXONOMIC REVISION AND BIOGEOGRAPHY OF *PHASSODES*
BETHUNE-BAKER, 1905 (LEPIDOPTERA: HEPIALIDAE), GHOST
MOTH DESCENDANTS OF A SUBDUCTION ZONE WEED IN THE
SOUTH-WEST PACIFIC

JOHN R. GREHAN & CARLOS G.C. MIELKE



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Cover illustration: Selection of scales from central forewing of *Phassodes* spp. (see page 14). Photos by James Boone, Miho Maeda, and Agnes Stubblefield.

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Taxonomic revision and biogeography of *Phassodes* Bethune-Baker, 1905 (Lepidoptera: Hepialidae), ghost moth descendants of a subduction zone weed in the south-west Pacific. Grehan, J.R. & Mielke, C.G.C. *Bishop Museum Occasional Papers* 136: 1–37 (2020)

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Taxonomic revision and biogeography of *Phassodes* Bethune-Baker, 1905 (Lepidoptera: Hepialidae), ghost moth descendants of a subduction zone weed in the south-west Pacific

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Abstract. *Phassodes* Bethune-Baker, 1905 is distributed in Fiji (*P. vitiensis* (Rothschild, 1895)), the Solomon Islands (*P. walteri* sp. n.), Samoa (*P. samoa* sp. n.), and American Samoa (*P. tutuila* sp. n.). It is the only genus of Hepialidae endemic to oceanic islands. Monophyly of the genus is supported by four unique features, and a sister group relationship with the Australian genus *Abantiades* Herrich-Schäffer, 1855 is supported by four shared derived features. There are also some features shared between *Phassodes* and other genera: a) the southern Andean genus *Andeabatis* Nielsen & Robinson, 1983 (shape and structure of the male genitalia), b) the Peruvian *Viridigigas* Grehan & Rawlins, 2016 and c) the Chilean *Puermytrans* Viette, 1951 (presence of a basal forewing scent gland). The distribution of *Phassodes* coincides with the Vitiáz Trench, an extinct subduction zone that marks a former boundary between the Indo-Australian and Pacific plates. It is proposed that the common ancestor of *Phassodes* and *Abantiades* diverged through vicariance when the subduction zone along the east coast of Australia (East Gondwana), along with its island arc, began retreating into the Pacific between 90 and 75 Ma. Survival of the genus on volcanic islands is attributed to metapopulation dynamics, with continuous transference of populations from older, subsiding islands to newly emergent ones. This model suggests that *Phassodes* species originated much earlier than the individual islands they now occupy.

INTRODUCTION

Phassodes Bethune-Baker, 1905 ranks among the larger-bodied genera of Hepialidae (Fig. 1), and is also one of the most poorly known. The first specimen (a single male from Fiji bought from a dealer) was briefly described by Rothschild (1895) under the genus *Leto* Hübner, [1820] (named for a South African species). A more detailed outline was given a decade later by Bethune-Baker (1905), who described the genus *Phassodes* for six proposed species from the island of Viti Levu [these were all later synonymized under *P. vitiensis* (Rothschild, 1895) by Nielsen *et al.* (2000)]. The only other literature records of *Phassodes* distribution refer to specimens collected from Samoa (Tams 1935) and American Samoa (Comstock 1966) that were also attributed to *Phassodes vitiensis* (Rothschild, 1895) by these authors.

The distribution of *Phassodes* is of considerable biogeographic interest as it is the only member of Hepialidae known to occupy oceanic archipelagos that lack continental crust. All other Hepialidae are restricted to continents or occur on archipelagoes where continental crust forms part of their geological structure such as New Zealand, New Caledonia, New Guinea, The Philippines, and Taiwan. Many genera and species of Hepialidae in Australasia have distributions spatially coinciding with geological features that were active in the Mesozoic and Cenozoic, and this supports the existence of a diverse East Gondwanan exoporian fauna in Mesozoic time (Grehan 2018, Grehan & Mielke 2018a, b, 2019a). Grehan & Mielke (2018a) suggested that the Pacific island distribution of *Phassodes* was either derived from an ancestor present in East Gondwana (and later the arcs that migrated away from it) or on existed on subaerial parts of the large igneous plateaus that formed in the central Pacific. These alternatives could not be further evaluated without knowledge of the sister group of *Phassodes*.

We recently had the opportunity to examine a new *Phassodes* specimen from the Solomon Islands and in order to assess its species status it became necessary for us to compare its morphology with specimens from the other island localities. This comparison was made possible by generous loans of material from Fiji, Samoa, and American Samoa held at the Bernice Pauahi Bishop Museum, Honolulu (USA), and further material from the National Museum of Natural History, Washington, DC (USA), and the New Zealand Arthropod Collection (Auckland). In this paper we describe three new *Phassodes* species and examine evidence of the phylogenetic and biogeographic relationships of the genus.

MATERIAL AND METHODS

Specimens of *Phassodes* examined in this study are deposited in collections of BPBM (including donation of the type specimen of the new species from Guadalcanal), NZAC (Landcare Research), and the USNM. Specimens of other genera compared in this study are *Abantiades magnificus* (Lucas, 1898), (NZAC), *Abantiades hyalinatus* (Herrich-Schäffer, 1853) (CMNH), *Andeabatis chilensis* (Ureta, 1951) (USNM), and *Abantiades latipennis* Tindale, 1932 (JRGC).

Morphological terminology follows Kristensen (2003) for wing venation, Mielke & Casagrande (2013) for most of the genitalia structures with reference to the tegumen (= intermediate plate), saccus (= vinculum), and fultura inferior (= juxta), Grehan & Mielke (2017) for fultura superior (= trulleum) and the tergo-sternal sclerite. We also refer to Dumbleton (1966) for wing venation patterns as ‘hepialine’ where Rs1+Rs2 and Rs3 are stalked.

Specimen preparation. The abdomen was removed and treated in a cold solution of 5% KOH. The abdominal integument was opened by a right lateral cut from the tergo-sternal bar to the genitalia; the genitalia were then removed and stained in Chlorazol black and are stored in alcohol or glycerine. Terminology follows Mielke & Casagrande (2013) for genitalia and Grehan & Mielke (2017) for the tergo-sternal connection. Outline diagrams of the wing were prepared by tracing over photographs using InkScape Scalable Vector Graphics (SVG) 1.1 (Second Edition), version <http://www.w3.org/TR/2011/REC-SVG11-20110816/>.

Holotype labels are written verbatim. A forward slash denotes a separate label.

Institutional Abbreviations

ANIC	Australian National Insect Collection, CSIRO, Canberra, ACT, Australia
BPBM	Bernice P. Bishop Museum, Honolulu, Hawai‘i, USA
JRGC	John R. Grehan Collection, Evans, New York, USA
NHMUK	Natural history Museum, London, UK
NZAC	New Zealand Arthropod Collection, Manaaki Whenua-Landcare Research, Auckland, New Zealand
USNM	National Museum of Natural History, Washington, D.C., USA

Other abbreviations

FW – Forewing; HW – Hindwing.

TAXONOMY*Phassodes* Bethune-Baker, 1905

Phassodes Bethune-Baker, 1905: 89. Type species: *Phassodes odorevalvula* Bethune-Baker, 1905, by original designation.

Monophyly. Supported by four uniquely derived character states (see discussion for validation): (a) Dorsal plate of female genitalia tall with convex lateral and inner margins, (b) ventral apex of pseudotegumen terminating as a shallow fork, (c) ridge extending lateral to pseudotegumen from base of postero-ventral tooth, and (d) wing pattern of sub-circular spots.

Diagnosis. Large moths with various shades of brown on body and appendages; FW marked by combinations of convex and concave (relative to wing base) lines between veins forming sub-circular spots, and a few to many silver markings (Figs. 1–5). The pattern of curved transverse lines between veins is similar to that found in many species of *Aenetus* Herrich-Schäffer, 1855, but these lack the sub-circular spots. Males distinguished from all other Old World Hepialidae by combined presence of HW androconia and FW scent gland. Short lobate valva with broad ovoid sacculus and laterally inflated intermediate zone of the tergosternal connection are similar to those of *Abantiades* Herrich-Schäffer, 1855. Females separated from all Old World Hepialidae by presence of elongate, digitiform dorsal extensions of the lateral lobes of the lamella antevaginalis.

Redescription. Wingspan: ~70–110 mm.

Head. Scales piliform, longer over clypeus anterior to base of antennae. Labial palp long, extending beyond anterior head margin, covered with digitiform scales, prelabium small, palpomeres subequal in length in males, longer in only female examined (*P. vitien-sis*), first and second palpomeres pale yellowish brown, distal palpomere pale reddish brown. Eyes prominent, no macro difference in size apparent between sexes. Intra antenna-ocular scales absent. Antennae filiform, 40–55 antennomeres, surface covered with numerous fine, short sensilla trichodea, terminal antennomere narrow, pointed, longer in male.

Thorax. Scales piliform, colour similar to head and abdomen. Anterior scutum III free of scales.

Legs. Tibia and tarsus with long lateral scales, length tapered distally. Epiphysis and arolium present. Metaleg proportionately long, ~90% of proleg length (Figs. 9a–9e).

Wings. FW longer than HW, ratio FW:HW ~1:0.6. FW costal pocket present; costal margin straight to outer 2/3, then convex to falcate apex; outer margin slightly concave then convex with posterior margin without distinct tornus. HW costal margin slightly convex to rounded apex, outer margin convex to tornus, posterior margin straight. Venation hepialine, Sc and R closely proximate, in HW only for the outer half before diverging at costal margin; common stalk of Rs1-Rs2 about 1/3 (FW) to 1/2 of distance from wing base; FW with four anal veins, 2A very thin and shorter than CuP, 3A extending just past base of outer edge of jugum, and 4A extending along inner edge of jugum (Figs. 10a–10b). Wing color pattern highly variable, ground color yellowish to grayish brown with transverse lenticular lines forming curves or ovoid shapes, variously shaded in darker or brighter tones of brown or silver, silvery markings extensive or more often limited to smaller stigmatic spots; dark brown spot sometimes present distally to junction of M₁ and CuA₁. Scales of central FW sub-rectangular to ovoid in shape (Fig. 11), distal margin smooth (in gross morphology) with shallow point or rounded (in scales of stigma). Male FW with basal ovoid scent gland posterior to 1A, with 1A lining the anterior margin of the gland (Figs. 12a, 12b); HW androconial tuft emerging at base close to the inner margin (Fig. 14).

Abdomen. Covered with piliform scales. Tergosternal sclerite with short lateral and dorsal brace, each with broad medial edge; intermediate zone forming a broad sub-rectangular region lightly sclerotized and bulging laterally. Tergum II (Figs. 15a–15d) rectangular, lateral ridge broad, posteriorly angled laterally, anterior ridge of tergum II not meeting across median. Sternum II (Figs. 17a–17d) with long anterolateral arms, sclerotized anteriomedially, central anterior edge strongly sclerotized, lateral ridge from outer apex of anterior arm slightly convex, angled laterally towards posterior of SII. Tergum III (Figs. 15a–15d) with lateral ridge along anterior half. Tergum VIII membranous in male and female. Sternites II–III wider than long. Sternum VII of male rectangular, longer than wide. Sternum VIII of male (Figs. 18a–18c) rectangular, slightly wider posteriorly, anterior margin convex, posterior margin broadly concave, with central edge connecting directly to ventral ridge projecting from central apodemal suture, postero-lateral corners narrow (Fig. 18b) or broad (Figs. 18a, 18c); sternum VIII of female (Figs. 18d–18e) wider than long, posterior margin a shallow W-shape with lateral concave depressions either side of central convex edge.

Genitalia, male (Figs. 19–23). Tegumen subtriangular, wider medially, free of pseudotegumen, medial edge concave. Saccus triangular, lateral margin extending to widest posteriorly either side of tegumen; apodemal suture with ventral projecting ridge that abuts the posterior margin of sternite VIII. Tergal lobes forming elongate digitiform process either side of dorsal median (Fig. 23a–23b). Pseudotegumen strongly sclerotized, heavily sclerotized along anogenital margin and apex of pseudoteguminal arm, latter fused across median with a central notch between two short points; postero-ventral tooth elongate, laterally extending as a shallow, straight ridge either side about half length of pseudotegumen; postero-dorsal tooth shallow or pointed, narrow dorsal process either side of the median lightly sclerotized. Fultura superior rectangular, narrowing slightly posteriorly, posterior margin with deep, broad notch. Fultura inferior subsquare, slightly narrower posteriorly. Valva short, broad sacculus with shallow point along posterior margin, distal valve lobed with extensive covering of setae.



Fig. 1. *Phassodes vitiensis*: Naviti Resort, Coral Coast, Fiji (Photo by Kirk Williams & Benny de Groof).

Genitalia, female (Figs. 26–28). Dorsal plate (tergum IX) forming a tall, broad arch narrowing at the point of fusion across dorsal median, inner and outer lateral edges convex. Subanal plates upright or inclined to median, narrow, slightly angled medially. Lamella antevaginalis with tall subrectangular, weakly sclerotized central lobe, lateral lobes sclerotized with dorso-medial digitiform process and sometimes laterally subtended by a shallow knob (Fig. 26b). Ductus bursae narrow, slightly less than half length of corpus bursae, latter cylindrical, narrowing proximally and distally.

Biology and host plants. There is no information on larval biology of *Phassodes*, but it is almost certain that the immature stages are ground dwellers. A stem boring habit would have likely been observed and recorded, and no evidence of stem boring was seen in trees and shrubs during a visit to Viti Levu (Fiji) by JRG when searching for *Phassodes vitiensis*.

Species composition, distribution and type depository

Phassodes vitiensis (Rothschild, 1895: 482). HT male: NHMUK

Distribution: Fiji, Viti Levu. Type locality – ‘Fiji’

Phassodes walteri Grehan & C. Mielke, **sp. n.** HT male: BPBM

Distribution: Solomon Islands. Type locality – Guadalcanal

Phassodes samoa Grehan & C. Mielke, **sp. n.** HT male: BPBM

Distribution: Samoa. Type locality – Upolu, Afiamalu

Phassodes tutuila Grehan & C. Mielke, **sp. n.** HT female: BPBM

Distribution: American Samoa. Type locality – Tutuila, near Pago Pago

Species Accounts

Phassodes vitiensis (Rothschild, 1895)

(Figs. 1, 2a–c, 6a–6b, 7a–b, 8a–d, 9a–9b, 14, 15a, 16a, 17a–b, 18a, 18e, 19a–c, 22a, 26a–b)

Leto vitiensis Rothschild, 1895: 482. HT male: NHMUK

Type locality – Fiji

Phassodes bimorpha Bethune-Baker, 1905: 91. HT [sex uncertain]*: NHMUK

Type locality – Fiji, Viti Levu, Rewa River

Phassodes guthrei Bethune-Baker, 1905: 90. Syntypes: NHMUK

Type locality – Fiji, Viti Levu, Rewa River

Phassodes nausori Bethune-Baker, 1905: 91. HT [sex uncertain]*: NHMUK

Type locality – Fiji, Viti Levu, Nausori, Rewa River

Phassodes odorevalvula Bethune-Baker, 1905: 90. HT male: NHMUK

Type locality – Fiji, Viti Levu, Nausori

Phassodes rewaensis Bethune-Baker, 1905: 91. HT [sex uncertain]*: NHMUK

Type locality – Fiji, Viti Levu, Nausori

Phassodes vitensis Bethune-Baker, 1905: 92. HT [sex uncertain]*: NHMUK

Type locality – Fiji, Viti Levu, Nausori

Monophyly. Supported by unique configuration of the postero-dorsal tooth of the pseudotegumen.

Diagnosis. Male genitalia with a postero-dorsal shark-fin tooth along margin of anogenital field distinguish this species from *P. samoa* sp. n. with a shallow convex lobe, and from *P. walteri* sp. n. with a subrectangular postero-dorsal projecting lobe with three blunt points (Fig. 22).

Species features. Male. *Wingspan*: ~70 mm (Figs. 1, 2a).

Head. (Fig. 6a, 7a, 7b) Prelabium small, first and second labial palpomeres pale yellowish brown, subequal, distal palpomere pale reddish brown, slightly shorter.

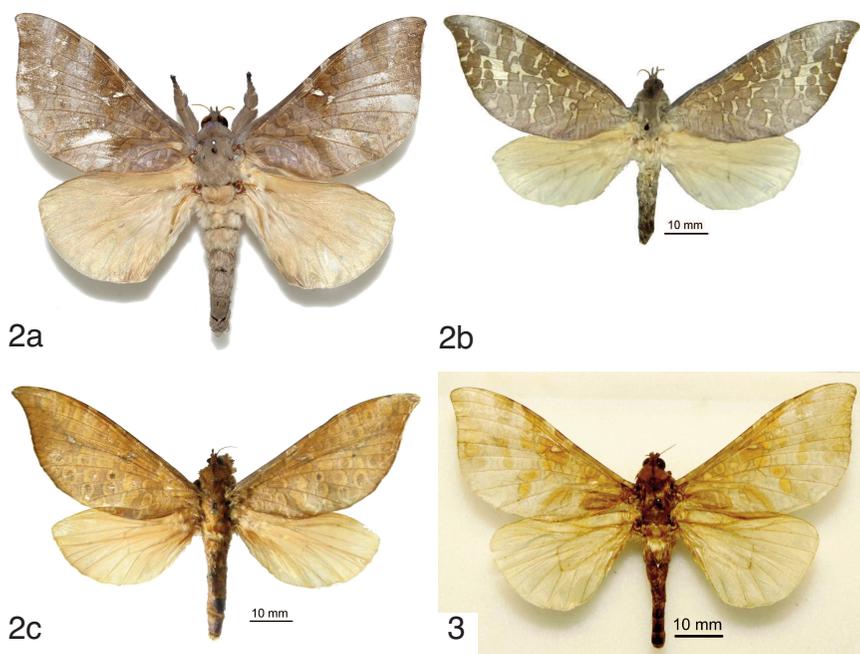
Thorax. As for genus.

Wings. As for genus.

Legs. (Figs. 8a–d, 9a) Leg proportions: pro:meso:meta: 1:1.16:0.86.

Abdomen. (Figs. 15a, 16a, 17a, 18a) As for genus.

* Bethune-Baker (1905) referred to male and female types of *P. guthrei* and males for the other species, but other than *P. odorevalvula*, his illustrations of each species do not show the FW scent gland and therefore they appear to be females. The correct sex of the holotypes will need to be verified by examination of the specimens at NHMUK in the future. Dissection and/or DNA extraction of all primary types will also be necessary to validate their synonymy under *P. vitiensis*.



Figs. 2–3. *Phassodes* species. **Fig. 2.** *Phassodes vitiensis*: (a) male, Fiji (ANIC, photo by J. Nielsen, unscaled), (b) female, Viti Levu, Fiji, 10 Nov 2014 (Benny de Groof Collection, photo by Benny de Groof), (c) female, Coral Coast, 17 km from Sigatoka Village, Naviti Resort, 17 Jul 2014 (Benny de Groof Collection, photo by Benny de Groof). **Fig. 3.** *Phassodes walteri* sp. n., holotype male, dorsal (photo by Victor Gurko).

Genitalia. (Fig. 19a–19c, 22a) Pseudotegumen postero-dorsal tooth forming a blunt shark-fin shape. Fultura superior posterior margin anterior to pseudotegumen with deep, broad notch. Fultura inferior slightly narrower posteriorly. Valva with shallow baso-posterior point.

Female. *Wingspan:* ~100 mm (Fig. 2b–c)

Head. (Fig. 6b) Palpomeres subequal, distal palpomere proportionately longer than in male, narrowing slightly distally.

Thorax. As for male

Legs. (Figs. 8d, 9b) Leg proportions: pro:meso:meta: 1:1.17:0.87.

Wings. As for genus.

Abdomen. (Fig. 17b, 18e) As for genus.

Genitalia. (Figs. 26a–b) Ductus bursae narrow, about half width and length of corpus bursae. Corpus bursae distally rounded, narrowing towards junction with ductus bursae.

Distribution. Fiji, island of Viti Levu (Fig. 30).

Type: Holotype ♂ (NHMUK): Fiji.



Fig. 4. *Phassodes samoa* sp. n., male holotype: (a) dorsal, (b) ventral (photos by James Boone), (c) male paratype (L35, NZAC) (photo by Jane Hyland, unscaled).

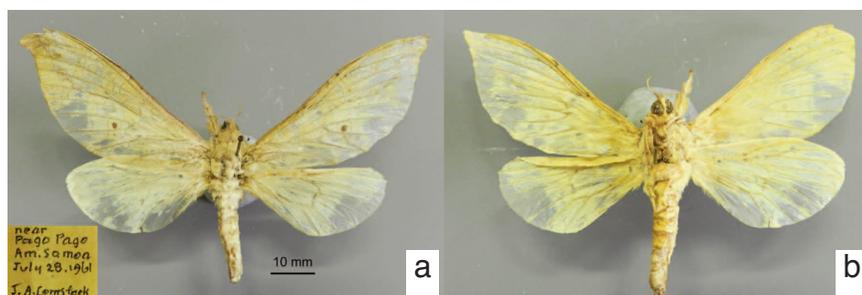


Fig. 5. *Phassodes tutuila* sp. n., female holotype: (a) dorsal, (b) ventral (photos by James Boone).

Material examined (1♂, 4♀). All Fiji, Viti Levu: 1♂, Nandarivatu, 31 Sep 1938, E.C. Zimmerman collection. Dissection JRG M278 (BPBM); 1♀, Nandarivatu, 7 Oct 1937, E.M. Valentine leg. Dissection JRG F304 (BPBM); 1♀, Nandarivatu, 1973, E.M. Valentine leg. Dissection JRG F301 (BPBM); 1♀, Savura Creek. Dissection L34, JSD [John S. Dugdale] (NZAC); 1♀, Nairayawa, 178°5'E, 17°56'S, UV trap, 20–23 Nov 1986, R. Brown & O. Pellmyr leg. [not dissected] (USNM).

Etymology. Not given at the original description. Presumably derived from the Fijian term 'Viti' for Fiji, the type locality.

***Phassodes walteri* Grehan & C. Mielke, sp. n.**

(Figs. 3, 6c, 6f, 7c, 9c, 11, 15b, 16b, 17c, 18b, 20a–c, 22b)

Diagnosis. Male genitalia with a subrectangular postero-dorsal projecting lobe with three blunt points along margin of anogenital field distinguish this species from the rounded lobe of *P. samoa* sp. n., and from *P. vitiensis* with a separate posteriorly curved point (Fig. 2b).

Description. Male. *Wingspan*: 95 mm (Fig. 3). FW length: 42 mm, width 22 mm; HW length 33 mm, width 24 mm.

Head. (Figs. 6c, 6f, 7c) Antenna with 42 antennomeres. Palps as for genus.

Thorax. As for genus.

Legs. (Fig. 9c) Leg proportions: pro:meso:meta 1:1.2:0.87.

Wings. (Fig. 11) As for genus.

Abdomen. (Figs. 15b, 16b, 17c, 18b) As for genus.

Genitalia. (Figs. 20a, 20b, 20c, 22b) Pseudotegumen strongly sclerotized along anogenital margin and ventral apex; postero-ventral tooth lateral ridge about half length of pseudotegumen; postero-dorsal tooth forming subrectangular lobe with an uneven edge. Fultura superior 'H' shaped, narrowing slightly posteriorly below pseudotegumen. Fultura inferior subsquare, narrower posteriorly with concave lateral margins.

Female unknown.

Distribution. Guadalcanal, Solomon Islands. Known only from the type locality (Fig. 30).

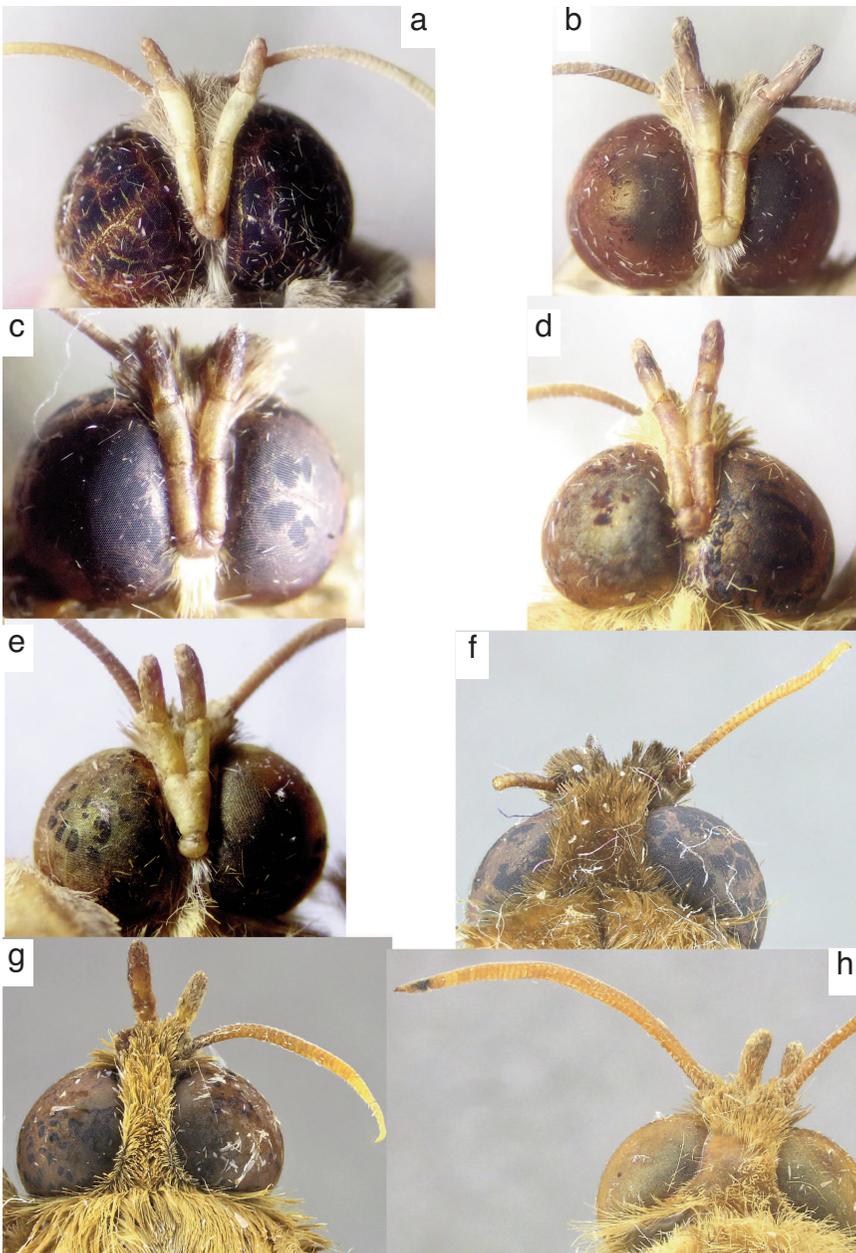


Fig. 6. *Phassodes* spp. Head, ventral view: (a) *P. vitiensis* male (M278), (b) *P. vitiensis* female (F301), (c) *P. walteri* sp. n., male holotype, (d) *P. samoa* sp. n., male holotype, (e) *P. tutuila* sp. n., female holotype (photos by John Grehan); dorsal view: (f) *P. walteri* sp. n. male holotype, (g) *P. samoa* sp. n., male holotype, (h) *P. tutuila* sp. n., female holotype (photos by James Boone).



Fig. 7. *Phassodes* spp. Antenna apex, lateral view: (a) *P. vitiensis* male (BPBM voucher), (b) *P. vitiensis* female (BPBM voucher), (c) *P. walteri* sp. n. male holotype, (d) *P. samoa* sp. n., male holotype, (e) *P. tutuila* sp. n. female holotype (photos by James Boone, Miho Maeda, and Agnes Stubblefield).

Type. Holotype ♂ (BPBMENT 20080134303): Solomon Islands, Guadalcanal Island, 50–80 m, Lunga River envt. [environment] 2–10 km S of Barana Village, Honiara Region, 23.XI–18.XII. 2016, St Jákl et V. Gurko leg. / *Holotypus*, *Phassodes walteri* Grehan & C. Mielke des. 2020 /. Dissection JRG M302. Donated to BPBM.

Etymology. Named for Walter Herman Grehan, in celebration of his 90th birthday, and in recognition of his many years of support for the entomological interests of JRG.

***Phassodes samoa* Grehan & C. Mielke, sp. n.**

(Figs. 4a–c, 6d, 6g, 7d, 9d, 10a, 11, 12a–b, 15c, 16c, 17d, 18c, 21a–c, 22c, 23a, 27a)

Phassodes vitiensis Rothschild; *sensu* Comstock (1966: 62).

Diagnosis. Male genitalia with a shallow postero-dorsal projecting convex lobe along margin of anogenital field distinguish this species from *P. vitiensis* with a postero-dorsal shark-fin tooth and *P. walteri* sp. n. with a subrectangular postero-dorsal projecting lobe with three blunt points (Fig. 22c).

Description. Male. *Wingspan*: 85 mm; *FW length*: 47 mm, width 20 mm; *HW length*: 30 mm, width 17 mm (Figs. 4a–c).

Head. (Fig. 6d, 6g, 7d) Antenna with 40 antennomeres. Palps as for genus.

Thorax. As for genus.

Legs. (Fig. 9d) Leg ratio 1:1.25:0.97.



Fig. 8. Leg morphology and scales. *Phassodes vitiensis*. Male (BPBM voucher, dissection M278): (a) proleg, (b) mesoleg, (c) metaleg; female (BPBM voucher, dissection F301) (d) distal tarsus and arolium. *Abantiades latipennis* (JRGc): (e) metaleg showing scales of femur (pale yellowish brown) and tibia (long grey scales) (photos by John Grehan).

Wings. (Figs. 10a, 11, 12a, 12b) As for genus.

Abdomen. (Figs. 15c, 16c, 17d, 18c) As for genus.

Genitalia. (Figs. 21a–c, 22c, 23a) Saccus broadly V-shaped. Pseudotegumen postero-ventral tooth lateral ridge extending 1/4 distance to dorsal edge; postero-dorsal tooth forming shallow, triangular knob merging with concave margin dorsally. Fultura superior sub-rectangular, wider than long, posterior margin with shallow notch medially, fultura inferior subsquare, narrower posteriorly with concave lateral margins.

Female (dissection available only). *Genitalia.* (Fig. 27a) Central lobe weakly sclerotized, narrower dorsally; dorso-medial digitiform process slightly taller than central lobe, angled medially, apex forming a sharp, acute point; bursa copulatrix damaged, only a portion of ductus bursae remaining – not described.

Distribution. Upolu Island, Samoa. Known only from the type locality (Fig. 30).

Types. Holotype ♂ (BPBMENT 2008013404): Afiamalu, Upolu, Samoa, vi-10-40 [10.IV.1940]/ At light / Swezey and Zimmerman collectors/ *Holotypus*, *Phassodes samoa* Grehan & C. Mielke des. 2020 / Dissection JRG M277 (BPBM). Paratypes (1♂, 1♀). All Samoa: 1♂, Samoa, 1914-1918. R. W. Tate Collection. Dissection L35, JSD [John S. Dugdale] (NZAC). Note: Robert Ward Tate was the New Zealand Governor of Samoa between 1919 and 1923. He is recorded as having an interest in the study of insects (Eteuati 1982); 1♀, Alafua, [Western] Samoa. Dissection L36, JSD (NZAC).

Etymology. Named for the country of Samoa.

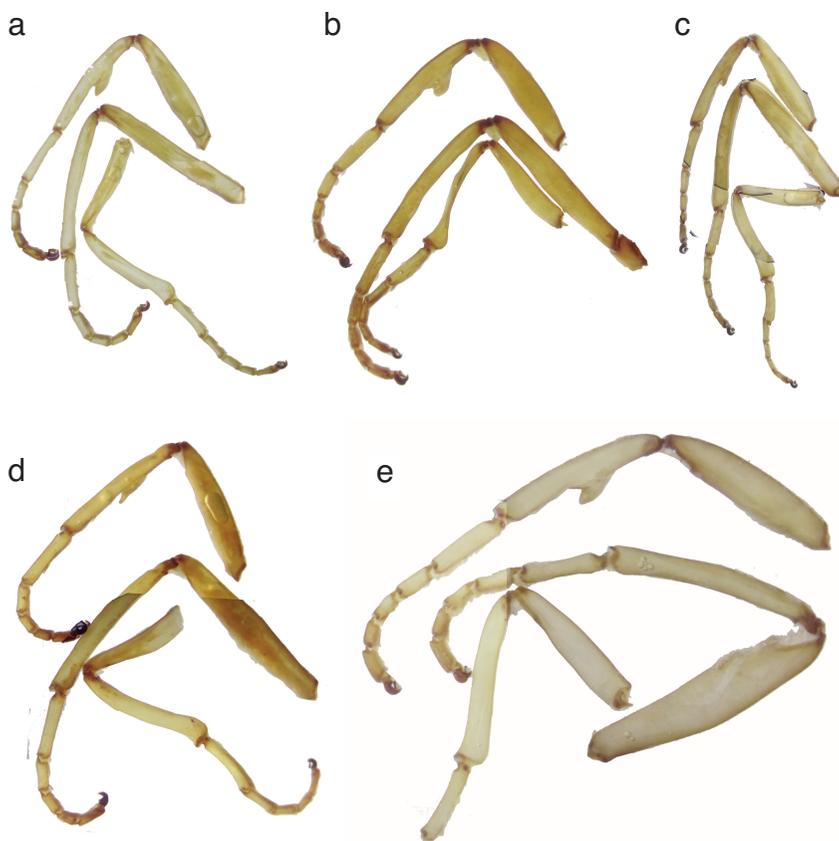


Fig. 9. *Phassodes* spp. leg morphology: (a) *P. vitiensis* male (M278), (b) *P. vitiensis* female (F301), (c) *P. walteri* sp. n. male holotype, (d) *P. samoa* sp. n. male holotype, (e) *P. tutuila* sp. n. female holotype (photos by John Grehan).

***Phassodes tutuila* Grehan & C. Mielke sp. n.**

(Figs. 5a–b, 6e, 6h, 7e, 9e, 10b, 11, 15d, 16d, 17e, 18d, 27b, 28)

Phassodes vitiensis (Rothschild); *sensu* Tams (1935; plate XII, fig. 1).

Diagnosis. Distinguished from the female of *P. vitiensis* by a narrower ductus bursae and from the female of *P. samoa* sp. n. by the narrower triangular shape of the central lobe of the lamella antevaginalis.

Description. Female. *Wingspan*: 88 mm; *FW length*: 45 mm, *width* 19 mm; *HW length*: 33 mm, *width* 17 mm (Figs. 5a–b).

Head. (Figs. 6e, 6h, 7e) Antenna with 54 antennomeres. Palps with basal palpomeres fused (may represent an aberration).

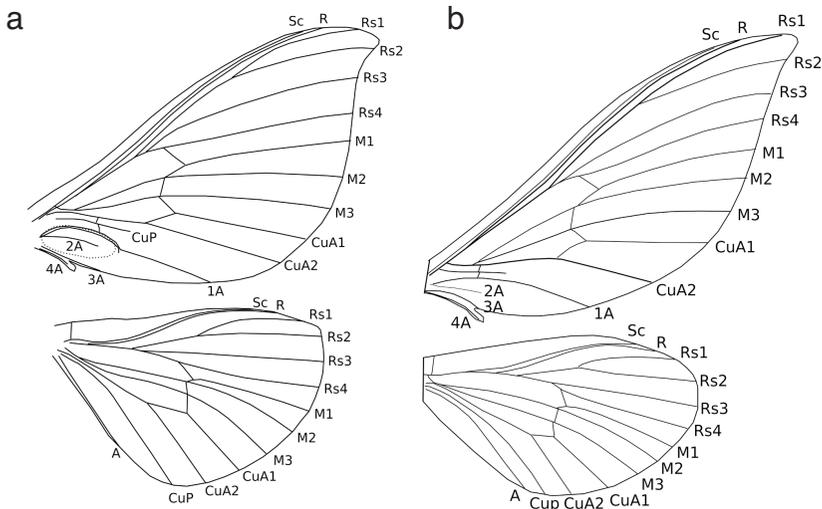


Fig. 10. *Phassodes* spp. wing venation: (a) *P. samoa* sp. n. male, (b) *P. tutuila* sp. n. female. Diagram by John Grehan.



Fig. 11. Selection of scales from central forewing (10 x magnification). Top row – *S. walteri* sp. n. male, central row – *S. tutuila* sp. n. female, bottom row – *S. samoa* sp. n. male. Photos by James Boone, Miho Maeda, and Agnes Stubblefield.

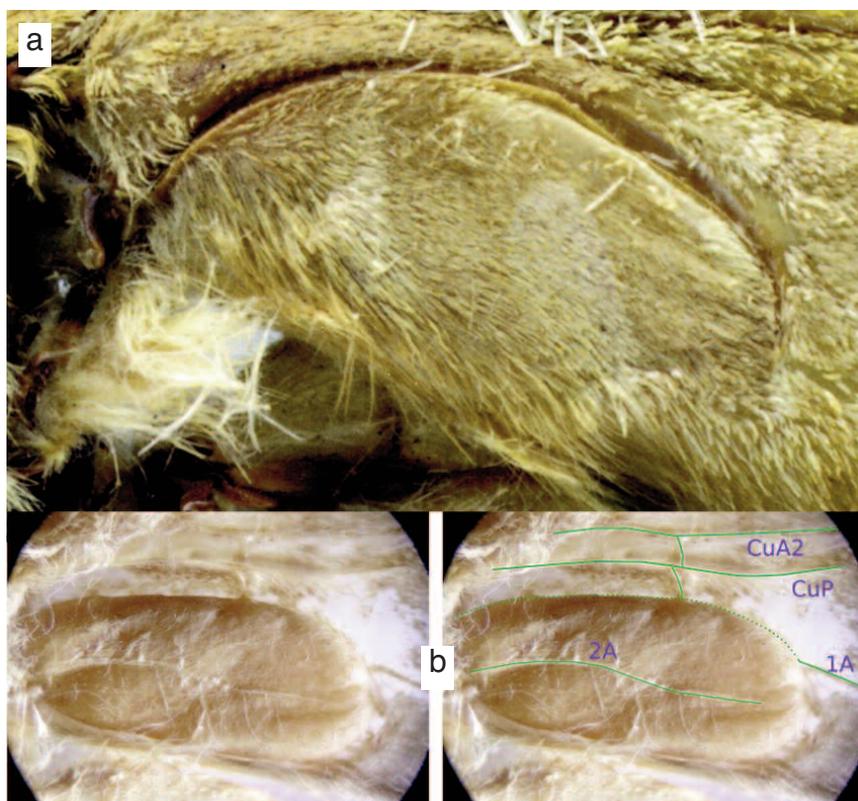


Fig. 12. *Phassodes samoa* sp. n. male holotype forewing scent gland and venation: dorsal (**a**) and ventral (**b** – right figure with veins highlighted) (dorsal photo by Jane Hyland, ventral by John Grehan).

Thorax. (Fig. 11) As for genus.

Legs. (Fig. 9e) As for genus. Tarsi missing from hind leg, precluding comparative length measurements.

Wings. (Fig. 10b) As for genus.

Abdomen. (Figs. 15d, 16d, 17e, 18d) As for genus.

Genitalia. (Figs. 27b, 28) Ductus bursae narrower than in *P. vitiensis*, distal apex of corpus bursae pointed.

Distribution. Tutuila Island, American Samoa. Known only from the type locality (Fig. 30).

Types. Holotype ♀ (BPBM 2008013405): near Pago Pago, Am. Samoa, July 28 1961, J.A. Comstock [leg.] / *Holotypus*, *Phassodes tutuila* Grehan & C. Mielke des. 2020 / Dissection JRG F276 (BPBM). Paratype (1♂). Same locality and collector as the holotype, 7 June 1961 (BPBM).

Etymology. Named for Tutuila, the main island of American Samoa.

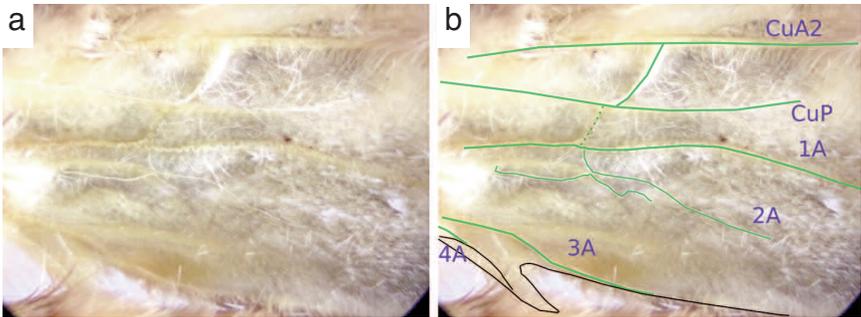


Fig. 13. Ventral view of *Abantiades latipennis* male forewing basal veins (JRGC). (a) *in situ*, (b) labeled (image by John Grehan).



Fig. 14. *Phassodes vitiensis* male hindwing androconial tuft arising from base of posterior hindwing margin close to basal sclerites.

DISCUSSION

In general color pattern, *Phassodes* are distinct from all other Hepialidae. The separation of *Phassodes* as a monophyletic group is supported by the following unique features that together provide strong corroboration for *Phassodes* being a phylogenetically valid genus.

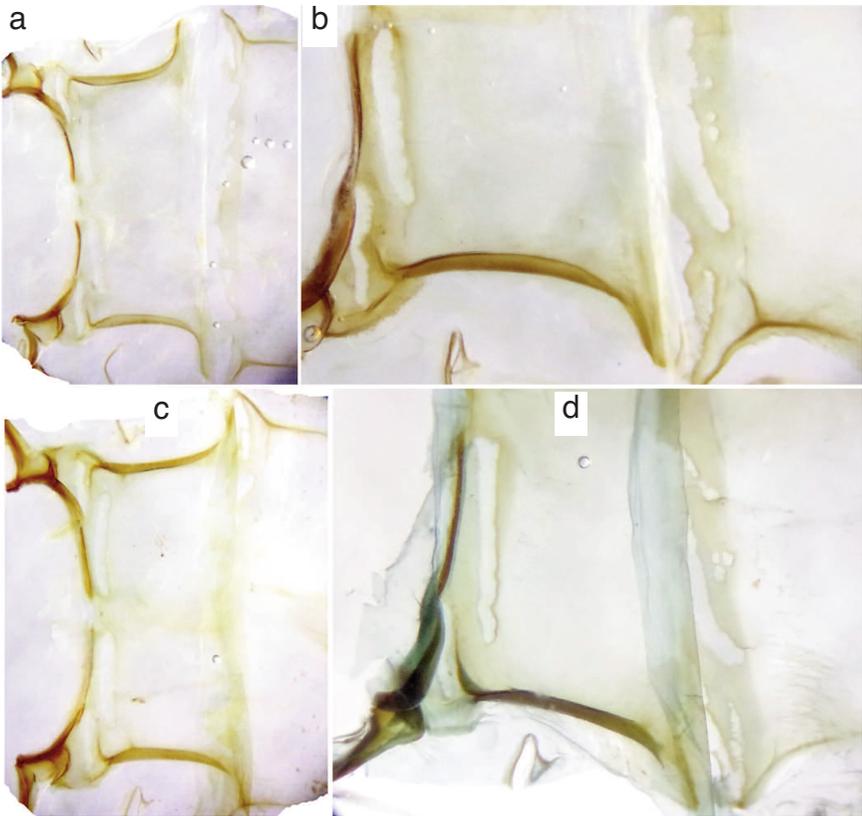


Fig. 15. *Phassodes* spp. Tergum II and III (partial): (a) *P. vitiensis* male (M278), (b) *P. walteri* sp. n. male holotype, (c) *P. samoa* sp. n. male holotype, (d) *P. tutuila* sp. n. female holotype (photos by John Grehan).

These features are phylogenetically derived as they are not present in an outgroup comprising the other exoporian families Anomosetidae (Kristensen 1978a), Neotheoridae (Kristensen 1987b, Simonsen & Kristensen 2017), Palaeosetidae (Davis *et al.* 1995), Prototheoridae (Davis 1996), and Mnesarchaeidae (Gibbs & Kristensen 2019) and are also absent from other Hepialidae (JRG & CGCM, pers. observ.).

- 1) **Shape of the dorsal plate** (Figs. 26a, 27a, 27b). The dorso-ventrally elongate dorsal plate of the female genitalia with convex inner and outer margins is unique within the Exoporia.
- 2) **Shape of the pseudoteguminal arms** (Figs. 19–22). The apex forms a short point on each pseudotegumen plate which is basally fused across the median giving the appearance of a short, two pronged fork.

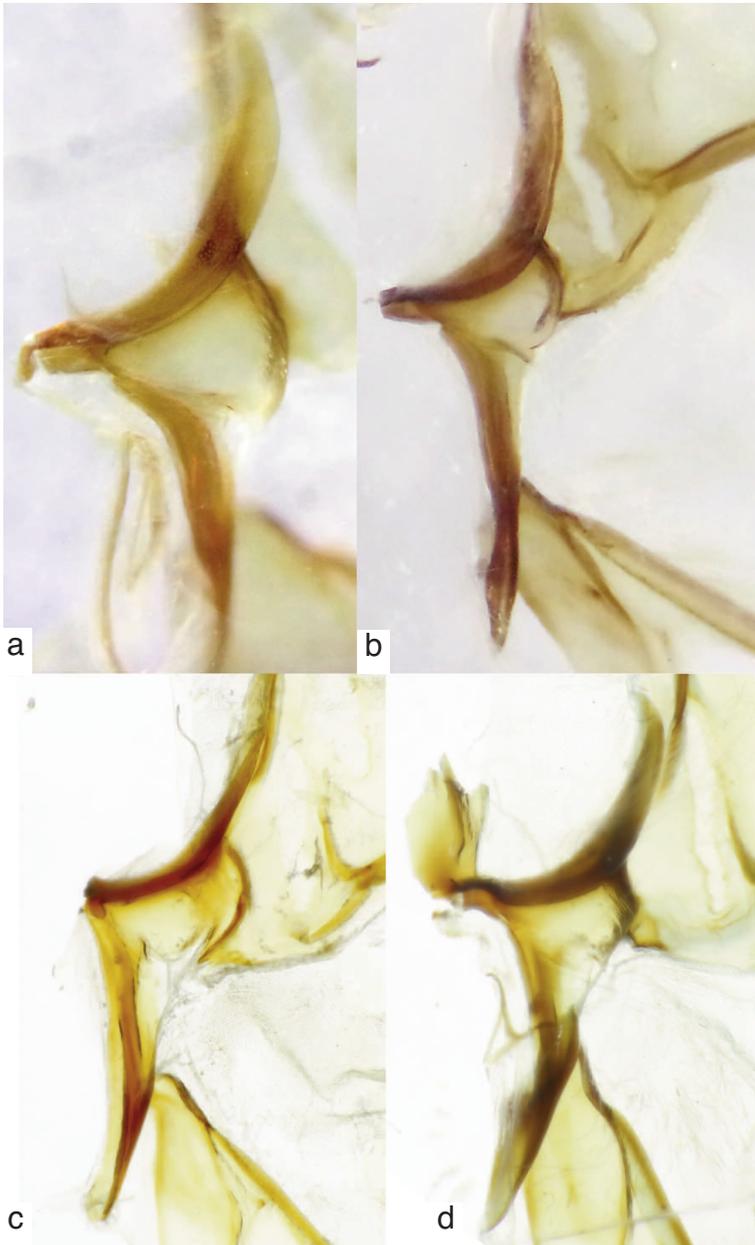


Fig. 16. *Phassodes* spp. Tergosternal connection: (a) *P. vitiensis* male (M278), (b) *P. walteri* sp. n. male holotype, (c) *P. samoa* sp. n. male holotype, (d) *P. tutuila* sp. n. female holotype (photos by John Grehan).

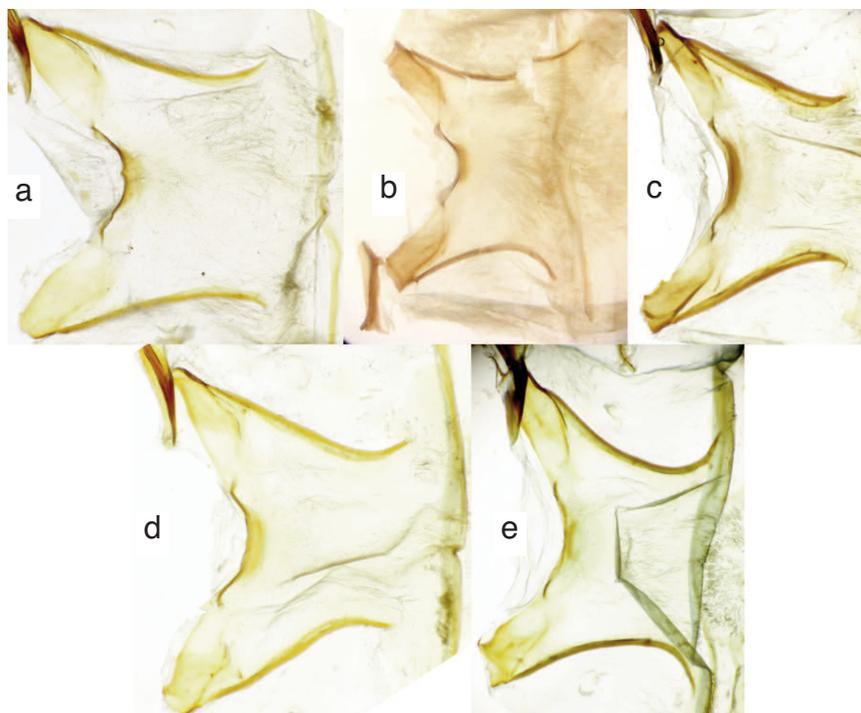


Fig. 17. *Phassodes* spp. Sternum II: (a) *P. vitiensis* male (M278), (b) *P. vitiensis* female (L34), (c) *P. walteri* sp. n. male holotype, (d) *P. samoa* sp. n. male holotype, (e) *P. tutuila* sp. n. female holotype (photos by John Grehan).

- 3) **Lateral ridge of postero-ventral tooth** (Figs. 19–22). On the side of each pseudotegumen plate there is a straight ridge extending back from the base of the postero-ventral tooth.
- 4) **Wing pattern** (Figs. 1–5). Although a more diffuse feature, the wing pattern involves a series of distinctly sub-circular spots of greater or lesser intensity scattered over most of the FW. Although some *Aenetus* species also have ovoid shapes to the ground pattern, they never form sub-circular spots as with *Phassodes*.

A potential fifth unique characteristic is the presence of two sclerotized patches present along the dorsal wall of the antrum. This feature is not recorded in other exoporian families, but we have not yet examined the antrum of all other Hepialidae to be certain of its presence or absence in other genera within the family. We note that the structure is absent at least from the Australian *Abantiades* (Simonsen 2018).

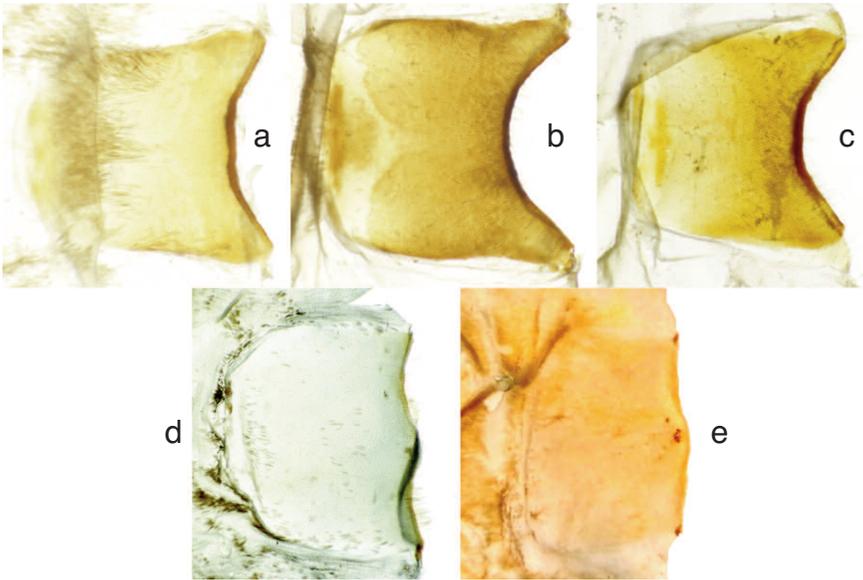
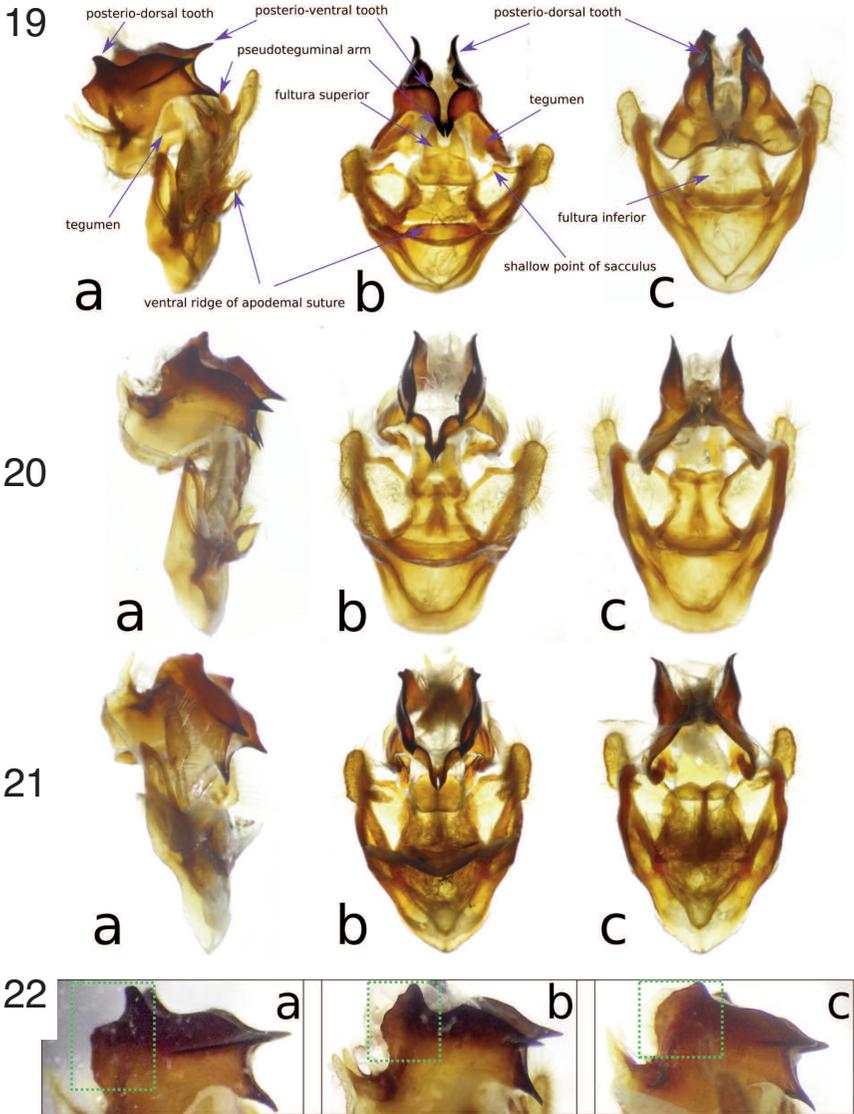


Fig. 18. *Phassodes* spp. Sternum VIII: (a) *P. vitiensis* male (M278), (b) *P. walteri* sp. n. male holotype, (c) *P. samoa* sp. n. male holotype, (d) *P. tutuila* sp. n. female holotype, (e) *P. vitiensis* female (F301) (photos by Ryan St Laurent).

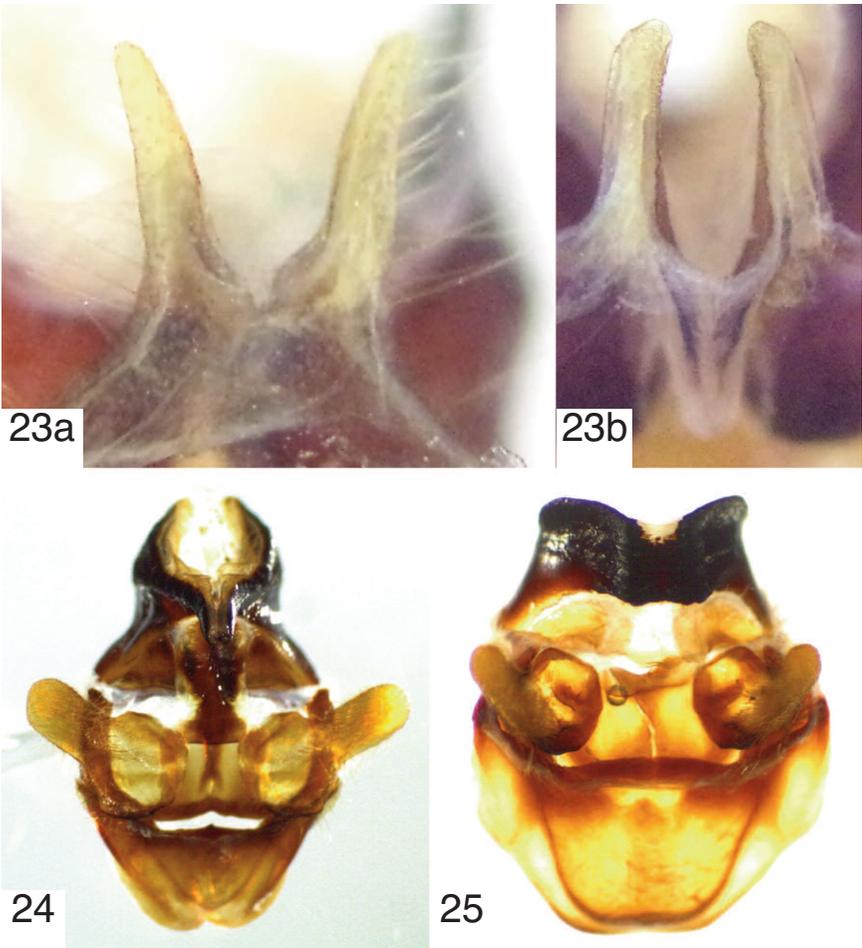
Species status

The three species with males known differ from each other by the shape of the postero-dorsal tooth of the pseudotegumen as illustrated in Fig. 22. These distinction are paralleled by differences in the shape of sternite II in the male where the lateral ridges are almost sub-parallel and only weakly curved posteriorly in *P. vitiensis* (Fig. 17a), broad and more angled postero-medially in *P. walteri* sp. n. (Fig. 17c) and narrow and postero-medially angled in *P. samoa* sp. n. (Fig. 17d). The medially sclerotized anterior margin of *P. vitiensis* and *P. samoa* sp. n. are more similar to each other than to *P. walteri* sp. n. by the lateral edge being more attenuated.

Although *P. tutuila* sp. n. is represented by a female only, the external genitalia are distinct with respect to the shape of the central lobe which forms a tapered sub-triangular dorsal projection (Fig. 27b), in contrast to *P. samoa* sp. n. where the dorsal projection is more sub-rectangular (Fig. 27a) and to *P. vitiensis* where it forms a broad triangular shape with a rounded dorsal margin (Fig. 26a). The bursa copulatrix of *P. tutuila* sp. n. has a narrow ductus bursae (Fig. 28) compared to that of *P. vitiensis* (Fig. 26b), but cannot be compared with *P. samoa* sp. n. due to damage to most of the internal genitalia. There is also evidence of species differences in the shape of the terminal segment of the antenna – elongate in *P. vitiensis*, narrow in *P. walteri* sp. n., broad in *P. samoa* sp. n., slightly falcate in *P. tutuila* sp. n. (Fig. 7) although the latter is only known for the female.



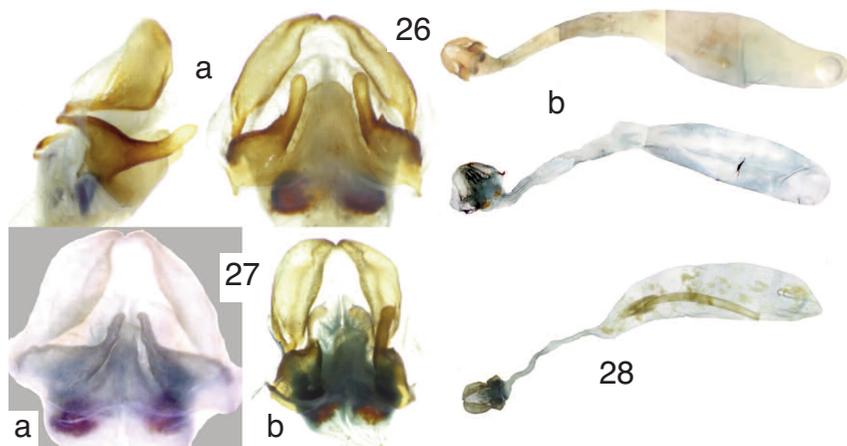
Figs. 19–22. *Phassodes* spp. Male genitalia. **Fig. 19.** *Phassodes vitiensis* male genitalia (M278): (a) ventral, (b) lateral, (c) dorsal. (photos by Ryan St Laurent). **Fig. 20.** *Phassodes walteri* sp. n. Holotype male genitalia: (a) ventral, (b) lateral, (c) dorsal. (photos by Ryan St Laurent). **Fig. 21.** *Phassodes samoa* sp. n. Holotype male genitalia: (a) ventral, (b) lateral, (c) dorsal. (photos by Ryan St Laurent). **Fig. 22.** *Phassodes* spp. Postero-dorsal tooth shape (within dotted square) of pseudotegumen: (a) *P. vitiensis* (M278), (b) *P. walteri* sp. n. holotype, (c) *P. samoa* sp. n. holotype.



Figs. 23–25. Hepialidae spp. Male genitalia. **Fig. 23.** Digitiform process of the tergal lobe: (a) *Phassodes samoa* sp. n. holotype, (b) *Abantiades magnificus*, dissection JRG M229 (NZAC) (photos by John Grehan). **Fig. 24.** *Abantiades hyalinatus*. Male genitalia, ventral view. Dissection JRG M220 (CMNH) (photo by John Grehan). **Fig. 25.** *Andeabatis chilensis*. Male genitalia, ventral view. Dissection JRG M211 (USNM) (photo by John Grehan).

Relationships between *Phassodes* and other Hepialidae

The general size and wing shape of *Phassodes* is reminiscent of some *Aenetus* species while the broad and short HW relative to FW length is similar to *Abantiades* (cf. Simonsen 2018). *Phassodes* also shares the presence of an epiphysis and arolium with most other Australasian Hepialidae (Table 2), but these features are also applicable to many genera and at least some other hepialoid families which preclude their shared presence being unequivocally informative within the Hepialidae. But several other features are potentially informative about



Figs. 26–28. *Phassodes* spp. Female genitalia. **Fig. 26.** *Phassodes vitiensis* female genitalia: (a) external genitalia in posterior (left) and lateral (right) views (photos by Ryan St Laurent) Dissection JRG D304 (BPBM), (b) bursa copulatrix; upper (L34) (NZAC), lower (F304) (photos by John Grehan). **Fig. 27.** Female external genitalia, (a) *Phassodes samoa* paratype (photo by John Grehan), (b) *Phassodes tutuila* holotype (photo by Ryan St. Laurent). **Fig. 28.** *Phassodes tutuila* holotype bursa copulatrix (photos by John Grehan).

close phylogenetic relationships between *Phassodes* and Australian or South American hepialid genera since these features are absent from other families of Exoporia and are therefore derived within the Hepialidae. These features are discussed next to assess their validity and significance for identifying the probable sister group of *Phassodes*.

(a) Metatibial androconia. Records of this structure being present in *Phassodes* (Nielsen & Robinson 1983, Grehan 2012, Grehan & Rawlins 2016) are incorrect. Detailed examination of the metatibia shows that while the long metatibial scales present the superficial appearance of an androconial scale tuft (Fig. 8c), the individual scales lack a fluid filled basal swelling found in metatibial androconial scales. Instead, the scales are uniformly thin, hair-like (not rod-like) and strongly attached to the tibia (instead of being loosely attached like the androconial scales, JRG pers. observ.). The metatibia is also well sclerotized and of even width from proximal to distal ends with no indication of localized swelling or thinning of the cuticle. Metatibial androconia are present in several genera, but they do not comprise a monophyletic entity (Table 2).

(b) Hindwing androconia. Only two genera of Hepialidae are recorded with this feature – *Phassodes* and the Chilean *Puermytrans* Viette, 1951 (Table 1). Hindwing androconia are also known in the hepialoid families Anomosetidae and Palaeosetidae (Kristensen 1978, Davis *et al.* 1995). In the Anomosetidae the HW androconia are located within the posterior margin which is folded up over the dorsal surface of the HW and enclosing the androconia (Kristensen 1978). For the Palaeosetidae, Davis *et al.* (1995) noted that the HW androconia of male *Ogygioses* Issiki & Stringer, 1932 are superficially similar to that of Anomosetidae, but the hair ultrastructure is different and suggested that different origins were involved as there were no other indications of a close relationship between these two

Table 1. Presence of epiphysis and arolium in some primitive exoporian families and Australasian genera.

	Epiphysis	Arolium	Reference
Neotheoridae	+		Simonsen & Kristensen (2017)
Palaeosetidae	+	+	Davis (1996)
Prototheoridae	+ (vestigial)	+	Davis (1996)
Hepialidae			
<i>Abantiades</i>	+	+	Simonsen (2018)
<i>Aenetus</i>	+	+	Simonsen (2018)
<i>Aoraia</i>	+	+	Dugdale (1994), JRG, pers. observ.
<i>Archaeo-aenetus</i>	+	+	Simonsen (2018)
<i>Cladoxycanus</i>	+	?	Dugdale (1994)
<i>Dioxycanus</i>	+	?	Dugdale (1994)
<i>Dumbletonius</i>	+	+	Dugdale (1994), JRG, pers. observ.
<i>Elhamma</i>	+	+	Simonsen (2015)
<i>Heloxycanus</i>	+	?	Dugdale (1994)
<i>Jeana</i>	+	+	E. Beaver, pers. comm.
<i>Oncopera</i>	+	+	Simonsen (2018)
<i>Oxycanus</i>	+	+	Beaver <i>et al.</i> (2020)
<i>Wiseana</i>	+	?	Dugdale (1994)
<i>Zelotypia</i>	+	+	Simonsen (2018)

taxa. Folding up over the dorsal surface and enclosing androconial hairs has also been documented for *Puermytrans* (Nielsen & Robinson 1983). In *Phassodes* the androconial tuft originates at the base of the posterior HW margin at the junction with the wing sclerites (Fig. 14), and this appears to be different from the arrangement in Anomosetidae and Palaeosetidae, but further comparative descriptions are necessary before definite conclusions may be reached. The shared presence of HW androconia in *Phassodes* and *Puermytrans* is phylogenetically equivocal due to the presence of apparently similar structures at least one other hepialoid family (Table 2). There are also other forms of androconia or similar scale formations in the Hepialidae such as the androconial tuft on the HW between CuA and CuP in *Fraus* Walker, 1856 (Nielsen & Kristensen 1989) and rows of long, erect rod-like scales occur on the hind and ventral FW of *Leto venus* (Cramer, 1780) (Grehan *et al.* 2019).

Table 2. Presence of three scent producing structures in Hepialoidea.

	Metatibial androconia	FW gland	HW androconia	Source
Palaeosetidae				
<i>Ogygioses</i>	+	+ (single species)	+	Davis <i>et al.</i> (1995)
Hepialidae				
<i>Aenetus</i>	+			Simonsen (2018)
<i>Archaeoaenetus</i>				Simonsen (2018)
<i>Hepialus</i>	+			Grehan & Rawlins (2016)
<i>Kozloviella</i>	+			Grehan & Mielke (2018c)
<i>Oncopera</i>	+	-		Simonsen (2018)
<i>Palpifer</i>		+		Grehan & Mielke (2019b)
<i>Pfitzneriella</i>	+			Grehan & Mielke (2018c)
<i>Phassodes</i>		+	+	Current study
<i>Phassus</i>	+			Mielke & Grehan (2015)
<i>Phthius</i>	+			Mielke & Grehan (2017)
<i>Phymatopus</i>	+			Wagner (1985)
<i>Puermytrans</i>	+	+	+	Nielsen & Robinson (1983)
<i>Schausiana</i>	+			Mielke & Grehan (2015)
<i>Sthenopsis</i>	+			Grehan & Rawlins (2016)
<i>Thitarodes</i>	+			Zhu <i>et al.</i> 2004
<i>Zenophassus</i>	+			Tindale (1941)
<i>Viridigigas</i>		+		Grehan & Rawlins (2016)

(c) Basal FW scent gland. This is a prominent structure in the male *Phassodes* FW, positioned posterior to 1A which curves along the anterior edge, and with 2A extending medially along the ventral surface. A FW gland is also present in *Puermytrans* (Nielsen & Robinson 1983) and *Viridigigas* Grehan & Rawlins, 2016 of Peru (Grehan & Rawlins 2016), both of which also share the presence of a prominent metatibial androconial tuft (unlike *Phassodes*). A scent gland in *Palpifer* Hampson, 1893 (Asia) is longitudinally bisected by the single A vein (Grehan & Rawlins 2016, Grehan & Mielke 2019b) and in this respect differs from the other hepialid genera. A basal FW scent gland is also present in *Ogygioses* (Palaeosetidae). However, Davis *et al.* (1995) noted that while this was strongly reminiscent of the scent gland of *Puermytrans*, the latter was invaginated behind, not within, vein 1A, and a strict homology seemed to be ruled out. This would preclude the structure constituting an ‘underlying’ synapomorphy (present in the common ancestor, but since lost in most descendants). However, the bisecting of the gland by 1A in *Palpifer*

is structurally similar in this respect. The ventral surface of the gland in *Phassodes* is devoid of scales or visible microtrichia, while very short scales (microtrichia?) line the inner surface of the gland in *Viridigigas* (Grehan & Rawlins 2016). The presence of this gland in various hepialoids may represent a common developmental genetic system that is switched on within different lineages and involves different structural genes. In this respect, the different morphological characteristics of the feature and its presence within genera that otherwise have no other strong evidence of close affinity may indicate that this structure is not immediately informative as to their phylogenetic relationships, but is in need of further study.

(d) Intermediate zone of the tergo-sternal connection. A structural similarity in the tergo-sternal sclerite shared between *Abantiades*, *Phassodes* and some South American genera was identified by Grehan (2010, 2012) as incorrect. There is a postero-lateral knob on the intermediate zone of the tergo-sternal sclerite that characterizes the cibyryne clade, a monophyletic group of Central and South American genera (Grehan 2012). The intermediate zone in *Phassodes* and *Abantiades* expands laterally and this initially seemed to represent a homologous condition, but close examination of *Phassodes* and *Abantiades* shows that this expansion involves the intermediate zone as a whole rather than a distinct postero-lateral knob. Nevertheless, the similarity shared by *Phassodes* and *Abantiades* does represent a derived feature within the Hepialidae that is potentially informative of a close affinity between these two genera, and it is recognized here as a shared derived character state.

(e) Male genitalia. The male genitalia of *Phassodes* show very strong similarities with those of the *Abantiades*, including the overall shape and proportions of individual structures. In some cases, the similarity is sufficiently strong that without knowing the provenance of a specimen, one might be forgiven mistaking *Phassodes* genitalia for those of an *Abantiades* species. General (non-unique) similarities include the shape of the valva described by Simonsen (2018) for *Abantiades* as "...large with a broad and rounded distal section and a well-defined sacculus" which is equally applicable to *Phassodes*. The two genera also share the presence of a large fultura inferior, a narrower elongate fultura superior, and a triangular tegumen (Fig. 24).

There are two features that represent uniquely shared character states. The first is the shape of the pseudoteguminal arms which are aligned next to each other, fused across the median, and are oriented anterior ventrally as a short (*Phassodes*) or longer (*Abantiades*) sub-tubular projection.

The second feature concerns the digitiform projection of the tergal lobe either side of the median (Figs. 23a, 23b). This structure was incorrectly referred to as a 'twin process' by Grehan (2012) but close examination shows the digitiform projections to be positioned on the dorsal margin of the pseudotegumen and form part of the membrane extending to the posterior margin of tergum VIII. This membrane represents a fusion of tergites IX and X, and since the digitiform projections are at the posterior of this membrane they represent modifications of the tergal lobe of tergum X (cf. Nielsen & Kristensen 1989). In addition, the digitiform projections are hollow and support setae, which is also a feature of the tergal lobe. In this respect the digitiform projection is different from the 'twin processes' that is part of the dorsal pseudotegumen enclosing the anogenital region as shown by Dugdale (1994).

(f) Female genitalia. The female genitalia do not show unequivocal evidence of close affinity between *Phassodes* and *Abantiades* or to any other genera. The external female genitalia in *Abantiades* is dorso-ventrally flattened, whereas in *Phassodes* it is tall and the lamella antevaginalis has a tall, subrectangular, central lobe with adjacent, dorsally-projecting, narrow digitiform processes. These lateral structures represent a derived feature within the Hepialidae and are absent from other exoporian families. *Phassodes* is the only Old World genus with this feature, while in the New World a similar structure is found in the genus *Phassus* Walker, 1856 of Central America. In the latter, the central lobe is strongly developed, varying from tall to broad, and the digitiform processes range from the short dorsal projections of *P. triangularis* Edwards, 1885 to long and thin in *P. huebneri* (Geyer, 1838) (JRG, pers. observ.).

(g) Lateral ridges of tergum III. All hepialids have a lateral ridge on tergum II, while a lateral ridge on tergum III is limited to *Phassodes*, *Afrotheora* Nielsen & Scoble, 1986, *Antihepialus* Janse, 1942, and *Aenetus*. Nielsen & Scoble (1986) noted that the lateral ridge is also present in some Prototheoridae and (weakly) in Anomosetidae. They believed that the tergum III ridge is unlikely to be the ground plan of the Hepialidae *sensu stricto* (Hepialidae exclusive of *Afrotheora*, *Antihepialus*, and *Gazoryctra* Hübner, 1820), which would mean that the shared similarity between the southern African *Afrotheora* and *Antihepialus* represents an apomorphic trait (Nielsen & Scoble 1986: 43). However, its presence in some other hepialoid families as well as *Phassodes* and *Aenetus* means that its phylogenetic significance is equivocal, as it could represent a hepialid plesiomorphy or it has evolved in some closely related genera (*Afrotheora*, *Antihepialus*) and others that are more distantly related to each other (*Phassodes*, *Aenetus*).

(h) Four FW anal veins. This shared condition has only been confirmed for two *Abantiades* species – *A. labyrinthicus* (Donovan, 1805) and *A. latipennis*. Presence of this condition in all *Abantiades* requires corroboration. Three of the veins are very small and 2A in particular is very thin, so these veins may be easily overlooked. A single vein only (probably 2A) was indicated for *A. hyalinatus* by Simonsen (2018). The relative size and position of the A veins is similar for *Abantiades* (Fig. 13) and *Phassodes*. In both vein 2A is extremely thin, and both 3A and 4A are close to the jugum, 3A extending just past base of outer edge of jugum, and 4A extending to or along the inner edge of jugum.

***Abantiades* and *Phassodes* as sister groups.** A sister group relationship is proposed between these genera on the basis of the following four uniquely shared character states. Although this phylogenetic relationship is not the result of a formal phylogenetic analysis, we have identified these character states with respect to all other Hepialidae with respect to the genitalia, and most other genera with respect to FW venation.

- 1) **Shape of tergo-sternal central region.** Both genera have a laterally inflated intermediate zone that is unique within the Hepialidae.
- 2) **Pseudoteguminal arms.** In both genera the apex of the pseudoteguminal arms are adjacent and extend ventrally as a short sub-tubular projection.
- 3) **Digitiform tergal lobes.** Tergal lobes form elongate, digitiform projections either side of the median (Figs. 23a and 23b).
- 4) **Forewing anal veins.** The four anal veins present in both genera share a similar form and arrangement.

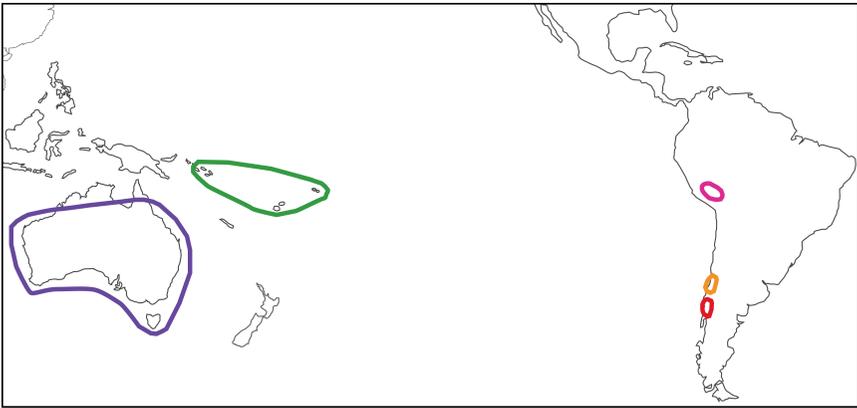


Fig. 29. Genera referred in the text on systematic relationships. Distribution ranges of *Abantiades* (blue outline), *Phassodes* (green outline), *Andeabatis* (red outline), *Puermytrans* (orange outline), and *Viridigigas* (purple outline). Distribution data from Nielsen & Robinson (1983), Grehan & Rawlins (2016) and Simonsen (2018)

There are also broader levels of shared similarity between *Phassodes* and *Abantiades*, although these are not unique. They include the general shape and relative size of the pseudotegumen and saccus, and elongate labial palps (the latter representing a plesiomorphic condition for the Hepialidae). These features are also evident in the southern Andean genus *Andeabatis* Nielsen & Robinson, 1983 (Fig. 25) which lacks the narrowly fused pseudoteguminal arms (instead having a broad barrel-shaped region of fusion). In particular, the short and relatively broad valva with a broad ovoid sacculus is unlike the valve of other southern South American genus (cf. Nielsen & Robinson 1983). It is also of potential phylogenetic interest that the FW color pattern of *Andeabatis* comprises concentric ovoid patches of gold bordered with black and within the Hepialidae this feature is only otherwise found in two species of *Abantiades* – *A. ocellatus* Tindale, 1932 and *A. sericatus* Tindale, 1932 (cf. Nielsen & Robinson 1983, Fig. 212; Simonsen 2018, plate 1, Figs. e–h). The potential relationship with *Andeabatis* requires further study. The FW of *Andeabatis* has dark-tipped wing scales that are also found in other New World genera such as *Druceiella* Viette, 1949, *Pfitzneriana* Viette, 1950, *Pseudodalaca* Viette, 1950, *Hampsoniella* Viette, 1950 and *Wallacella* C. Mielke, Grehan & Cock, 2020 (Nielsen & Robinson 1983; JRG & CGCM pers. observ.). The shared presence of the digitiform lateral lobes of the lamella antevaginalis in *Phassodes* and *Phassus*, the wing scent organs in *Phassodes* and *Puermytrans*/*Viridigigas*, and structural similarities of the male genitalia in *Phassodes* and *Andeabatis* also represent alternative potential relationships involving South American taxa (Fig. 29), or they are indicative of broader relationships that have yet to be analyzed in detail. Molecular studies may provide further clarification.

A further morphological similarity concerns the size and shape of scales on the metatibia of *Phassodes* (Fig. 8c) and *Abantiades* (Fig. 8e). While the metatibial scales are not androconia, they do form a considerable tuft of long thin scales that may give the

superficial appearance of androconia. This scale formation may represent a derived condition for members of the Hepialidae but this cannot be assessed at this time due to the lack of documentation of metatibial scale formation in exoporian genera.

Biogeographic analysis

The method applied here uses biogeographic-tectonic correlation, a panbiogeographic method, to estimate the age of clades (Croizat 1958, 1964; Craw *et al.* 1999; Heads 2012a). Fossils are used to provide constraints on minimum ages only. The tectonic correlation method contrasts with other methods that use fossil-based calibrations to incorrectly provide maximum clade ages. Tectonic correlation involves the following steps: (1) identify sister clades, (2) identify geographic location of phylogenetic breaks between sister clades, and (3) identify tectonic features coinciding with distributional boundaries or phylogenetic discontinuities.

Tectonic correlation provides evidence for a historical relationship between extant distribution and the geological history of the region. The geographic break is identified with respect to the minimum distance criterion, based on the premise that in the absence of any other evidence to the contrary, the shortest geographic distance between disjunct sister taxa is more likely to reflect the historical origin of that disjunction (Page 1987, Craw *et al.* 1999).

The continental (Australian) *Abantiades* is allopatric and disjunct with its putative sister group *Phassodes*, restricted to oceanic islands at the western edge of the Pacific Plate. The *Phassodes* localities of Fiji and the Solomon Islands lie near the Australian-Pacific Plate margin. Along with Vanuatu and Tonga, these islands once formed a continuous island arc which was rifted apart into the separate arcs by sea-floor spreading (Heads 2006). The Vanuatu segment was pushed to the southwest by the opening of the North Fiji basin (Pelletier & Auzende 1995, Ruelland & Lagabrielle 2005). The overall distribution of *Phassodes*, as well as the disjunction between the Solomon Islands and Fiji, follows the trend of the Vitiāz Trench (Fig. 30), a former Indo-Australia-Pacific plate boundary that was extinct by ~20–15 Ma (Pelletier & Auzende 1995, Mann & Taira 2004, Price *et al.* 2014). *Phassodes* is also present on the Samoan islands, which are formed by a hotspot, not subduction zone volcanism. The island of Upolu has an age of about 3 Ma, while the adjacent island of Savai'i is estimated to be ~5 Ma (Koppers *et al.* 2008). The Samoan hotspot, however, is much older than this, with former Samoan volcanoes extending west and reaching a maximum age of ~22 Ma. Hart *et al.* (2004) suggest that the Samoan hotspot has been active since at least 40 Ma and earlier volcanoes would have been lost by subduction at the Vitiāz Trench. The lifespan of some of these volcanoes may also be prolonged by rejuvenated volcanism (Koppers *et al.* 2011, Konter & Jackson 2012).

While the Samoan islands are not directly part of the Vitiāz Trench, the hotspot trail has been merging with the Trench for at least 40 million years and perhaps throughout the existence of the former trench. These ancestral Samoan islands along the northern edge of the Vitiāz Trench would likely have been occupied by *Phassodes*. The geographic disjunction between *Phassodes* and its potential Australian sister group, *Abantiades*, spatially coincides with the basin that has opened between the subduction zone and Australia. The subduction zone originally ran along the east coast of Gondwana (Australia), but began to move eastwards in a process termed slab or trench rollback (Fig. 31). This rollback began at ~100 Ma and continues to the present day (Heads 2017).

The regional geology and the biogeography of *Phassodes* are consistent with a vicariance model in which the range of the *Phassodes* + *Abantiades* ancestor was broken

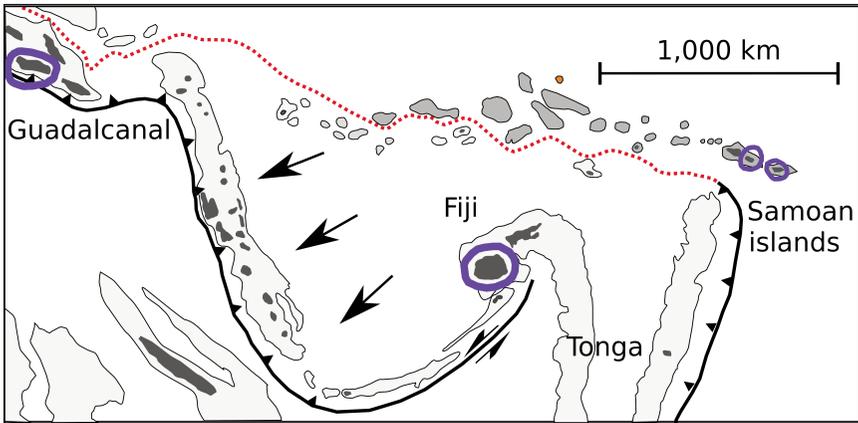


Fig. 30. Distribution map for *Phassodes* (blue outlines) and local tectonics. Thick black lines – major plate boundaries pointing in the direction of subduction beneath over-riding plate with barbs on the over-riding plate; dotted red line – Vitiaz Trench; arrows – direction of expansion of North Fiji Basin; half arrows – direction of plate movement either side of transform fault; Dark grey shading – current islands; pale and intermediate shading – submerged ridges, seamounts, and island slopes (from Pelletier & Auzende 1995).

apart with slab rollback. The continental (Australian) component became *Abantiades* while the island arc component became *Phassodes*. There is a 2000 km disjunction in *Phassodes* between the Solomons and Fiji. This could be explained by extinction during the south-westward rollback of the subduction zone between these two areas with the opening of the North Fiji basin. This explanation is also consistent with the existence of the same disjunction in many other animal and plant groups, such as *Dictyophlebes* (Angiosperms: Araliaceae) in Fiji and the Solomons (Plunkett & Lowry 2012), the frog sister group subgenera *Platymantis* (*Yanuboto*) (Fiji) and *Platymantis* (*Discodeles*) (Solomons) (Brown *et al.* 2015), *Phasmotaenia* stick insects (Fiji, Solomon Islands, New Guinea, Philippines, and Micronesia), *Heterospathe* palms (Fiji, Solomon Islands, New Britain, New Guinea, Maluku Islands, Philippines), and *Allorthorhinus* beetles (Fiji, Solomons, Philippines) (Heads 2014). These examples show that the Vitiaz trench disjunction in *Phassodes* is a general pattern and is shared by taxa with widely varying means of dispersal.

***Phassodes* species as descendants of a subduction zone weed**

Little is known about the detailed ecology of *Phassodes*. In Fiji *P. vitiensis* has a broad elevation range between c.1100 m at Nandarivatu (near the highest point of Fiji, Mt Tomanivi/Victoria, 1800 m with distinctly montane vegetation) and the coast at Nausori and Rewa (two of Bethune's types). The species are almost certainly forest inhabitants, probably root feeders since this is the larval habit of *Abantiades* (Simonsen 2018), but

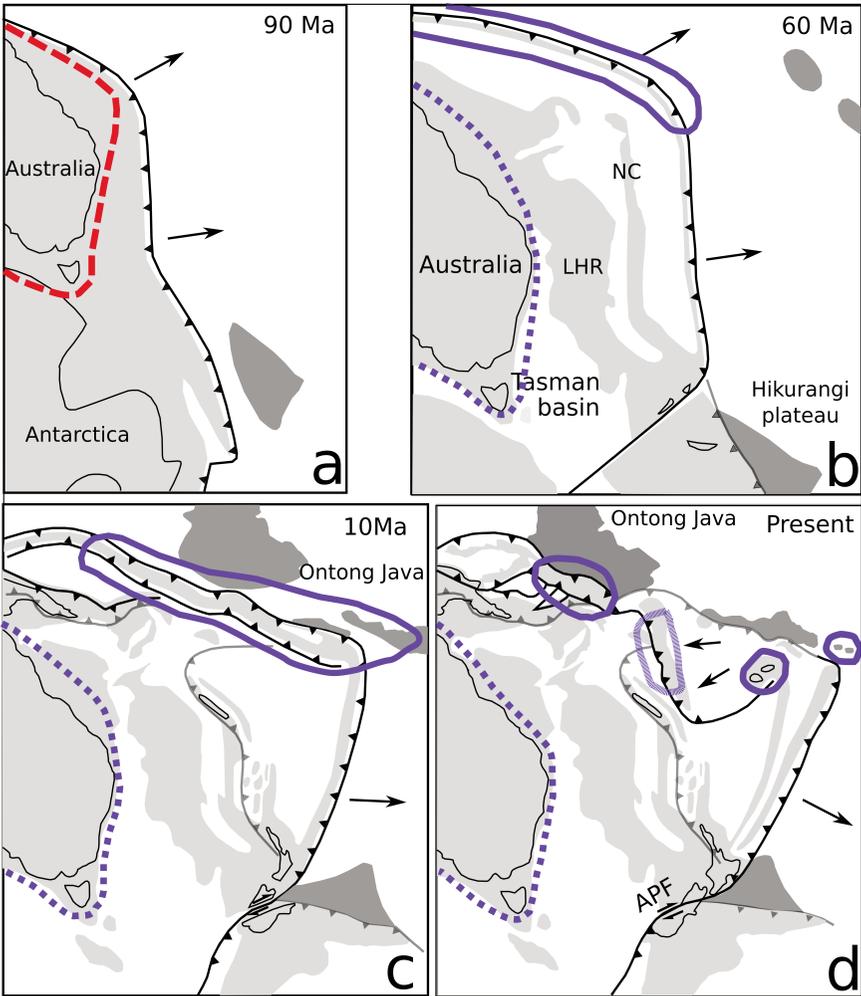


Fig. 31. Conceptual diagram of possible historical relationship between eastwards rollback of East Gondwana subduction zone and vicariance of the *Abantiades/Phassodes* ancestor: **(a)** hypothetical range of ancestor, **(b)** initial separation between 90-70 Ma isolating *Phassodes* along subduction zone volcanic islands, **(c)** contiguous island arc distribution of *Phassodes*, including the Samoa hotspot trail, **(d)** tectonic disruption of the Solomon-Tonga island arc displacing the Vanuatu segment to the southwest where it is possible that *Phassodes* may still persist. Red dashed line – hypothetical ancestral range, blue line – *Phassodes* distribution, dotted blue line – *Abantiades* distribution (shown just for the eastern range), pale blue line – potential persistence of *Phassodes* in Vanuatu archipelago.

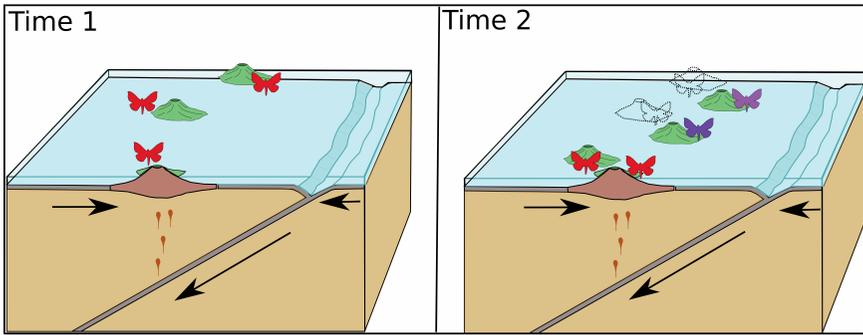


Fig. 32. Conceptual diagram of *Phassodes* as a subduction zone weed at a converging plate margin where the genus is able to persist along a plate margin as a series of metapopulations. Initial species populations in Time 1 (red silhouettes) establish new populations in Time 2 (blue and purple silhouettes) by dispersing onto new volcanoes (adjacent or very close) that are sequentially formed along the subduction zone while older islands are eroded or subside (dotted outlines in Time 2). Arrows – direction of plate movement. See Heads (2019) for discussion of the metapopulation concept.

they have not been recorded as forest or agricultural pests. The moths have been collected at lights within inhabited areas, which suggests that they can survive in disturbed environments. *Phassodes* is distributed along a plate margin in environments that are prone to periodic disruption by volcanic activity.

In the traditional model of Pacific biogeography, young volcanic islands such as Fiji were colonized by recent, long-distance dispersal from the mainland. Instead, in the model proposed here, *Phassodes* and its ancestors have occupied the island arc at the subduction zone ever since this separated from the mainland at ~90 Ma. The individual islands in the arc are ephemeral, but *Phassodes* has persisted at the subduction zone by colonizing new volcanic strata and new islands by normal, local dispersal. When volcanic activity subsides, older islands erode and submerge and their populations become extinct.

Movement of organisms between habitat islands or geographic islands in a region is a normal ecological process that allows a species to persist as a metapopulation (a population of populations) more or less *in situ*, in the region, even when individual islands have a patchy, disjunct distribution, and are ephemeral over time (Heads 2012b, 2018, 2019).

Normal dispersal is an observable ecological process and may result in habitat (or island) colonization and range expansion, but not differentiation—this requires a cessation of normal dispersal. In this respect ecological dispersal is different from long-distance dispersal, a theoretical mode of speciation that is often invoked to explain the origin of allopatric taxa by singular, chance events (Heads 2012b).

The ecological dispersal of *Phassodes* is probably very limited, since large Hepialidae appear to be poor fliers. This is especially true for heavy-bodied females where in flight the speed of flight in gravid moths may barely reach walking pace and the abdomen droops almost vertically (JRG pers. observ. of *Aenetus virescens* (Doubleday, 1843)). Adult moths are non-feeding and rarely survive beyond a single night in the wild. Their proportionately large body and rapid wing beat preclude gliding or drifting over long distances, unlike many other moths and butterflies. This limited dispersal ability is also consistent with the different species in Samoa and American Samoa being separated by only 70 km.

Metapopulation dynamics, with constant dispersal among the islands in a region, can result in old taxa inhabiting geologically young islands (Heads 2018, 2019) and this process is inferred here for *Phassodes*. We propose that the ancestral *Phassodes* was first isolated from its continental sister group when the subduction trench and its island arc along the east coast of Gondwana began to retreat eastwards (slab rollback). As the Tonga-Kermadec Trench migrated east and the Vitiaz Trench moved northeast, the subduction zone continued to generate volcanic islands. As long as there were sufficient volcanoes in contact or close proximity, populations of *Phassodes* could persist along the subduction zone by dispersing onto newer islands, while older islands eroded and were submerged (Fig. 32).

Following their formation, the original continuity of island arcs between the Solomon Islands and Tonga was subsequently disrupted by tectonic extension and rifting. This would have also affected the ancestral distribution of *Phassodes*, and could explain the apparent disjunction between Fiji and the Solomons. By the constant dispersal and colonization of new islands along the subduction zone, ancestral *Phassodes* was functioning ecologically as a ‘subduction zone weed’ (Heads 2012b), effectively occupying vacant habitats in a similar way to weeds occupying a cultivated garden.

Current information on the distribution of *Phassodes* species is still limited. Samoa and Fiji each comprise two main islands in close proximity, but there are records of *Phassodes* for only one island in each country. To help clarify the biogeography of *Phassodes* its presence or absence in Vanuatu should be determined, along with the distribution limits within the Solomon Islands. There also remains the outstanding question of the Bismarck Archipelago. These islands comprise island arcs of Pacific origin and for which there are no records of any Hepialidae, a characteristic noted by Pagenstecher (1900). And while Bethune-Baker’s (1905) new species of *Phassodes* were all from the same locality or area and synonymized by Nielsen *et al.* (2000), there has been no detailed assessment of their phylogenetic status. *Phassodes* should be a high priority target group for future surveys of Lepidoptera in this region.

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REFERENCES

- Beaver, E., Moore, M., Velasco-Castrillon, A. & Stevens, M.I. 2020. Three new ghost moths of the genus *Oxycanus* Walker, 1856 from Australia (Lepidoptera: Hepialidae). *Zootaxa* 4732: 351–374.

- Bethune-Baker, G.T.** 1905. Notes on a small collection of Heterocera from the Fiji Islands, with descriptions of some new species. *Proceedings of the Zoological Society of London* **1**: 88–95.
- Brown, R.M., Siler, C.D., Richards, S.J., Diesmos, A.C. & Cannatella, D.C.** 2015. Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae). *Zoological Journal of the Linnean Society* **174**: 130–168.
- Comstock, J.A.** 1966. Lepidoptera of American Samoa with particular reference to biology and ecology. *Pacific Insect Monographs* **2**: 1–74.
- Craw, R.C., Grehan, J.R. & Heads, M.J.** 1999. *Panbiogeography. Tracking the history of life*. Oxford University Press, New York. 229 pp.
- Croizat, L.C.** 1958. *Panbiogeography*. 3 vols. Published by the author, Caracas. 2749 pp.
- Croizat, L.C.** 1964. *Space, time, form. The biological synthesis*. Published by the author, Caracas. 881 pp.
- Davis, D.R., Karsholt, O., Kristensen, N.P. & Nielsen, E.S.** 1995. Revision of the genus *Ogygioses* (Palaeosetidae). *Invertebrate Taxonomy* **8**: 1231–1263.
- Davis, D.R.** 1996. A revision of the southern African family Prototheoridae (Lepidoptera: Hepialoidea). *Entomological Scandinavica* **27**: 393–439.
- Dugdale, J.** 1994. Hepialidae (Insecta: Lepidoptera). *Fauna of New Zealand* **30**: 1–164.
- Dumbleton, L.J.** 1966. Genitalia, classification and zoogeography of the New Zealand Hepialidae (Lepidoptera). *New Zealand Journal of Science* **9**: 920–981.
- Eteuati, K.S.** 1982. *Evaevaga A Samoa: Assertion of Samoan Autonomy 1920–1936*. Unpublished PhD Thesis. Canberra, Australian National University, Canberra. 350 pp.
- Gibbs, G.W. & Kristensen, N.P.** 2019. Mnesarchaeidae (Insecta: Lepidoptera: Hepialoidea). *Fauna of New Zealand* **78**: 1–105.
- Grehan, J.R.** 2010. Structural variants in the morphology of the first abdominal tergite supporting the monophyly of the Latin American genera *Cibyra* Walker, *Druceiella* Viette, *Pfitzneriana* Viette and *Trichophassus* Le Cerf (Lepidoptera: Hepialidae). *Bulletin of the Buffalo Museum of Science* **39**: 43–63.
- Grehan, J.R.** 2012. Morphological evidence for phylogenetic relationships within the Hepialidae (Lepidoptera: Exoporia). *Bulletin of the Buffalo Museum of Science* **42**: 33–62.
- Grehan, J.R.** 2018. Ghost moth fragments of Gondwana. *Botanical Society of Otago Newsletter* **84**: 12–15.
- Grehan J.R. & Mielke, C.G.C.** 2017. Re-characterization of *Gymelloxes* with a re-description of *Gymelloxes terea* from Central America (Lepidoptera: Hepialidae). *Zootaxa* **4663**: 434–440.
- Grehan, J.R. & Mielke, C.G.C.** 2018a. Evolutionary biogeography and tectonic history of the ghost moth families Hepialidae, Mnesarchaeidae, and Palaeosetidae in the Southwest Pacific (Lepidoptera: Exoporia). *Zootaxa* **4415**: 243–275.
- Grehan, J.R. & Mielke, C.G.C.** 2018b. Research on the evolutionary age and origin of ghost moths (Hepialidae). *News of the Lepidopterists' Society* **60**: 90–93.
- Grehan, J.R. & Mielke, C.G.C.** 2018c. New species of *Dugdaleiella*, gen. nov., *Kozloviella*, gen. nov., and *Pfitzneriella* Viette from upper elevation Andes of Ecuador and Peru (Lepidoptera: Hepialidae). *Zootaxa* **4497**: 1–28.

-
- Grehan, J.R. & Mielke, C.G.C.** 2019a. Evidence for ghost moths and relatives as fragments of a Gondwana biota (Lepidoptera: Exoporia). *The Weta* **53**: 24–34.
- Grehan, J.R. & Mielke, C.G.C.** 2019b. Two new species of *Palpifer* Hampson, 1893 from South East Asia (Lepidoptera: Hepialidae). *Bishop Museum Occasional Papers* **125**: 1–23.
- Grehan, J.R., Ralston, C.D. & van Nort, S.** 2019. Specialized wing scales in the male of the South-African moth *Leto venus* (Cramer, 1780) (Lepidoptera: Hepialidae). *Metamorphosis* **30**: 43–45.
- Grehan, J.R. & Rawlins, J.E.** 2016. A remarkable new genus and species of ghost moth from Peru (Lepidoptera: Exoporia: Hepialidae). *Annals of the Carnegie Museum* **84**: 47–57.
- Hart, S.R., Coetzee, M., Workman, R.K., Blusztajn, J., Johnson, K.T.M., Sinton, J.M., Steinberger, B. & Hawkins, J.W.** 2004. Genesis of the Western Samoa seamount province: age, geochemical fingerprint and tectonics. *Earth and Planetary Science Letters* **227**: 37–56.
- Heads, M.** 2006. Seed plants of Fiji: an ecological analysis. *Biological Journal of the Linnean Society* **89**: 407–431.
- Heads, M.** 2012a. Bayesian transmogrification of clade divergence dates: a critique. *Journal of Biogeography* **39**: 1749–1756.
- Heads, M.** 2012b. *Molecular panbiogeography of the tropics*. Berkeley, University of California Press. 562 pp.
- Heads, M.** 2014. *Biogeography of Australasia. A molecular analysis*. Cambridge, Cambridge University Press. 493 pp.
- Heads, M.** 2017. *Biogeography and evolution in New Zealand*. CRC Press, Boca Raton, Florida. 635 pp.
- Heads, M.** 2018. Metapopulation vicariance explains old endemics on young volcanic islands. *Cladistics* **32**: 392–212.
- Heads, M.** 2019. Recent advances in New Caledonian biogeography. *Biological Reviews* **94**: 957–980.
- Konter, J.G. & Jackson, M.G.** 2012. Large volumes of rejuvenated volcanism in Samoa. Evidence supporting a tectonic influence on late-stage volcanism. *Geochemistry, Geophysics, Geosystems* **13**: 1–23.
- Koppers, A.A.P., Russell, J.A., Jackson, M.G. & Konter, J.** 2008. Samoa reinstated as a primary hotspot trail. *Geology* **36**: 435–438.
- Koppers, A.A.P., Russell, J.A., Roberts, J., Jackson, M.G. & Konter, J., Wright, D.J., Staudigel, H. & Hart, S.R.** 2011. Age systematics of two young en echelon Samoan volcanic trails. *Geochemistry, Geophysics, Geosystems* **12**: 1–40.
- Kristensen, N.P.** 1978a. Observations on *Anomoses hylecoetes* (Anomosetidae), with a key to the hepialoid families (Insecta: Lepidoptera). *Steenstrupia* **5**: 1–19.
- Kristensen, N.P.** 1978b. A new family of Hepialoidea from South America, with remarks on the phylogeny of the subordo Exoporia (Lepidoptera). *Entomologica Germanica* **4**: 272–294.
- Kristensen, N.P.** 2003. 4. Skeleton and muscles: adults, pp. 39–1131. In: Kristensen, N.P. (ed.), *Handbook of Zoology*. Part IV. Volume 4: Arthropoda: Insecta, Part 36: Lepidoptera, Moths and Butterflies, Volume 2: Morphology, Physiology, and Development. De Gruyter, Berlin. 564 pp.

- Mann, P. & Taira, A.** 2004. Global tectonic significance of the Solomon Islands and Ontong Java Plateau convergent zone. *Tectonophysics* **389**: 137–190.
- Mielke, C.G.C. & Casagrande, M.M.** 2013. A new *Cibyra* Walker, 1856 from southern Brazil with taxonomic notes (first note) (Lepidoptera, Hepialidae). *Nachrichten des Entomologischen Vereins Apollo* (Neue Folge) **34**: 73–86.
- Mielke, C.G.C. & Grehan, J.R.** 2015. Description of a new species of *Phassus* Walker, 1856 from Costa Rica, *Pallas*, gen. n., with a new species from Guatemala, and taxonomic notes on *Sthenopsis* Packard, [1865] (Lepidoptera, Hepialidae). *European Entomologist* **7**(4): 113–134.
- Mielke, C.G.C. & Grehan, J.R.** 2017. Description of *Phthius* gen. n., with a new species from southeastern Brazil with possible vicariance relationships to Mesoamerica (Lepidoptera, Hepialidae). *Nachrichten des Entomologischen Vereins Apollo* (Neue Folge) **38**: 132–137.
- Nielsen, E.S. & Kristensen, N.P.** 1989. Primitive ghost moths. *Monographs on Australian Lepidoptera* **1**: 1–206.
- Nielsen, E.S. & Robinson, G.S.** 1983. Ghost moths of southern South America (Lepidoptera: Hepialidae). *Entomograph* **4**: 1–192.
- Nielsen, E.S., Robinson, G.S. & Wagner, D.L.** 2000. Ghost-moths of the world: a global inventory and bibliography of the Exoporia (Mnesarchaeoidea and Hepialoidea) (Lepidoptera). *Journal of Natural History* **34**: 823–878.
- Nielsen, E.S. & Scoble, M.J.** 1986. *Afrotheora*, a new genus of primitive Hepialidae from Africa (Lepidoptera: Hepialoidea). *Entomologica Scandinavica* **17**: 29–54.
- Page, R.D.M.** 1987. Graphs and generalized tracks; quantifying Croizat's panbiogeography. *Systematic Zoology* **37**: 254–270.
- Pagenstecher, A.** 1900. *Die Lepidopterenfauna des Bismarck-Archipels*. Zweiter Theil. Die Nachtfalter. E. Nägele, Stuttgart. 451 pp.
- Pelletier, B. & Auzende J.M.** 1995. Geometry and structure of the Vitiáz Trench (SW Pacific). *Marine Geophysical Researches* **18**: 305–335.
- Plunkett, G.M. & Lowry, P.P.** 2012. Phylogeny and diversification in the Melanesian *Schefflera* clade (Araliaceae) based on evidence from nuclear rDNA spacers. *Systematic Botany* **37**: 279–291.
- Price, A.A., Jackson, M.G., Blichert-Toft, J., Hall, P.S. Sinton, J.M., Kurz, M.D., & Blusztajn, J.** 2014. Evidence for a broadly distributed Samoan-plume signature in the northern Lau and North Fiji Basins. *Geochemistry, Geophysics and Geosystems* **15**: 986–1008.
- Rothschild, W.** 1895. On two new moths and an aberration. *Novitates Zoologicae* **2**: 482.
- Ruellan, E. & Lagabrielle, Y.** 2005. Subductions et ouvertures océaniques dans le Sud-Ouest Pacifique. *Géomorphologie* **2**: 121–142.
- Simonsen, T.J.** 2018. Splendid ghost moths and their allies. A revision of Australian *Abantiades*, *Oncopera*, *Aenetus* and *Zelotypia*. *Monographs of Australian Lepidoptera* **12**: 1–312.
- Simonsen, T.J. & Kristensen, N.P.** 2017. Revision of the endemic Brazilian 'neotheorid' hepialids, with morphological evidence for the phylogenetic relationships of the basal lineages of Hepialidae (Lepidoptera: Hepialoidea). *Arthropod Systematics & Phylogeny* **75**: 282–301.

-
-
- Tams, W.H.T.** 1935. *Insects of Samoa and Other Samoan Terrestrial Arthropoda: Lepidoptera. Heterocera (exclusive of Geometridae and the Microlepidoptera)*. Parts 3–4. Trustees of the British Museum (Natural History), London. 129 pp.
- Tindale, N.B.** 1941. Revision of the ghost moths (Lepidoptera Homoneura, family Hepialidae). Part IV. *Records of the South Australian Museum* 7: 15–46.
- Wagner, D.L.** 1985. The biosystematics of the Holarctic Hepialidae, with special emphasis on the *Hepialus californicus* species group. Unpublished PhD Dissertation. University of California, Berkeley. 395 pp.
- Zhu, H., Wang, K. & Han, H.** 2004. *Fauna Sinica Insecta*. Vol. 38. Lepidoptera, Hepialidae, Epiplemlidae. Science Press, Beijing. 952 pp. [In Chinese with English summary]