



A new species of *Proterhinus* Sharp, 1878 (Coleoptera: Curculionoidea: Belidae) from Miti‘aro, Cook Islands, South Pacific

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Abstract

Proterhinus tauai Brown, **new species** is described from specimens collected on the island of Miti‘aro in the Cook Islands, South Pacific. It differs from congeners by the combination of having a dorsal vestiture of decumbent brown clavate scales, lacking erect elongate setae, anterior pronotal angles projecting forwards, and having short antennae that do not reach the posterior margin of the pronotum. This species shows strong sexual dimorphism in the shape of the rostrum, with males having a large semicircular rostrum, compared with a stout subrectangular rostrum in females. Fitting allometric models to the relationship of morphometric variables with body length show that rostrum width and area have significantly different allometric relationships between the sexes, consistent with hypotheses of sexual selection. *Proterhinus tauai* was collected from coastal scrub vegetation. Collection data and observation of captive specimens indicate a host relationship with the parasitic vine *Cassytha filiformis* L. (Lauraceae).

Key words: Oxycoryninae, Aglycyderini, biogeography, allometry, Mitiaro

Introduction

The genus *Proterhinus* Sharp, 1878 has undergone a large radiation with species found in a wide variety of habitats on both high and low islands throughout the Central Pacific (Figure 1). Over 150 species have been described from Hawaii (Perkins 1900, 1910, 1926, 1931a, Zimmerman 1940), three species are known from the Marquesas (Perkins 1931b, 1936), three species from the Society Islands (Zimmerman & Perrault 1989), one species (*P. phoenix* Perkins, 1931) from Enderbury Island in the Phoenix Archipelago (Figure 1, Perkins 1931a) and one species (*P. samoae* Perkins, 1907) with a broad distribution in the South Pacific, as a result of anthropogenic movement of coconuts (Zimmerman 1948, Zimmerman & Perrault 1989). Adults have been collected on a wide range of host-plants (Swezey 1938) and there appears to be a range of host specificity in the genus. Some species are apparently restricted to a particular plant (e.g. *P. abnormis* Perkins on *Broussaisia arguta* Gaud., Hydrangeaceae), while others have been frequently collected from several different plant species in unrelated families (e.g. *P. angustiformis* Perkins on *Coprosma waimeae* Wawra, Rubiaceae, and *Alyxia stellata* (J.R.Forst. & G.Forst.) Roem. & Schult., Apocynaceae) (Swezey 1938). The larvae of Hawaiian species of *Proterhinus* can be found in fern fronds and stems, under tree bark, in dead twigs, or mining in leaves (Anderson 1941), while the larvae of most non-Hawaiian species are unknown.

Proterhinus was placed by Sharp (1878) in the Aglycyderidae. This taxon was recognised as being close to the Belidae and Oxycorynidae based on larval characters (Böving & Craighead 1931, van Emden 1938, Anderson 1941); however, its rank has been variously regarded as a family (Crowson 1981, Thompson 1992, Zimmerman 1994) or as subfamily of Belidae (Kuschel 1992, 1995, Oberprieler *et al.* 2007). Phylogenetic studies that have included aglycyderine weevils have consistently nested them within the Belidae as a tribe of the Oxycoryninae (Marvaldi *et al.* 2006, McKenna *et al.* 2009).

Miti‘aro is a small (29 km²) island in the Southern Group of the Cook Islands with a maximum elevation of 15 m (Land Information New Zealand 2014). The island has a roughly 1 km wide ring of coral-derived limestone (*makatea*) surrounding a central swamp in which four areas of volcanically derived soils are located (Stoddart

et al. 1990). The vegetation of these fertile volcanic soils has been strongly modified by agricultural use, while the swamp is dominated by the sedge *Cladium jamaicense* Crantz. Extensive areas of largely undisturbed vegetation remain on the makatea, owing to the treacherous nature of the landform. Here, the vegetation is a low, open forest primarily made up of *Pandanus tectorius* Parkinson ex Du Roi, with scattered *Guettarda speciosa* L. and *Pisonia grandis* R. Br. (Sykes 1980, Franklin & Merlin 1992). The age of the island remains uncertain, as there are no unweathered volcanic rock outcrops that might yield samples for radioisotope dating. It is certain that the island was completely submerged for an extensive period of time, with uplift estimated to have begun in the Pliocene (Lambeck 1981).

Miti'aro has a rich human history, with the earliest evidence of human occupation on the island estimated to date to the 16th century AD (Walter & Campbell 1996). Nearby Ma'uke has sites indicating occupation in the 14th century AD (Walter 1998), and it is likely that Miti'aro was inhabited at that time also. Extensive trade and cultural exchange with other islands, both in the Cook Islands (Sheppard *et al.* 1997) and further afield, particularly with the Society and Austral Islands (Allen & Johnson 1997, Rolett 2002), has resulted in a substantial anthropogenic component to the fauna. For example, the land snail fauna of Miti'aro contains 27 widespread species which are inferred to have been dispersed to Miti'aro through human agency, out of a total of 34 species known from the island (Brook *et al.* 2010). However, the insects of Miti'aro have been poorly collected to date, and little is known about the composition and origin of the insect fauna of the island.

This paper describes a new species of *Proterhinus* recently discovered on Miti'aro. It also discusses the sexual dimorphism in the genus in the context of sexual conflict evolutionary processes and provides an outline of the biogeography of Miti'aro.

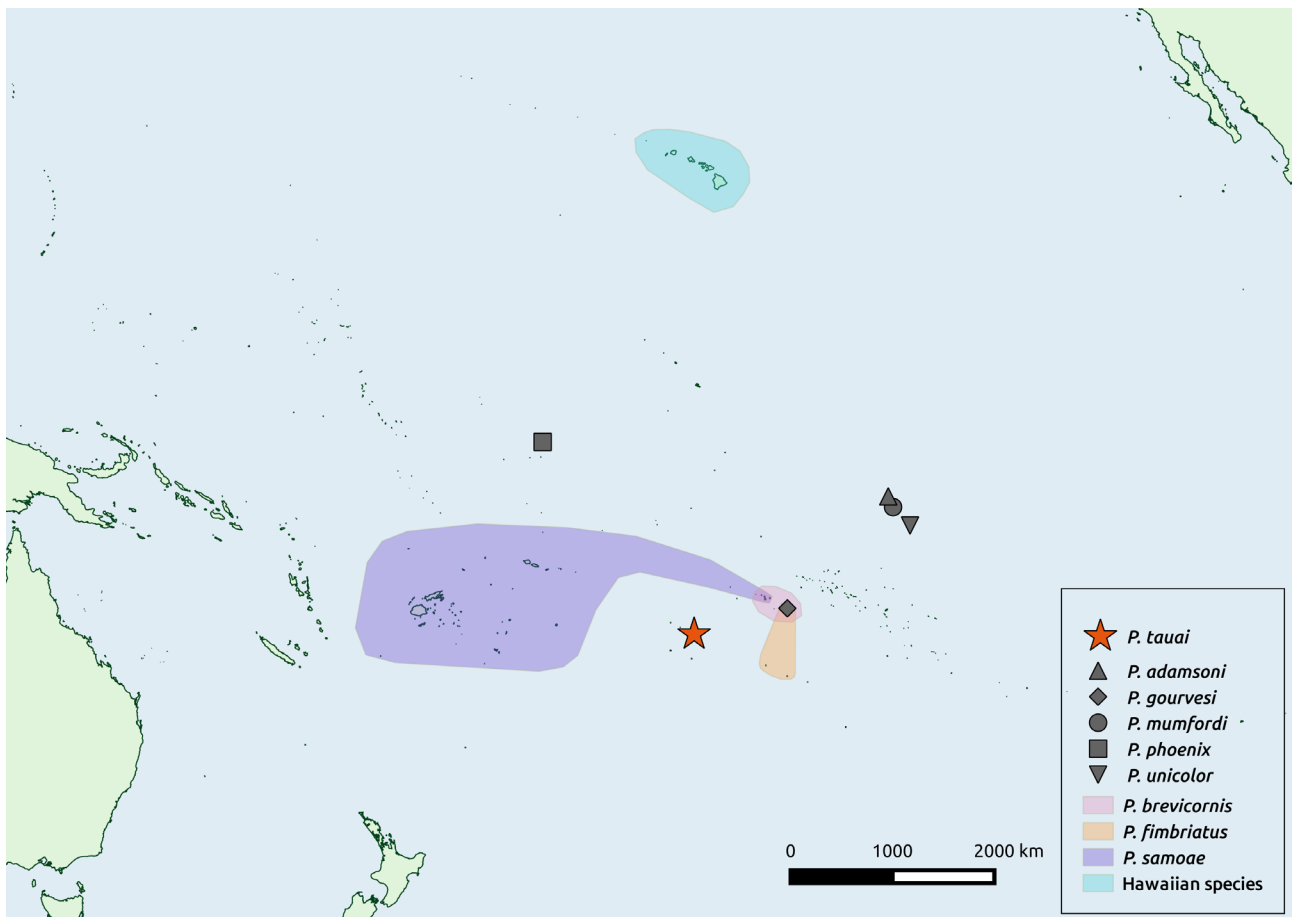


FIGURE 1. Distribution of known *Proterhinus* species

Materials and methods

Specimens were collected by beating vegetation over a fabric tray. Host plants were identified by the author using

Sykes (2016). Plant specimens were collected and deposited in the Allan Herbarium (CHR; Manaaki Whenua Landcare Research, Lincoln, New Zealand) with catalogue numbers CHR 644578 and CHR 644577.

Specimens retained for behavioural observations were kept in a 400 ml (64 mm × 64 mm × 110 mm) clear PET plastic container (LabServ, Waltham, MA, USA). To provide ventilation, 4 × 10 mm diameter holes were bored in the opaque white polypropylene lid and covered with fabric. Sprigs of associated plant material were kept in water in a 5 ml (15 mm × 52 mm) flat-based polystyrene tube (LabServ) filled with water. Eight specimens were retained in captivity for five days, with sprigs of *Suriana maritima* L. (Surianaceae) and *Cassytha filiformis* L. (Lauraceae). Observations were made daily, for approximately 15 min in the mornings.

Morphological terminology follows Oberprieler *et al.* (2014), Lawrence *et al.* (2010) and Wanat (2007). Colour descriptors follow the National Bureau of Standards (Kelly & Judd 1976), which provides a dictionary of 267 colours with natural-language descriptions. Digital representations of these colours in the RGB colorspace have been provided by Jaffer (2011).

Genitalia were examined by removing the abdomen and cleared using undiluted lactic acid. After dissection, the genitalia were photographed before being mounted in dimethyl hydantoin formaldehyde (DMHF) (Liberti 2005) on a card pinned below the specimen.

Body length was measured in lateral view from the anterior margin of the eyes to the apex of the elytra. Body height was measured in lateral view from the hind coxa to the dorsal margin of the elytra, perpendicular to the longitudinal axis of the insect. Rostrum length was measured in anterior view from the anterior margin of the eyes to apex of the rostrum (Figures 8, 9, \overline{EF}). Rostrum width was measured in two places in both sexes. The first was immediately anterior to the eyes, at the base of the rostrum (Figures 8, 9, \overline{AB} , ‘basal width’). The second place (‘distal width’) was across the apex of the rostrum in females (Figure 8, \overline{CD}); while in males this was the widest point of the

rostrum, slightly apicad of the base (Figure 9, \overline{CD}). Rostrum area in females was calculated as $A_f = \frac{(\overline{AB} + \overline{CD})\overline{EF}}{2}$.

The rostrum area in males was calculated as $A_m = \frac{\pi r^2}{2}$, where r was the radius of the circumscribed circle of $\triangle CDE$. Specimens were examined using a Nikon AZ100M stereomicroscope fitted with a Nikon DS-Ri 1 digital camera, and measurements were made using Nikon NIS Elements (v. 4.10). The same microscopy platform was used to prepare habitus photographs with the focus stacking capabilities of NIS Elements.

Analyses of the allometric relationships between rostrum dimension and body length were undertaken to evaluate hypotheses of their function. Linear models of log-transformed traits were fitted to estimate the parameters a and b of the allometric equation $Y = aX^b$ (Bonduriansky 2007). Rostrum area was square-root transformed prior to model fitting. Analyses were conducted using R (R Core Team 2017).

Specimens have been deposited in the following collections:

ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia
BPBM	Bernice Pauahi Bishop Museum, Honolulu, Hawaii, United States of America
CMNC	Canadian Museum of Nature, Ottawa, Ontario, Canada
NHM	Natural History Museum, London, United Kingdom
NZAC	New Zealand Arthropod Collection, Manaaki Whenua Landcare Research, Tamaki, Auckland, New Zealand
USNM	Smithsonian Institution National Museum of Natural History, Washington D.C., United States of America

***Proterhinus tauai* Brown, new species**

<http://zoobank.org/urn:lsid:zoobank.org:act:A648AAF8-FB12-41BF-B800-3CE1AEFDD10F>

Figures 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18

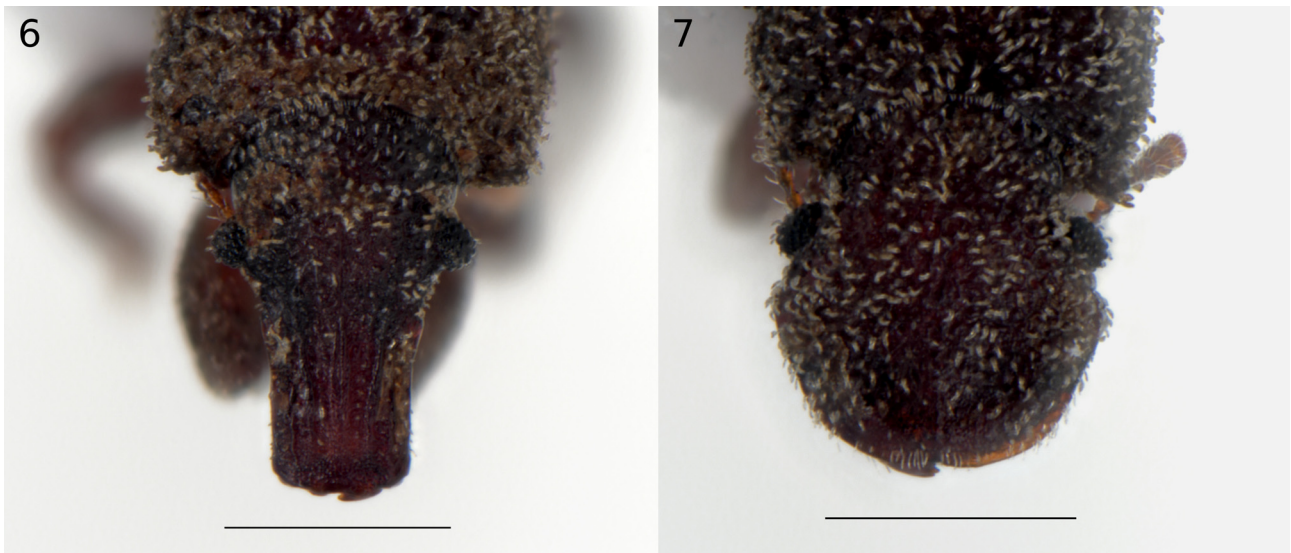
Diagnosis. Dorsum covered with decumbent to suberect brown clavate scales (Figures 2, 3); lacking long setae on lateral regions of elytra. Antennae short, not reaching posterior margin of pronotum when directed backwards (Figures 4, 5). Pronotum with lateral margins subparallel, anterior angles produced anteriorly.



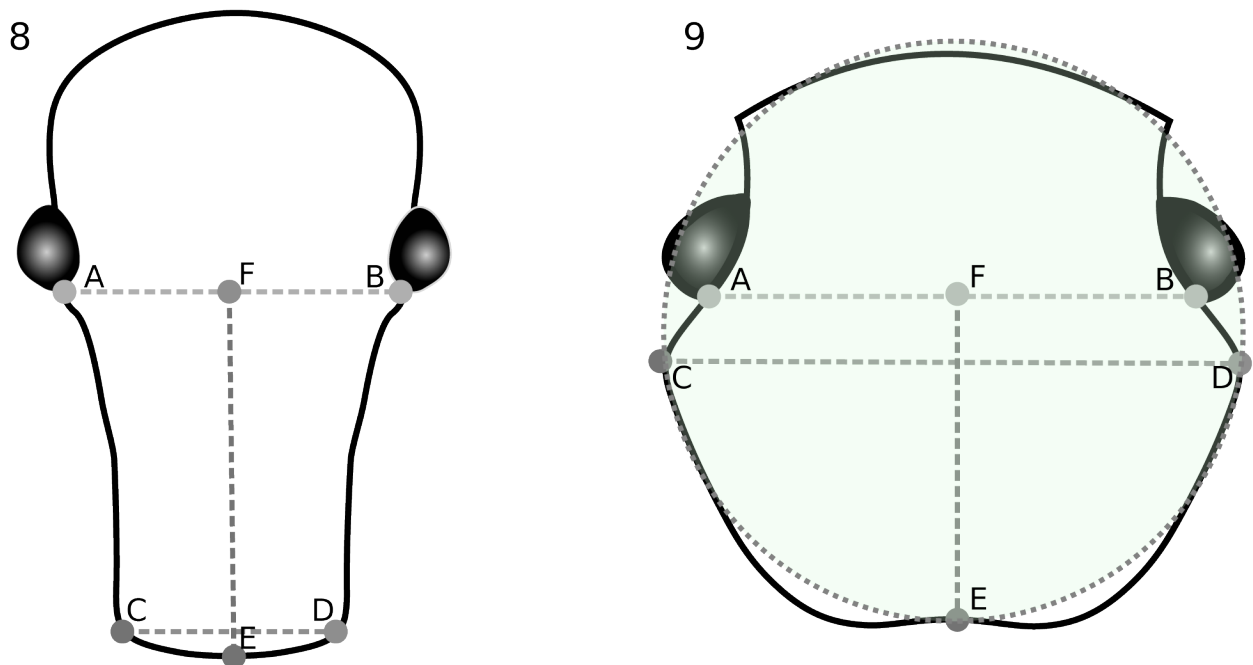
FIGURES 2–5. Habitus photographs of *Proterhinus tauai* new species. 2, 4: female. 3, 5: male. Scale bars = 1 mm.

Description. Body length 1.52 mm to 2.53 mm (\bar{X} = 2.02 mm, s = 0.25, n = 33), height 0.44 mm to 0.70 mm (\bar{X} = 0.57 mm, s = 0.07, n = 33). Integument black; sometimes with diffuse dark red to strong red maculae on the lateral regions of the elytra, occasionally extending onto the pronotum. Dorsum covered with decumbent to suberect light greyish yellowish brown clavate scales, variably condensed into maculae (Figures 2, 3). **Mouthparts.** Females with mandibles subtriangular, left overlapping the right; prementum subquadrate. Males with mandibles large, fal-ciform, laterally with fine setae; prementum large, triangular. **Rostrum.** Females with narrower, subrectangular rostrum in dorsal view (Figure 6); widest immediately in front of eyes, gently tapering towards apex; multicarinate, dorsum with five low blunt carinae which are devoid of scales; ventrolateral margin with multiple erect setae; underside with inconspicuous fine setae, appears nude; length 0.37 mm to 0.52 mm (\bar{X} = 0.44 mm, s = 0.05, n = 12), distal width (Figure 8, \overline{CD}) 0.25 mm to 0.31 mm (\bar{X} = 0.28 mm, s = 0.02, n = 12), length/width ratio 1.42 to 1.74 (\bar{X} = 1.61, s = 0.10, n = 12). Males with broad semicircular rostrum in dorsal view; widest approximately one eye diameter in front of eyes, sharply constricted between this point and eyes (Figure 7); underside with sparse, fine setae. Length 0.23 mm to 0.49 mm (\bar{X} = 0.36 mm, s = 0.07, n = 21), distal width (Figure 9, \overline{CD}) 0.37 mm to 0.84 mm (\bar{X} = 0.59 mm, s = 0.14, n = 21), length/width ratio 0.56 to 0.69 (\bar{X} = 0.61, s = 0.04, n = 21). **Antennae.** At full length reaching about midpoint of pronotum. Segment 1 pyriform, as long as segment 2 + 1/2 segment 3, inserted ventrally. Segment 2 pyriform, as long as segment 3 + 1/4 segment 4, about as wide as segment 1. Segments 3–6 pyriform, subequal in length and width, about 1/2 width of segment 2. Segments 7–11 getting progressively longer and wider, with segments 9–11 forming a loose club. **Head.** Eye hemispherical, strongly protuberant; coarsely faceted; interocular scales present. Males with underside having large scattered punctures. Females with underside unpunctured. **Pronotum.** Length 0.43 mm to 0.72 mm (\bar{X} = 0.57 mm, s = 0.08, n = 33), width 0.53 mm to 0.89 mm (\bar{X} = 0.71 mm, s = 0.10, n = 33), length/width ratio 0.73 to 0.90 (\bar{X} = 0.81, s = 0.04, n = 33). Anterior angles produced anteriorly in both sexes. Lateral margins subparallel. Disc strongly punctured. Surface matte, without distinct microsculpture. **Elytra.** Length 0.93 mm to 1.67 mm (\bar{X} = 1.26 mm, s = 0.17, n = 33), width 0.65 mm to 1.07 mm (\bar{X} = 0.86 mm, s = 0.11, n = 33), length/width ratio 1.31 to 1.61 (\bar{X} = 1.47, s = 0.07, n = 33). Striae confused, not forming clear rows, coarsely punctured. Surface matte, without distinct microsculpture. **Thoracic ventrites.** Anterior end of metanepisterna reduced, not protruding into lateral elytral margin. Metaventrite coarsely punctured, vestiture sparse and fine. **Abdomen.** Ventrites impunctate, clothed with short, fine, inconspicuous setae. **Legs.** Femora stout, maximum girth in distal 1/3; scales more numerous apicad of widest point. Tibiae subcylindrical;

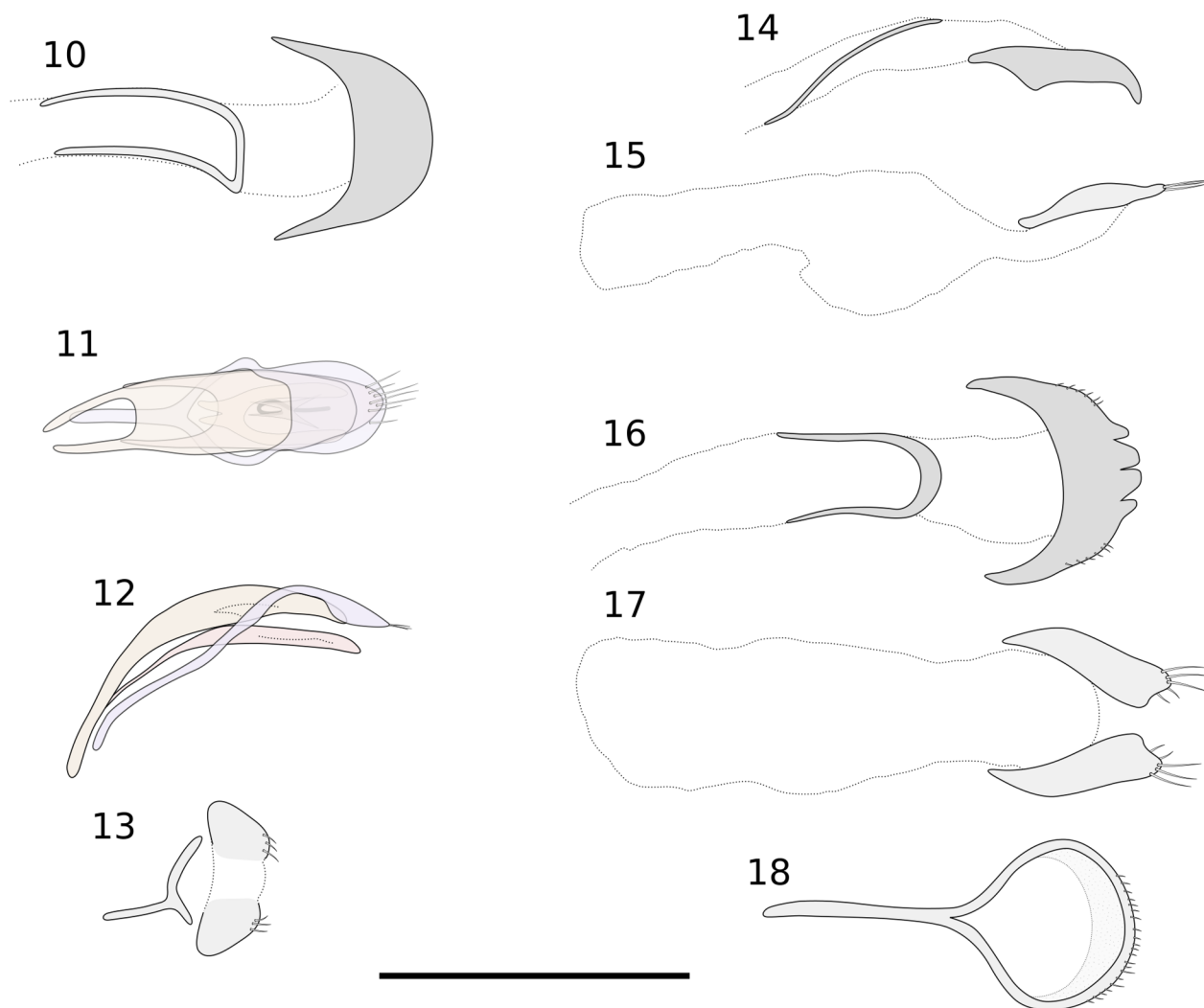
setae on dorsal margin short, inconspicuous. Tarsi pseudotrimerous; segment 1 short; segment 2 bilobed, about 3 times as long as segment 1, clothed underneath with dense setae, lobes normally developed and symmetrical on all legs in both sexes; segment 3 concealed; segment 4 about as long as rest of tarsal segments combined; claws large, divergent. **Male genitalia.** Figures 10–13. Tergite 8 concealed, retractable under tergite 7, posterior margin entire; rectal loop open anteriorly. Sternite 8 largely membranous, lightly sclerotised. Sternite 9 asymmetrical; spiculum gastrale short, barely as long as longest lateral arm of the sternite. Tegmen with parameral sector broadly rounded, bearing scattered setae. Pedon longer than tectum; pedon narrowly rounded at apex, tectum broadly rounded, nearly truncate. **Female genitalia.** Figures 14–18. Tergite 8 with 4 teeth on posterior margin; rectal loop open anteriorly. Sternite 8 a lightly sclerotised loop with small setae on the posterior margin. Gonocoxites narrow, about 3.5 times longer than wide; styli absent.



FIGURES 6–7. Head and rostrum of *Proterhinus tauai* new species. 6: female. 7: male. Scale bars = 0.5 mm.



FIGURES 8–9. Diagrams of head and rostrum of *Proterhinus tauai* new species, with dashed lines showing where measurements were taken. 8: female. 9: male. Basal width = \overline{AB} . Distal width = \overline{CD} . Rostrum length = \overline{EF} . The circumscribed circle of $\triangle CDE$ forming the basis of the calculation of male rostrum area is shown as a dotted line with green fill.



FIGURES 10–18. Genitalia of *Proterhinus tauai* new species. 10: male tergite 8, dorsal view, showing rectal loop; 11, aedeagus, dorsal view (tegmen coloured blue, tectum yellow, pedon red); 12, aedeagus, lateral view (tegmen coloured blue, tectum yellow, pedon red); 13, male sternite 8, ventral view; 14, female tergite 8, lateral view, showing rectal loop; 15, ovipositor, lateral view; 16, female tergite 8, dorsal view, showing rectal loop; 17, ovipositor, dorsal view; 18, female sternite 8, ventral view. Scale bar = 0.5 mm; all figures to same scale.

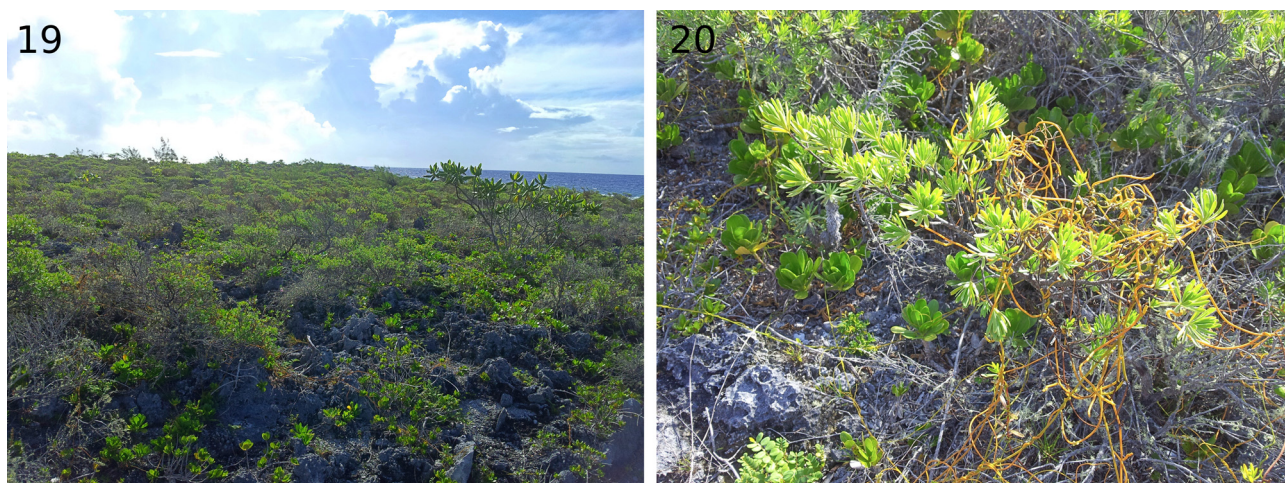
Type material examined: Holotype. Male (NZAC). Specimen mounted on card triangle; abdomen removed, dissected and mounted in DMHF on white card below specimen. Labelled ‘COOK ISLANDS / Airport, Kaapoto / Mitiaro / 17 March 2017 / SDJ Brown’ [printed, off-white card], ‘Beaten from *Suriana / maritima* / 19.8401°S 157.7094°W’ [printed, off-white card], ‘HOLOTYPE / *Proterhinus / tauai* / Brown 2018’ [printed, red card].

Paratypes. A total of 32 specimens (20 males, 12 females) designated as paratypes, bearing blue paratype label. Paratype specimens deposited in NZAC, ANIC, BPBM, CMNC, NHM, USNM.

Miti‘aro: Airport, Kaapoto, 17 Mar 2017, SDJ Brown, beaten from *Suriana maritima*, 19.8401°S 157.7094°W (BPBM: 1, NZAC: 1); Villages, 17 Mar 2017, SDJ Brown, beaten from dying coconut frond, 19.8601°S 157.7196°W (NHM: 1); Vaikoua, 18 Mar 2017, SDJ Brown, beaten from *Chamaesyce fosbergii*, 19.8453°S 157.7179°W (NZAC: 1). Vainano, 18 Mar 2017, SDJ Brown, beaten from *Suriana maritima*, 19.8406°S 157.7131°W (BPBM: 1, CMNC: 1, NHM: 1, NZAC: 4, USNM: 1); Te Unu, 22 Mar 2017, SDJ Brown, beaten from *Chamaesyce fosbergii*, 19.8882°S 157.6912°W (ANIC: 1, BPBM: 1, NHM: 2, NZAC: 4, USNM: 1); Oavea, 22 Mar 2017, SDJ Brown, beaten from *Chamaesyce fosbergii*, 19.8960°S 157.7108°W (CMNC: 1, NZAC: 6); Northeast coast, 23 Mar 2017, SDJ Brown, beaten from *Suriana maritima* and *Cassytha* tangle, 19.8498°S 157.6828°W (ANIC: 1, BPBM: 1, NZAC: 3);

Distribution. This species is known only from Miti‘aro, Cook Islands, South Pacific (Figure 1).

Biology: Specimens were collected from coastal scrub (Figure 19), especially from *Suriana maritima* and *Chamaesyce fosbergii* (Sherff) Croizat & O.Deg (Euphorbiaceae) which were entwined with the parasitic vine *Cassytha filiformis* (Figure 20). All specimens were collected by beating vegetation over a fabric tray.



FIGURES 19–20. Habitat of *Proterhinus tauai* new species. 19: coastal scrub in northwest Miti'aro. 20: *Suriana maritima* parasitised by *Cassytha filiformis*.

Remarks. *Proterhinus tauai* is closely related to *P. brevicornis* Zimmerman and Perrault, 1989, as evidenced by the similarities between the two species in the form of the dorsal vestiture, shortened antennae and the shape of the rostrum in both sexes. It differs from *P. brevicornis* by having the anterior angles of the pronotum produced anteriorly and ventrite 1 being impunctate.

It is also similar to *P. phoenix*, with both species having similar dorsal vestiture, and being similarly found on a low relief island. However, *P. tauai* differs from *P. phoenix* by having the anterior angles of the pronotum produced anteriorly and the dorsal surfaces more coarsely punctured. The males of *P. phoenix* also have a remarkably long spine on the ventral surface of all tarsal segments 1, which is not present in *P. tauai*.

Although superficially similar in facies to species of *Aralius*, especially *A. wollastoni* (Sharp) from New Zealand, *P. tauai* can be readily placed in *Proterhinus* by the following characters which distinguish the two genera (Kuschel 2003): antennal segments 1 are longer than segments 2, ventrites 1–4 are smooth, without grooves or impressions laterally; males do not have a setiferous pit behind the postmentum; and females have only four teeth on the apical margin of tergite 8.

This species was not found on 'Atiu, Mangaia or Rarotonga, despite searches by the author in similar habitats to those in which it had been found on Miti'aro.

Etymology. Named after Taua, first missionary on Miti'aro. Originally from Taha'a in the Society Islands, he arrived on Miti'aro in 1823 through the agency of the London Missionary Society (Williams 1837, Lange 2005). He faithfully served on Miti'aro for 18 years before returning with his family to Taha'a.

Behavioural observations. Unfortunately, captive rearing offered few insights into the behaviour and biology of *P. tauai*. Specimens observed during the day were found deep in the leaf clusters of *S. maritima* or on the stems of *C. filiformis*. No unequivocal feeding damage was seen, though some oval abrasions were observed on the leaves of *S. maritima* and on the stems of *C. filiformis*. One possible oviposition hole was observed in the node where *C. filiformis* was parasitising *S. maritima*. The weevils were generally lethargic, with little movement occurring during observation periods. No inter-individual interactions were observed.

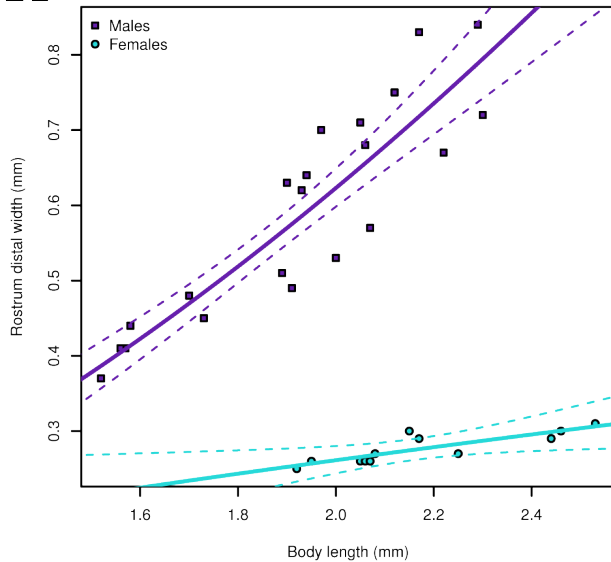
Rostrum allometric relationships. Rostrum traits varied between males and females in three of the four traits investigated. The distal width of the rostrum presented the greatest disparity between the two sexes. Males had a positively allometric relationship ($b_{\text{male}} = 1.739$) between distal width and body length, while the same trait in females was negatively allometric ($b_{\text{female}} = 0.675$) (Figure 21; Table 1). Basal width and rostrum area showed similar patterns of being positively allometric in males ($b_{\text{male}} = 1.566$ and $b_{\text{male}} = 1.745$ respectively), and negatively allometric in females ($b_{\text{female}} = 0.702$ and $b_{\text{female}} = 0.858$ respectively). Rostrum length was the exception where sex did not significantly improve the model. This trait was positively allometric for both sexes ($b = 1.438$).

In contrast, none of the models fitted for the non-rostral traits showed significant differences between the sexes,

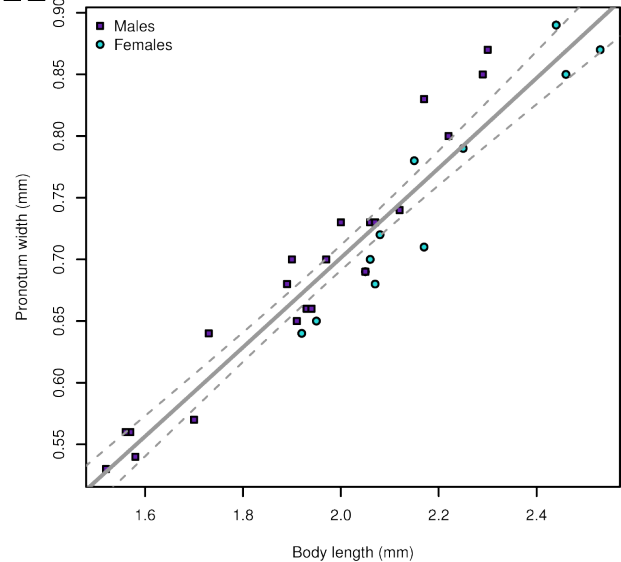
resulting in a single line being fitted for these traits (Table 1). Pronotum width (Figure 22) was isometric ($b = 1.036$), while elytral width and body height were both slightly negatively allometric ($b = 0.9$).

Comparing the distributions of male rostrum distal width, female pronotum width and female elytral width, shows some overlap between the first two traits (Figure 23), but minimal overlap between male rostrum distal width and female elytral width (Figure 23). A total of 43% of males had rostral widths that were greater than the female with the narrowest pronotum, while 75% of females had pronotal widths that were less than the widest male rostrum (Figure 24). The top 20% of males had rostrum widths that were wider than the pronotum width of 50% of females.

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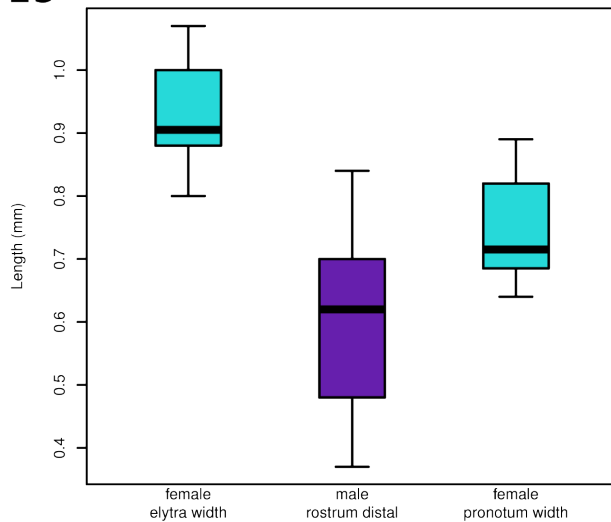


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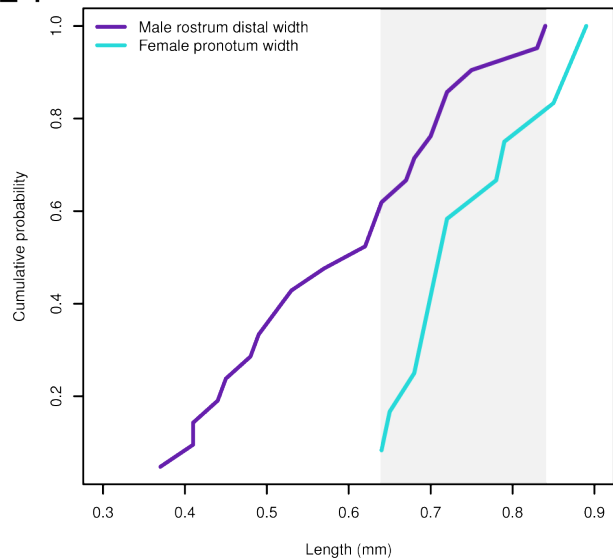


FIGURES 21–22. Allometric relationships of two traits with body length. 21: Distal width of rostrum. Regression lines are fitted separately for males and females. 22: Pronotum width. Regression line indicates the best fit for males and females combined. Dark blue squares indicate males, light blue circles females.

23



24



FIGURES 23–24. Relationship of male and female traits. 23: Boxplots showing the distribution of the pronotum width and elytral width of females and distal rostrum width of males. 24: Cumulative probability plot showing the overlap between male distal rostrum width and female pronotal width. Shaded area indicates zone of overlap between the two traits.

TABLE 1. Parameter estimates and standard errors for the allometric model $Y = aX^b$, where X = body length. p : probability that $b_{male} = b_{female}$.

Trait	a	b	a_{female}	b_{female}	a_{male}	b_{male}	p	R^2
Rostrum traits								
Distal width	—	—	-1.810 ± 0.22	0.675 ± 0.29	-1.679 ± 0.24	1.739 ± 0.32	0.002	0.960
Basal width	—	—	-1.509 ± 0.19	0.702 ± 0.24	-1.718 ± 0.21	1.566 ± 0.27	0.004	0.900
Length	-1.957 ± 0.08	1.438 ± 0.12	—	—	—	—	0.20	0.833
Area	—	—	-1.628 ± 0.22	0.858 ± 0.28	-2.146 ± 0.24	1.745 ± 0.32	0.010	0.836
Other traits								
Pronotum width	-1.073 ± 0.04	1.036 ± 0.06	—	—	—	—	0.471	0.917
Elytra width	-0.797 ± 0.04	0.916 ± 0.05	—	—	—	—	0.638	0.901
Body height	-1.224 ± 0.04	0.940 ± 0.05	—	—	—	—	0.840	0.907

Discussion

Sexual dimorphism and allometric trait relationships. Sexually dimorphic traits that have been exaggerated in males have been inferred as performing various functions: as ornaments to attract females (Spieth 1974), as weapons for conflict with conspecific males for access to females (Emlen 2008), or as structures used for coercively mating with females (Arnqvist & Rowe 2005, Bergsten & Miller 2007). Although these functions are not necessarily mutually exclusive (Berglund *et al.* 1996, McCullough *et al.* 2016), these broad categories provide a useful construct in which to consider trait utility.

Ornaments for attracting females require high visual acuity and tend to evolve in animals with good eyesight. Beetles generally are considered to have poor visual acuity (Crowson 1981), and thus it is unlikely that the vision of *P. tauai* attains a sophistication that enables the rostrum to function as an ornament.

The exaggerated development of weapons used in intraspecific competition between males for mates results from a combination of intense competition, a limited and readily defendable resource, and involving combat where strength of the individual is the primary determinant of the outcome (Emlen 2014). The traits in question are often positively allometric, and frequently show a sigmoid relationship or discontinuity between “major” and “minor” male morphs (Emlen & Nijhout 2000). Within the weevils, traits that have been identified as weapons during male–male conflict include legs (Wcislo & Eberhard 1989), prosternal horns (Eberhard *et al.* 2000) and massively elongated rostra (Painting & Holwell 2013). There are no apparent resources for the male *P. tauai* to defend, nor is the combat utility of the male rostrum shape immediately obvious. For these reasons, it is unlikely that these processes are occurring in this system.

Sexual conflict processes, where the evolutionary interests of each sex oppose each other, can lead to exaggerated traits which overcome female resistance to mating (Arnqvist & Rowe 2005, Perry & Rowe 2015). Examples of grasping traits which promote mating include the modified antennae and legs of male water striders (Westlake & Rowe 1999) and tarsal suckers of male dytiscid diving beetles (Bergsten & Miller 2007). Based on the linear scaling relationship observed between male *P. tauai* rostrum width and body size and the correlation between male rostrum width and female pronotum width, this is inferred to be the process responsible for the development of the male rostrum in *P. tauai*.

The mating behaviour of *P. tauai* is here hypothesised to involve the use of the exaggerated male mandibles to grasp the female while mating, most likely on the pronotum. This predicts that males with larger mandibles/rostra are better able to retain mates, thereby increasing their reproductive success and driving the observed positive allometric relationship. This hypothesised behaviour also provides an explanation of the differences between the sexes’ pronotum width allometry, as sexual conflict processes may select for females with wider pronota as they mate with fewer, but higher-quality males.

In this study, the dorsal dimensions of the rostrum were measured and analysed. However, the hypothesised behaviour given above suggests that selection pressure is likely to be occurring on a trait such as mandible shape or length. Thus, the differences in the shape of the rostrum are likely to be a consequence of the pressures on this associated trait, rather than being directly selected for.

It is also possible that exaggerated structures may arise through genetic phenomena such as linkage disequilibrium or pleiotropy. In these cases, size variation is a consequence of selection on other genes in proximity to, or a

different manifestation of the same genes involved with, the genes responsible for the development of the structure (Paaby & Rockman 2013, Johnsson 2015). While pleiotropic events have been found to be involved in some speciation processes (Nosil 2012), there are few examples of exaggerated sexually dimorphic structures that are affected by these mechanisms. In the diopsid fly *Teleopsis dalmanni* (Wiedemann, 1830), increases in eyespan are related to the absence of a meiotic driving X chromosome (Wilkinson *et al.* 1998, Cotton *et al.* 2014). If these phenomena are operating in *P. tauai*, the benefits of the unknown trait under selection must presumably outweigh the costs involved with producing the exaggerated rostrum. Further work to explore this possible mechanism will require detailed investigation into the genes responsible for rostrum development (Davis 2018) and the genetic architecture of *P. tauai*.

The rostrum of *P. tauai* differs between the sexes to a much greater degree than is usual within the genus *Proterhinus*. The majority of the Hawaiian species have males with an elongate, subrectangular rostrum (Perkins 1900), which differs from females in its dorsal sculpture and vestiture (Perkins 1931b), while most species found outside of Hawaii, including *P. phoenix*, *P. adamsoni* Perkins, 1931, *P. brevicornis* and *P. fimbriatus* Zimmerman and Perrault, 1989 have males with substantially wider rostra than females. The other genera in the tribe (*Aralius* Kuschel, 1990 and *Aglycyderes* Westwood, 1864) have males with similarly broad rostrum shapes (Kuschel 2003, 2008, Knížek 2012), suggesting that this is an example of phylogenetic conservatism. If true, the extra-Hawaiian species of *Proterhinus* may be paraphyletic with respect to the Hawaiian radiation, with implications for the origin of the genus.

Other sexually dimorphic traits in *Proterhinus* species include: males with a long spine on the ventral surface of tarsal segment 1 (*P. phoenix*), males with enlarged profemora (*P. perkinsi* Zimmerman, 1940), and males with enlarged metafemora (*P. pachycnemis* Perkins, 1900 and *P. podagricus* Perkins, 1910). These traits can also be interpreted as grasping structures, and suggest that mate coercion may be common within *Proterhinus*.

The negative allometric relationship seen in female rostral width traits is consistent with a hypothesis of constraints on the form of the rostrum relating to its role in preparing oviposition sites (Zwölfer & Brandl 1989, Eber *et al.* 1999). Research on other curculionine weevils has shown that the rostrum length of females co-varies with traits such as pericarp thickness of the host plant (Toju 2008). However, less consideration has been given to the role of rostrum width and the constraints on its evolution. Interestingly, the allometric coefficient for rostrum length seen here in *P. tauai* is the same as that recorded for *Curculio elephas* (Gyllenhal) and *C. glandium* Marsham (Bonal *et al.* 2011), despite vastly different ratios between rostrum length and body length.

Although secondary sexual traits often show increased allometric slopes (Voje 2016), it does not necessarily hold true that these traits have arisen through sexual selection. Recent work on modelling the evolution of allometric traits reveals that similar allometric relationships can arise from different origins, making it difficult to infer the processes that produced these observed morphometric relationships (Bonduriansky & Day 2003) in the absence of additional behavioural data.

The hypotheses presented above will require careful observation of mating behaviour to test their validity. Unfortunately, the isolation of Miti'aro will hinder the field work necessary for making these observations. The New Zealand aglycyderine weevil *Aralius wollastoni* Sharp, which has a similarly-shaped sexually dimorphic rostrum, may provide a more accessible model for researchers to investigate the sexual behaviour of the Aglycyderini.

Host specificity and larval habitat. *Proterhinus* larvae have been described from a wide range of habitats, including leaf mines, dead bark and dead twigs, dead fern stems (Anderson 1941, Swezey 1938). This diversity makes it difficult to predict where the larvae of *P. tauai* might be most likely. Based on observations of where specimens were collected, coupled by observations of specimens in captivity, it is hypothesised that *P. tauai* is associated with *Cassytha filiformis* and that larvae are stem borers of live *Cassytha* stems.

The association of *P. tauai* with *Suriana* is the first record of *Proterhinus* on this plant family and brings the number of families associated with the genus to 36 (Table 2). While the biology of some species (e.g. those that feed on dead wood or twigs) may predispose them to being on a wide variety of host plants, even those species of *Proterhinus* that are potentially host specific are found across a wide variety of plant families. This breadth suggests that *Proterhinus* species have been able to rapidly overcome a diverse range of plant defences, which may be a factor in the radiation of the genus.

Miti'aro biogeography. Miti'aro along with 'Atiu and Ma'uke make up what is known as the Nga Pu Toru Group within the Cook Islands and distances between the islands are relatively short (40 km to 'Atiu, 50 km to Ma'uke). Each island has an independent volcanic origin as evidenced by bathymetric profiles (Summerhayes 1967). However, the three islands have a shared cultural history, with Miti'aro and Ma'uke being under 'Atiuan political influence for long periods of time, especially at the time of first interaction with Europeans (Gill 1856).

However, despite this close proximity to these other islands, Miti‘aro has many unusual features of its biota. These include being the only island in the Cook Islands to have sandalwood (*Santalum insulare* Bert.) (Sykes 1980) and the palm *Pritchardia mitiaroana* J.Dransf. & Y.Ehrh. The island has two endemic plant species, a daisy *Tetramolopium mitiaroense* Lowrey, Whitkus & Sykes (Asteraceae) and a cress *Lepidium makateanum* Sykes (Brassicaceae) (Sykes 2016), and an endemic bird subspecies, the reed warbler *Acrocephalus kerearako kaoko* Holyoak. Conversely, Miti‘aro has no endemic land snails, unlike the other islands in the Southern Cook Islands (Brook *et al.* 2010). This paper reports the first endemic insect from Miti‘aro.

TABLE 2. Table of plant families and genera from which *Proterhinus* has been collected or associated. † indicates plant genera which host potentially highly specific species of *Proterhinus*.

Family	Genera	Reference
Amaranthaceae	<i>Charpentiera</i>	Swezey 1938
Apocynaceae	<i>Alyxia</i> †, <i>Pteralyxia</i>	Swezey 1938
Araliaceae	<i>Cheirodendron</i>	Swezey 1938
Arecaceae	<i>Cocos</i> , <i>Pritchardia</i>	Zimmerman & Perrault 1989
Asteraceae	<i>Argyroxiphium</i> †, <i>Bidens</i> †, <i>Lipochaeta</i> , <i>Dubautia</i>	Swezey 1938
Campanulaceae	<i>Clermontia</i> , <i>Cyanea</i> , <i>Lobelia</i>	Swezey 1938
Convolvulaceae	<i>Ipomoea</i>	Swezey 1938
Cunilaceae	<i>Weinmannia</i>	Zimmerman & Perrault 1989
Davalliaceae	<i>Davallia</i>	Zimmerman & Perrault 1989
Dicksoniaceae	<i>Cibotium</i> †	Anderson 1941
Dipentodontaceae	<i>Perrottetia</i>	Anderson 1941
Ebenaceae	<i>Diospyros</i> (as <i>Maba</i>)	Swezey 1938
Elaeocarpaceae	<i>Elaeocarpus</i>	Swezey 1938
Euphorbiaceae	<i>Aleurites</i> , <i>Antidesma</i> , <i>Chamaesyce</i> , <i>Euphorbia</i> †	Swezey 1938, Perkins 1926, this paper
Fabaceae	<i>Acacia</i> †	Swezey 1938
Gesneriaceae	<i>Cyrtandra</i>	Swezey 1938
Goodeniaceae	<i>Scaevola</i>	Swezey 1938
Hydrangeaceae	<i>Broussaisia</i> †	Swezey 1913, 1921, 1938 Anderson 1941, Perkins 1931a
Lauraceae	<i>Cryptocarya</i> , <i>Cassytha</i>	Swezey 1938, this paper
Liliaceae	<i>Astelia</i> †, <i>Cordyline</i> , <i>Dracaena</i> , <i>Smilax</i>	Swezey 1938
Malvaceae	<i>Gossypium</i> , <i>Hibiscadelphus</i> , <i>Hibiscus</i>	Swezey 1938
Myoporaceae	<i>Myoporum</i>	Swezey 1938
Myrsinaceae	<i>Myrsine</i> †(as <i>Suttonia</i>)	Swezey 1938
Myrtaceae	<i>Metrosideros</i> , <i>Syzygium</i>	Zimmerman & Perrault 1989, Swezey 1938
Nyctaginaceae	<i>Pisonia</i>	Swezey 1938
Oleaceae	<i>Osmanthus</i>	Swezey 1938
Poaceae	<i>Digitaria</i> †	Perkins 1931a
Polypodiaceae	<i>Dryopteris</i> , <i>Pteris</i> , <i>Sadleria</i>	Zimmerman & Perrault 1989
Rutaceae	<i>Melicope</i> (as <i>Pelea</i>), <i>Xanthoxylum</i> †	Anderson 1941, Perkins 1931a
Rubiaceae	<i>Bobea</i> , <i>Coprosma</i> , <i>Gouldia</i> †, <i>Rubus</i> , <i>Straussia</i> †	Anderson 1941, Swezey 1938
Sapotaceae	<i>Sideroxylon</i>	Swezey 1938
Sterculiaceae	<i>Waltheria</i>	Perkins 1931b
Surianaceae	<i>Suriana</i>	This paper
Thelypteridaceae	<i>Phegopteris</i>	Swezey 1938
Thymelaeaceae	<i>Wikstroemia</i> †	Anderson 1941
Urticaceae	<i>Pipturus</i> †	Swezey 1938

Based on the morphological similarity of *P. tauai* and *P. brevicornis*, this species indicates a link with the Society Islands. Other taxa with sister taxa in the Cook Islands and the Societies include the broad-nosed weevil genus *Rhyncogonus* (Claridge *et al.* 2017), and *Partula* land snails (Lee *et al.* 2014). Overall, within the broader context of Polynesian biogeography, there are strong connections in the biota between the Cook and Society Islands (Hembry & Balukjian 2016).

However, there are taxa that show links with Hawaii and the Austral Islands. Both endemic plants have their closest relatives in the Hawaiian Islands (Sykes 2014, 2016). Molecular phylogenies indicate that *T. mitiaroense* is sister to the Hawaiian species of the genus, and is inferred to have dispersed to Miti'aro from Hawaii (Lowrey *et al.* 2001, 2005). Genetic studies of sandalwood (*Santalum insulare*), show that Miti'aro specimens share their chlorotype with those from Raivavae (Butaud *et al.* 2005). A connection with the Austral Islands is also revealed by the relationships of the reed warbler, which has two subspecies endemic to Mangaia and Miti'aro respectively, and with its sister species (*A. rimitarae*) endemic to Rimatara (Cibois *et al.* 2011).

Conclusion

Proterhinus tauai is described from specimens collected in coastal scrub on Miti'aro, Cook Islands. This species differs from its congeners by the combination of: dorsal vestiture of decumbent brown clavate scales, lacking erect elongate setae; short antennae, not reaching the posterior margin of the pronotum; anterior pronotal angles projecting forwards; and males with a sexually dimorphic rostrum which is semicircular in dorsal view. Based on collection data and limited observation of captive specimens, the parasitic vine *Cassytha filiformis* (Lauraceae) is hypothesised to be the host plant of *Proterhinus tauai*. The scaling relationship of rostral and pronotal widths was measured in relation to body length, and showed that male rostrum width was strongly positively allometric, and the dimensions overlapped with female pronotal width. These results led to the hypothesis that *P. tauai* males use their mandibles to grasp females by the pronotum while mating. This coercive mating system has led to sexual selection being important in the evolution of the morphology of both males and female *P. tauai*. However, further behavioural observations will be necessary to confirm and refine these hypotheses.

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