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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. samoana* 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 *Puermymytrans* Viette, 1951 (presence of a basal forewing scent gland). The distribution of *Phassodes* coincides with the Vitiaz 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 *A. magnificus* (Lucas, 1898), (NZAC), *A. hyalinatus* (Herrich-Schäffer, 1853) (CMNH), *A. chilensis* (Ureta, 1951) (USNM), and *A. 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 tergosternal 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 tergosternal 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 tergosternal 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
JRGCC   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


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 posterio-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. vitiensis), first and second palpomeres pale yellowish brown, distal palpomere pale reddish brown. Eyes prominent, no macro difference in size apparent between sexes. Intra antenn-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 margin, 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 CuA2. 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. Stermites 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 apodermal suture, posterio-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; apodermal 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 pseudotegumal arm, latter fused across median with a central notch between two short points; posterio-ventral tooth elongate, laterally extending as a shallow, straight ridge either side about half length of pseudotegumen; posterio-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.
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 samoas 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 vitiensis Bethune-Baker, 1905: 92. HT [sex uncertain]*: NHMUK
Type locality – Fiji, Viti Levu, Nausori

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

Diagnosis. Male genitalia with a posterior-dorsal shark-fin tooth along margin of anogenital field distinguish this species from P. samoas sp. n. with a shallow convex lobe, and from P. walteri sp. n. with a subrectangular posterior-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.
Genitalia. (Fig. 19a–19c, 22a) Pseudotegumen posterio-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).

**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, 7c, 11, 15b, 16b, 17c, 18b, 20a–c, 22b)

**Diagnosis.** Male genitalia with a subrectangular posterio-dorsal projecting lobe with three blunt points along margin of anogenital field distinguish this species from the rounded lobe of *P. samoas* 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; posterio-ventral tooth lateral ridge about half length of pseudotegumen; posterio-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).
Phassodes samoanGrehan & C. Mielke, sp. n.
(Figs. 4a–c, 6d, 6g, 7d, 9d, 10a, 11, 12a–b, 15c, 16c, 17d, 18c, 21a–c, 22c, 23a, 27a)


Diagnosis. Male genitalia with a shallow posterio-dorsal projecting convex lobe along margin of anogenital field distinguish this species from Phassodes vitiensis with a posterio-dorsal shark-fin tooth and Phassodes walteri sp. n. with a subrectangular posterio-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.
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 posterio-ventral tooth lateral ridge extending 1/4 distance to dorsal edge; posterio-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).


Etymology. Named for the country of Samoa.
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. samoas* 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. samoae* 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. samoae* sp. n. male. Photos by James Boone, Miho Maeda, and Agnes Stubblefield.
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).


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

**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.
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.

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**Fig. 15. Phassodes spp. Tergum II and III (partial):** (a) *P. vitiensis* male (M278), (b) *P. walteri* sp. n. male holotype, (c) *P. samoai* sp. n. male holotype, (d) *P. tutuila* sp. n. female holotype (photos by John Grehan).
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).
3) **Lateral ridge of posterio-ventral tooth** (Figs. 19–22). On the side of each pseudotegumen plate there is a straight ridge extending back from the base of the posterio-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).

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**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).
Species status
The three species with males known differ from each other by the shape of the posteriodorsal tooth of the pseudotegumen as illustrated in Fig. 22. These distinctions 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 posterio-medially in *P. walteri* sp. n. (Fig. 17c) and narrow and posterio-medially angled in *P. samoas* sp. n. (Fig. 17d). The medially sclerotized anterior margin of *P. vitiensis* and *P. samoas* 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. samoas* 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. samoas* 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. samoas* 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. Posterio-dorsal tooth shape (within dotted square) of pseudotegumen: (a) *P. vitiensis* (M278), (b) *P. walteri* sp. n. holotype, (c) *P. samoa* sp. n. holotype.
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

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**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).
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 *Puermia trypsis* 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 genera.
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 1. Presence of epiphysis and arolium in some primitive exoporian families and Australasian genera.

<table>
<thead>
<tr>
<th></th>
<th>Epiphysis</th>
<th>Arolium</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neotheoridae</td>
<td>+</td>
<td></td>
<td>Simonsen &amp; Kristensen (2017)</td>
</tr>
<tr>
<td>Palaeosetidae</td>
<td>+</td>
<td>+</td>
<td>Davis (1996)</td>
</tr>
<tr>
<td>Prototheoridae</td>
<td>+ (vestigial)</td>
<td>+</td>
<td>Davis (1996)</td>
</tr>
<tr>
<td>Hepialidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abantiades</td>
<td>+</td>
<td>+</td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Aenetus</td>
<td>+</td>
<td>+</td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Archaeoaenetus</td>
<td>+</td>
<td>+</td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Cladoxycanus</td>
<td>+</td>
<td>?</td>
<td>Dugdale (1994)</td>
</tr>
<tr>
<td>Dioxycanus</td>
<td>+</td>
<td>?</td>
<td>Dugdale (1994)</td>
</tr>
<tr>
<td>Dumbletonius</td>
<td>+</td>
<td>+</td>
<td>Dugdale (1994), JRG, pers. observ.</td>
</tr>
<tr>
<td>Elhamma</td>
<td>+</td>
<td>+</td>
<td>Simonsen (2015)</td>
</tr>
<tr>
<td>Heloxycanus</td>
<td>+</td>
<td>?</td>
<td>Dugdale (1994)</td>
</tr>
<tr>
<td>Jeana</td>
<td>+</td>
<td>+</td>
<td>E. Beaver, pers. comm.</td>
</tr>
<tr>
<td>Oncopera</td>
<td>+</td>
<td>+</td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Oxycanus</td>
<td>+</td>
<td>+</td>
<td>Beaver et al. (2020)</td>
</tr>
<tr>
<td>Wiseana</td>
<td>+</td>
<td>?</td>
<td>Dugdale (1994)</td>
</tr>
<tr>
<td>Zelotypia</td>
<td>+</td>
<td>+</td>
<td>Simonsen (2018)</td>
</tr>
</tbody>
</table>
(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 medi-
ally along the ventral surface. A FW gland is also present in Puermyntrans (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 Oggioses (Palaeosetidae). However, Davis et al. (1995) noted that while this was strongly reminiscent of the scent gland of Puermyntrans, 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

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

<table>
<thead>
<tr>
<th></th>
<th>Metatibial androconia</th>
<th>FW gland</th>
<th>HW androconia</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td>Palaeosetidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oggioses</td>
<td>+</td>
<td>(single species) +</td>
<td>Davis et al. (1995)</td>
<td></td>
</tr>
<tr>
<td>Hepialidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aenetus</td>
<td>+</td>
<td></td>
<td></td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Archaeoaenetus</td>
<td>+</td>
<td></td>
<td></td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Hepialus</td>
<td>+</td>
<td></td>
<td></td>
<td>Grehan &amp; Rawlins (2016)</td>
</tr>
<tr>
<td>Kozloviella</td>
<td>+</td>
<td></td>
<td></td>
<td>Grehan &amp; Mielke (2018c)</td>
</tr>
<tr>
<td>Oncapera</td>
<td>+</td>
<td>-</td>
<td></td>
<td>Simonsen (2018)</td>
</tr>
<tr>
<td>Palpifer</td>
<td>+</td>
<td></td>
<td></td>
<td>Grehan &amp; Mielke (2019b)</td>
</tr>
<tr>
<td>Pfitzeriella</td>
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<td>Grehan &amp; Mielke (2018c)</td>
</tr>
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<td>Phassodes</td>
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<td>+</td>
<td>+</td>
<td>Current study</td>
</tr>
<tr>
<td>Phassus</td>
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<td></td>
<td></td>
<td>Mielke &amp; Grehan (2015)</td>
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<tr>
<td>Phthius</td>
<td>+</td>
<td></td>
<td></td>
<td>Mielke &amp; Grehan (2017)</td>
</tr>
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<td>Phymatopus</td>
<td>+</td>
<td></td>
<td></td>
<td>Wagner (1985)</td>
</tr>
<tr>
<td>Puermyntrans</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Nielsen &amp; Robinson (1983)</td>
</tr>
<tr>
<td>Schausiana</td>
<td>+</td>
<td></td>
<td></td>
<td>Mielke &amp; Grehan (2015)</td>
</tr>
<tr>
<td>Sthenopis</td>
<td>+</td>
<td></td>
<td></td>
<td>Grehan &amp; Rawlins (2016)</td>
</tr>
<tr>
<td>Thitarodes</td>
<td>+</td>
<td></td>
<td></td>
<td>Zhu et al. 2004</td>
</tr>
<tr>
<td>Zenophassus</td>
<td>+</td>
<td></td>
<td></td>
<td>Tindale (1941)</td>
</tr>
<tr>
<td>Viridigigas</td>
<td>+</td>
<td></td>
<td></td>
<td>Grehan &amp; Rawlins (2016)</td>
</tr>
</tbody>
</table>
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 tergosternal connection. A structural similarity in the tergosternal sclerite shared between *Abantiades*, *Phassodes* and some South American genera identified by Grehan (2010, 2012) is incorrect. There is a posterio-lateral knob on the intermediate zone of the tergosternal sclerite that characterizes the cibyrine 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 posterio-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 tergosternal central region.** Both genera have a laterally inflated intermediate zone that is unique within the Hepialidae.

2) **Pseudoteguminial arms.** In both genera the apex of the pseudoteguminial 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.
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, *Pfitzeriana* 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 *Puermymtrans/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 Vitiaz 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 Vitiaz 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 Vitiaz 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 Vitiaz 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
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 Solomons-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.
they have not been recorded as forest or agricultural pests. The moths have been collected at lights within inhabited areas, which suggest 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 moth 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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