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# Description of the Female and Egg of *Theramenes mandirigma* Zompro & Eusebio, 2001 (Phasmatodea: Heteropterygidae: Obriminae: Obrimini)

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## Abstract

The morphology of the female and egg of *Theramenes mandirigma* are described. The time from mating to depositing of the eggs, the time from deposition until hatching, and the food plants are reported.

## Key words

Phasmatodea, Obrimini, *Theramenes mandirigma*, egg capsule structure, Cebu biodiversity.

## Introduction

So far, only three specimens of *Theramenes mandirigma* were ever collected, all were males:

1. Date: August 17, 1974, Locality: Camp-7 forest, Collector: David A. Pahilan, a student of the University of San Carlos.
2. Date: April 01, 2000, Locality: a secondary forest in Alcoy, Collector: M. Pedregosa. This male specimen was used by Zompro & Eusebio to describe the new species in 2001. The collected specimen became the type specimen and was deposited in the Museum of Natural History, University of the Philippines Los Baños, [UPLBMNHC No. PHA-00329L].
3. Date: August 09, 2009, Locality: Camp-7 forest, Collector: Reagan Villanueva.

The female form remained unknown to science. On August 6, 2015, the female form of this species was discovered by the author. Copulation, the laying of eggs as well as the hatching could be observed in captivity.

The species *Theramenes mandirigma* is so far considered as an endemic to Cebu Island, Philippines.

## Description

Female (Figs. 1-3), general colour of head and body brown, similar to the male, but larger body and without the large dark brown tubercles. Abdomen significantly wider than in male. Only abdominal segments VI, VII and VIII bright yellowish brown, whereas whole abdomen bright brown in male.

### Head

Same as male, slightly larger, subquadrate, vertex slightly elevated. Eyes dark brown, projecting hemispherically, surrounded by a yellow ring.

### Antennae

As in male, light brown, outer half dark brown, with 25 segments, projecting beyond median segment. Scapus slightly flattened, pedicellus slightly more than half as long and two thirds as wide, subcylindrical. Succeeding segments increasingly longer.

### Prothorax

Slightly wider than long, as long as head,



Figure 1. *Theramenes mandirigma*, female, dorsal view



Figure 2. *Theramenes mandirigma*, mating position (lateral view)

*Mesothorax*

Trapezoidal, posterior end significantly wider. The two prominent tubercles of the male absent in the female, or extremely reduced. Median line visible throughout.

*Metathorax*

Slightly wider than mesothorax, The prominent tubercle of the male absent in the female, or extremely reduced. Median line visible throughout.

*Abdomen*

Median segment, about one half as long as metathorax into which it is fused or fully integrated, rectangular, more than twice as wide as long, not almost quadrate as in male. Abdominal segments II to VI significantly wider than in male. Abdominal segment II longer than and wider than median segment, slightly wider posteriorly. Abdominal segment III, wider than segment II, dilating posteriorly, with symmetrical yellow markings at the posterior end. Abdominal segment IV rectangular, widest abdominal segment, shorter but slightly wider than previous and following segments. Abdominal segments VI, VII and VIII lighter yellowish brown.

*Legs*

Profemora quadrate in cross-section. Protibiae slightly shorter, curved basally slightly elevated dorso-apically. Mesofemora and mesotibia quadrate in cross-section. Mesotibia slightly longer than mesofemora. Metafemora not strongly broadened, similar to profemora and mesofemora. Metatibia slightly longer than metafemora.



Figure 3. *Theramenes mandirigma*, the female depositing the eggs

Table 1 gives the measurements of the body parts. The measurements for the male are taken from Zompro, O. & Eusebio O. L. (2001).

### The egg

Measurements of the egg (in mm): length 6.5-7, width 2, height 2.5

Structure of the egg capsule of *Theramenes mandirigma*: Egg bullet-shaped, tapering towards the polar end. Surface shiny. Operculum elliptic, without capitulum. Micropylar plate oblong to slightly elliptical in shape, longer sides nearly parallel, with two lobes towards the posterior end, and rounded towards the anterior end. Micropylar cup located at the posterior end of the micropylar plate. Median line not separated, running up to the pole. The dorsal view of the egg capsule structure is shown in Fig. 4.

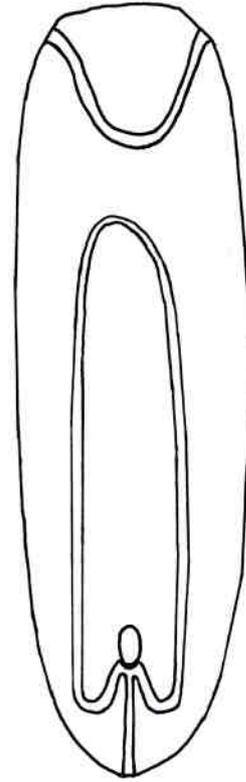


Figure 4. The egg, dorsal view

### The first instar (Fig. 8)

Body length after hatching: 1.32mm.  
Segments of the flagellum: 7.

### Remarks about the biology

Foodplants of *Theramenes mandirigma*: *Diospyros philippinensis* (Ebenaceae), and at least two other *Diospyros* species as well as *Swietenia macrophylla*.

Reproduction: The female deposited 19 eggs, a few millimetres deep into dead soft wood and into the soil.

Time from mating until depositing the eggs: 23 days.

Time from depositing the eggs until the first hatching: 83 days.

### Distribution

Endemic to Cebu island, Philippines. So far only known from two localities: Municipality Minglanilla and Municipality Alcoy.

### References

Zompro, O. & Eusebio O. L. (2001) A new species of stick insect (Phasmatodea: Heteropterygidae: Obriminae: Obrimini) from Cebu Island, Philippines. *The Philippine Entomologist* 14(2): 131. 135.

Table 1: Comparison of measurements of female and male body (in mm).

	Female	Male
Head:	7.0	5.0
Prothorax:	7.0	4.5
Mesothorax:	15.0	9.0
Metathorax:	8.0	5.2
Median segment:	4.0	2.9
Abdomen:	33.0	17.6 (computed)
Total length (head, thorax and abdomen):		
	70	41.3
Legs		
Profemora:	14.0	9.0
Protibia:	13.0	8.0
Mesofemora:	12.0	6.8
Mesotibia:	13.0	6.6
Metafemora:	16.0	8.9
Metatibia:	17.0	10.0
Antennae		
Length:	32	
Segments:	25	26



Figure 5. The egg, egg shape



Figure 6. The egg: , operculum



Figure 7. The egg, polar end of micropylar plate and median line



Figure 8. First instar of *Theramenes mandirigma*

# Colour variation in the Spiny Leaf Insect (*Extatosoma tiaratum* Macleay, 1826)

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## Abstract

*Extatosoma tiaratum* (Family Phasmatidae: Tropidoderinae) is native to the tropical regions of northern Australia where they begin life as ant mimics, initially being dark brown in colour, as they mature colours range from light orange-red, to brown, or a very pale green. This study documents the exoskeleton colour variation of daughters produced parthenogenetically by a green adult female, and whether the colour changes over time. We also investigated whether their exoskeleton colour changes in response to their environment, and whether variation in colour correlates with the protein composition of their exoskeleton. The dominant colours of fourth instar *E. tiaratum* included orange, yellow to reddish brown – colouration that provides these large, sedentary insects with effective camouflage amongst foliage. Whilst different proteins were observed in the various coloured exoskeletons no consistent correlations were apparent. Results of the preliminary protein analysis of the exoskeleton of this intriguing insect were inconsistent but warrant further investigation.

## Key words

*Extatosoma*, Phasmatidae, exoskeleton colour, exoskeleton proteins

## Introduction

*Extatosoma tiaratum* Macleay, 1826, is native to the tropical regions of northern Australia but has become a popular pet in the southern states. *E. tiaratum* (family Phasmatidae) belongs to subfamily Tropidoderinae which comprises mainly large, winged species that resemble leaves rather than twigs (Key 1991). Unlike other phasmids, *E. tiaratum* has numerous spines and integumental expansions on the abdomen and legs (Fig 1). It often hangs inverted amongst foliage with its procrystic abdomen curled over its back. The 1st instar of this species is black with an orange head mimicking ants from the genus *Leptomyrme* (Key 1991).

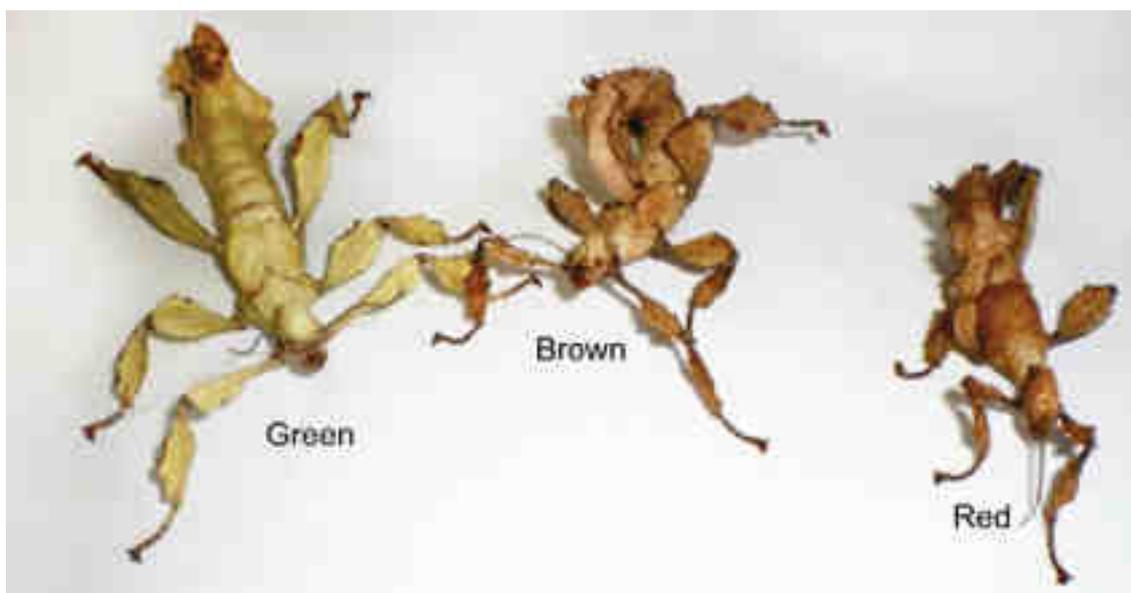


Figure 1. Colour variation in *E. tiaratum*. All three are daughters produced parthenogenetically by a single pale green female.

This phasmid (PSG9) is an interesting study model for many reasons, including: the female's ability to reproduce parthenogenetically (Brock 2003) and the propensity of the exoskeleton to exhibit colour change as well as the variation in colour. When a female *E. tiaratum* reproduces by parthenogenesis, all daughters have the same genotype (More 1996). However, it has been observed that a female that has reproduced by parthenogenesis can produce daughters with different exoskeleton colours.

*Extatosoma tiaratum* colours range from light orange-red, to brown, or a very pale green. This study documents the colour of daughters produced parthenogenetically by a pale greenish yellow (colour to be referred to as "green") adult female and investigates whether the variation in exoskeleton colour correlates with the protein composition of the exoskeleton of these insects.

The insect exoskeleton is composed of chitin, tanned lipoprotein, waxes, polyphenols and cements as well as protein (Prosser 1973). In other phasmid species such as *Carausius morosus* (Sinety 1901), the colour pigments including: brown (melanin), orange-red and yellow (lipochromes), and green are located in hypodermal cells (chromatophores), and are moved throughout these cells via microtubules (Prosser 1973). The intensity of colour is determined by how close to the surface of the exoskeleton the pigments are located (Berthold 1980). Prosser (1973) also found that the brown and orange-red pigments have the ability to migrate throughout the cells, whereas the yellow and green pigments do not.

Some phasmid species have the ability to gradually change the colour of their exoskeleton to blend with their environment. Mangelsdorf (1926) reported that altering the colour of the environment of *Dixippus morosus* (synonym of *Carausius morosus*) resulted in a change in exoskeleton colour. Few similar studies on exoskeleton colour change in *E. tiaratum* have been published. Variations in humidity and light have resulted in colour change in *C. morosus* (Prosser 1973), and Brock (2003) reported that *E. tiaratum* fed on *Eucalyptus* spp. leaves were brown in colour whereas when fed on leaves of *Acacia* or *Rosa* spp. their exoskeleton was usually green. In common with other phasmids, the survival of *E. tiaratum* depends almost entirely on its ability to remain unseen, making the colour of its exoskeleton of vital importance for camouflage.

The aims of this study were firstly, to categorise, monitor and document colour variation and change in exoskeleton colour in a sample population of *E. tiaratum* early instars – daughters of one pale green female that reproduced by parthenogenesis, and secondly to investigate the protein composition of three different coloured exoskeletons.

## Materials and Methods

*Extatosoma tiaratum* early instars (n = 84), all daughters of a single pale green female, were kept at room temperature (20-23°C) in a terrarium lined with damp paper towel and all were fed *Eucalyptus* spp. leaves. The terrarium was misted with water every 1 – 2 days to keep the environment moist. Exoskeleton colour of the ventral surface of the abdomen (which is curled over the insect's back) of all *E. tiaratum* was determined using Royal Horticultural Society (RHS) colour charts. The RHS colour codes were later matched to Universal Colour Language (UCL) names (Kelly & Judd 1976) and observations recorded on a weekly basis.

### *Exoskeleton colour change with maturity*

Ten of the 84 1st instar phasmids were placed in separate tanks i.e. one phasmid per tank. They were photographed and colour coded using the RHS colour charts at the beginning and the end of the study and their exoskeleton colour compared at 1st and 4th instar stage.

### *Monitoring of exoskeleton colour change in response to environment*

To determine whether exoskeleton colour can be altered by changing the colour of the phasmid's environment, four tanks were wrapped in coloured cellophane (either blue, green, red or yellow) plus one control tank without cellophane. Three phasmids of varying colours were housed in each tank,

one light greenish grey, one greyish brown and one reddish brown. All tanks were placed in a well lit position.

*Protein analysis of exoskeleton – preliminary study*

The protein composition of *E. tiaratum* exoskeleton was characterised using discontinuous sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) following the methods of Neil et al. (1993) and Mykles (1985a, 1985b) using Bio-Rad Mini-Protean II slab gel apparatus. Samples of exoskeleton were collected from one light greenish grey (labelled green), one greyish brown (brown) and one reddish brown (red) phasmid (all late instar) to compare protein composition. Pieces of exoskeleton were removed from integumental expansions on the hind leg, making sure not to take muscle or any other tissue. The exoskeleton samples were placed in solubilising buffer (2.3 mL distilled water; 0.5 mL 0.5M Tris HCl, pH 6.8; 0.4 mL glycerol; 0.8 mL 10% (w/v) sodium dodecyl sulphate (SDS) and ground using a Metabo hand drill with Eppendorf disposable polypropylene micro-pestles to minimize cross contamination. Ground samples were left on a Ratek rocker overnight and then stored at -20 oC.

Molecular weight markers (SigmaMarker wide molecular weight range Catalogue No: M 4038) were loaded into lane one of the gel. The 15 µL samples containing dissolved protein were loaded onto the gel and run at 200V for approximately 50 minutes. The gel was stained with Coomassie Blue overnight on a Ratek rocker, then destained for approximately 2 hours with a solution of 40% methanol and 10% acetic acid. Digital images were then taken with a ChemiDoc-It® Imaging System and images stored for later analysis. Gels were then dried and stored for later reference.

<b>RHS code</b>	<b>UCL colour name</b>	<b>1st instar</b>	<b>2nd instar</b>	<b>3rd/4th instar</b>	<b>Total No. individuals</b>
164C,165C	moderate orangish yellow		1	14	15
165D	pale orangish yellow		1	10	11
177B	light reddish brown	2	7		9
166D, 173D	moderate orange			9	9
174C, 174D	greenish reddish orange		4	2	6
177C, 177D	greyish reddish orange	1	4	1	6
11B, 160B	light yellow			6	6
187A, 187B	dark red	4			4
173D	moderate yellowish pink			4	4
166A	greyish brown	2			2
164B	moderate orangish	2			2
174A, 177A	moderate reddish brown	1	1		2
160D, 164D	pale yellow		1	1	2
165D	brownish orange			1	1
198D	light greenish grey			1	1
175D	moderate reddish orange			1	1
161B	moderate yellow			1	1
160C	pale greenish yellow			1	1
166B	reddish brown		1		1
<b>No. Individuals</b>		<b>12</b>	<b>20</b>	<b>52</b>	<b>84</b>

Table 1. Eighty-four *E. tiaratum* assigned to 19 different colour categories using RHS colour charts and UCL names.

## Results

### *Exoskeleton colour variation*

The eighty-four early instar *E. tiaratum* were assigned to 19 different colour categories using RHS colour charts and UCL colour names (Table 1). First instar hatchlings (n = 12) were found to be dark reddish brown in colour with an orange head, with both colours becoming dull brown pre-ecdysis. Second instar individuals (n = 20) on the other hand displayed a wider range of 10 RHS (8 UCL) colours while 3rd and 4th instars (n = 52) showed 17 RHS (13 UCL) colours. The most common colours overall were: moderate orangish yellow (n = 15), pale orangish, yellow (n = 11), followed by light reddish brown (n = 9) and moderate orange (n = 9).

### *Exoskeleton colour change with maturity*

Generally, as the 10 hatchlings kept in individual tanks matured they became progressively lighter and more orange in colour (Table 2). This colour change was first observed after the 1st and 2nd moult, and all phasmids remained the lighter colour for successive instars.

### *Monitoring of exoskeleton colour change in response to environment*

The colour change study involving *E. tiaratum* phasmids kept in tanks with different coloured light yielded inconsistent results. Overall individuals did become lighter in colour, but there was no discernible trend in exoskeleton colour change in response to environment, however two interesting changes were observed. The light greenish grey phasmid in the yellow cellophane covered tank became brown over a period of approximately 3 – 4 months, but no colour change was seen in the other

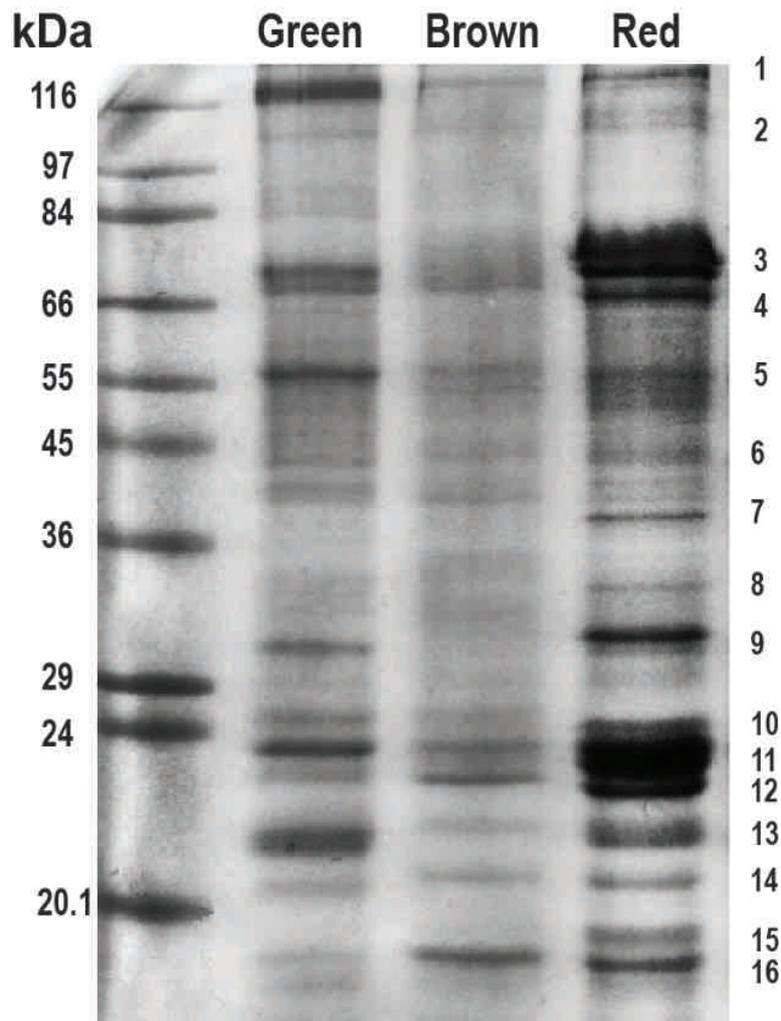


Figure 2. Protein composition of *E. tiaratum* exoskeleton characterised using gel electrophoresis (SDS-PAGE) 16 proteins with molecular weights between 116 and 18 kDa were observed.

two phasmids kept in the same tank. Another light greenish grey phasmid in the control tank also became brown, but again no other changes were observed in any of the other individuals in this tank.

#### *Protein analysis of exoskeleton – preliminary study*

Protein composition of *E. tiaratum* exoskeleton of three different colours (labelled green, brown and red for simplicity), characterised using gel electrophoresis (SDS-PAGE) yielded 16 major proteins with molecular weights between 116 and 18 kDa (Fig 2). Positive identification of the 16 proteins extracted in this preliminary study was not possible as little information about characterisation of phasmid exoskeleton proteins has been published. Consequently bands have been labelled numerically to facilitate comparison. Differences were detected and these were: the red exoskeleton sample produced the greatest number of bands (16) and brown, the least with 12. Green exoskeleton produced 14 bands with bands 4 (66 kDa) and 8 (approximately 34 kDa) present in the other two but absent in this sample. Bands 3 (approximately 70 kDa), 7 (approximately 39 kDa), 8, and 9 (approximately 27 kDa) were not apparent in the brown exoskeleton sample.



Figure 3A. *Extatosoma tiaratum* – final instar with typical orangish yellow colouration is well camouflaged when hanging from a drying eucalypt twig.

Figure 3B. An ant mimicking, 1st instar *E. tiaratum* with an orange head, dark brown thorax and abdomen.

## Discussion

The findings of this study were that there was variation in *E. tiaratum* exoskeleton colour, with 19 different colour categories noted, colour did change with maturity among the hatchlings produced parthenogenetically by one green female, and that the proteins extracted from the exoskeleton varied.

#### *Exoskeleton colour variation*

The dominant exoskeleton colours of over half the phasmids assessed ( $n = 44$ ) included orange, yellow or reddish brown. This colouration provides these large, increasing more sedentary insects with effective camouflage when attached to the reddish brown eucalypt twigs, the food source they were provided with, or drying leaves (see Fig 3A).

*Factors affecting exoskeleton colour*

It was observed that ten *E. tiaratum* hatchlings monitored in this study were initially dark brown (Fig 3B) but became lighter brown and more orange as they matured (Fig 3A). This correlates with the *E. tiaratum* life history, where hatchlings begin life as ant mimics inhabiting ant nests (Key 1991). To remain well camouflaged and safe from predation, the maturing phasmids must become lighter once they leave the safety of an ant's nest and move up into foliage. Interestingly few hatchlings in this study had the pale green colouration (refer to example in Fig. 4) of the mother despite having the same genotype. A longer term study tracking colour change from hatchling to adulthood is warranted.

1st instar	RHS code	UCL colour name	4th instar	RHS code	UCL colour name
	177B	light reddish brown		177D	greyish reddish orange
	166A	greyish brown		166C	brownish orange
	177B	light reddish brown		174C	greenish reddish orange
	187A	dark red		177B	light reddish brown
	187A	dark red		177B	light reddish brown
	177D	greyish reddish orange		166C	brownish orange
	187B	dark red		166C	brownish orange
	187A	dark red		166B	reddish brown
	177B	light reddish brown		175C	dark reddish orange
	165C	moderate orangish yellow		166C	brownish orange

Table 2. Observed exoskeleton colour change in *E. tiaratum* (n = 10) kept in individual tanks comparing 1st with 4th instar colouration



Figure 4. An example of a 3rd instar female *Extatosoma tiaratum* with pale green colouration.

*Extatosoma tiaratum* colour change in response to environment

No discernible trend in exoskeleton colour change in response to different coloured light was observed. Change in colour was seen in one individual in the control tank as well as one of the phasmids kept in yellow light. Both individuals that became brown were light greenish grey initially suggesting that this change was not a response to the colour of their environment.

*Protein composition of the exoskeleton*

Differences in the number of proteins extracted may not be due solely to the difference in exoskeleton colour. Little information about phasmid exoskeleton protein composition is available, but according to Wheeler et al. (2001) and Whiting et al. (2003) phasmids belong among the basal winged insect orders (Polyneoptera), and while their sister group is unknown, Orthoptera is a likely candidate. Andersen et al. (1986) extracted approximately 100 different proteins from orthopteran exoskeleton. Andersen et al. (1995) later noted that post-ecdysial proteins can be rendered inextractable as a result of sclerotization, and observed an abrupt change in cuticular proteins extracted from orthopterans post-ecdysis. The phasmids used in this study were the progeny of one female, but not all eggs hatched simultaneously, so individuals may have been different stages of the instars – either pre or post ecdysis when exoskeleton samples were taken, hence the variation in proteins extracted. Andersen et al. (1995) found that the majority of orthopteran pre-ecdysial, cuticular proteins had molecular weights between 8 and 50 kDa. This may explain the extra bands between 50 and 18 kDa seen in exoskeleton samples from the red, and the green coloured *E. tiaratum*.

Although the results of this preliminary study found differences in the protein composition of exoskeletons of different colours, further investigation is warranted to determine what these proteins are.

**Acknowledgements**

We would like to thank Professor Marjory Martin for providing us with the RHS colour charts, Cuong Huynh and Jessica Bywater for their excellent technical assistance.

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# Phasmid collection and bibliography of the Phasmida works of J. T. C. Sellick

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J. T. C. Sellick (in earlier works he published under the name J. T. Clark) obtained his undergraduate degree in Zoology from St John's College, Cambridge and later studied for an MSc and PhD in Entomology at the University of London. His teaching career included Harrow County School, the Royal Grammar School and Uppington School where he was Head of Biology. Sellick is best known among phasmatologists for his work on the morphology of the phasmid egg capsule, his terminology of which has now become widespread in phasmid publications. His collection, comprising of pinned insects, eggs mounted on cards and eggs in tubes has been donated to the Natural History Museum, London along with original drawings of eggs from his publications and a copy of his PhD thesis. The Museum also holds copies of his other publications related to the Phasmida.

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# A new genus and species of Phasmida, *Pseudososibia albidotarsi* (Phasmida: Necrosiinae) from South Andaman Island, India

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## Abstract

A new species of Phasmida belonging to family Diapheromeridae, subfamily Necrosiinae was collected from South Andaman Island during a survey in the month of December, 2013 to January 2014. A single male, a female and egg has been collected. The species belongs to a new genus *Pseudososibia*. The species has been assigned the name *albidotarsi* due to the presence of strikingly white tarsi.

## Key words

*Pseudososibia albidotarsi*, new genus and species, Phasmida, Necrosiinae, Andaman Island, India.

## Introduction

According to literature records, so far 6 genera and 6 species of Phasmida (listed below) are known from Andaman and Nicobar Islands. The Island fauna seems to be poorly known as is evident from the high number of genera compared to species. Certainly many islands are totally virgin and inaccessible to date. So far one genus and one species *Trachythorax atrosignatus* (Brunner von Wattenwyl, 1893) under the subfamily Necrosiinae is known from this region. Here is the addition of a new genus, *Pseudososibia* along with the description of a new species, *Pseudososibia albidotarsi*.

## Species of Phasmida previously known from Andaman and Nicobar Islands

*Abrosoma virescens* Redtenbacher, 1906 (doubtful as per PSF).

*Lonchodes verrucifer* Wood-Mason, 1876.

*Ramulus westwoodi* (Wood-Mason, 1873).

*Sceptrophasma hispidulum* Wood-Mason, 1873.

*Trachythorax atrosignatus* (Brunner von Wattenwyl, 1893).

*Phyllium (Phyllium) westwoodii* Wood-Mason, 1875.

## Description

### Diagnosis

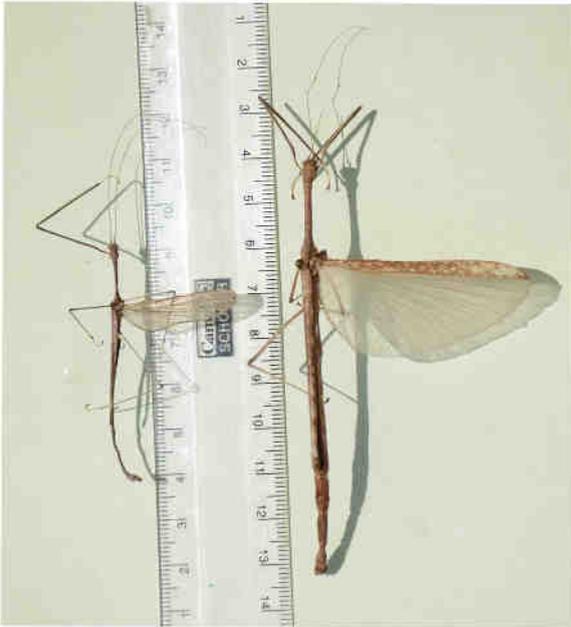
Head globose; ocelli distinct; eyes colourless; antennae shorter than body; elytra short, oval costal area of hind wing brown with pale whitish spots and similar patches towards tip; all tarsi shining white.

### Male (Figs 1-4)

Head posteriorly globose, not elevated into cone or hump; margins around ocelli and antennal carina with black lines; vertex of head smooth, of uniform grey coloured. Eyes big, round, grey coloured. Ocelli distinct with the rim of cup black lined. Basal 2 segments of antennae grey coloured; dorsally the segments are whitish to grey, black spotted at joints; ventrally segments are dark brownish to blackish.

Prothorax rectangular, grey coloured, a little narrowed behind where is a thin transverse, black line. Mesothorax uniformly narrow, carinated, rounded, and almost smooth with very few minute tubercles at anterior end; ventrally with one median and two pairs of longitudinal carinae. Metathorax and median segment blackish; median segment a little more than half of metathorax.

Elytra oval elongated, apex conically round; densely reticulate; hump distally placed from middle; costal area, base and a narrow posterior area of anal area pale grey coloured; area adjoining hump is



**Fig. 1**



**Fig. 2**



**Fig. 3**



**Fig. 4**



**Fig. 5**

Fig. 1: Holotype male and allotype female of the new species.

Fig. 2: Holotype male.

Fig. 3: Head and thorax of holotype male.

Fig. 4: Last abdominal segments of holotype male.

Fig. 5: Host plant

black. Hind wing extends up to middle of 5th abdominal segment; long veins of costal area blackish spotted; long veins of anal area pale grey; anterior ½ of costal area with opaque cells, rest cells colourless; anal area colourless.

Legs are smooth. Foreleg incurved at base; femur and tibia pale blackish with black lined carinae; tarsi except claw are shiny white; distal joints of tibia and femora black. In the middle and hind legs, femora with black bands which are less distinct on tibiae; their distal joints and tarsi coloured as forelegs.

Abdominal segments are blackish dorsally, smooth and rounded, faintly hairy; segments 5-9 at mid-posterior point with minute black tubercles; segments 2-5 very little longer; 6-10 shorter gradually; 8th nearly half of 7th; 9th and 10th carinated; 10th at extremity conical and deflexed ventrally; ventrally the segments are irregularly black patched.

Poculum long, extends up to apex of 9th segment; its basal part carinated; apex conically narrowed at distal end. Cerci short, straight, cross each other beneath 10th segment.

Material examined: Holotype male, Bamboo Teri near Ferrargunj in South Andaman, 12.12.2013, 11.72 N, 92.65 E, 109 mts, 12.xii.2013, coll. G. Srinivasan.

Measurements (mm): Total length 53; antenna 38; head 1.8; prothorax 2.4; mesothorax 8.4; metathorax 7.2; median segment 4.8; elytra 1.5; hind wing 26; foreleg 17+17.5+6.5; middle leg 12.5+11.5+5; hind leg 16+17+5.5.

#### *Female* (Figs 6-9)

Head without black line on antennal carinae and rim of ocelli. Antennae similar to male; spots at joints of segments less distinct. Vertex with 8 longitudinal blocks of brownish patches (each such block consists of spots of brownish and pale white mixed together); each longitudinal patch with a distinct round black spots at its front.

Thorax similar to male, but without posterior transverse black band. Mesothorax similar to male; carina in the form of a very fine groove along the entire length; dorsally smooth except for few very distinct black almost rounded tubercles. Mesosternum with one median and two lateral ridges. Pleura of mesothorax with 6-7 black minute tubercles. Metathorax and median segment similar to male; pleura of metathorax with 4 pairs of black minute tubercles and scattered white patches; latter less on abdominal segments. Legs similar to male.

Elytra as in male. Hind wing same as in male but extends nearly up to the distal end of the 5th abdominal segment. Costal area dirty brown, with irregular pale spots along length; these spots fuse at distal end forming ovoid pale patches; both anterior half and posterior half of costal area are opaque along the length; veins of anal area colourless.

Abdominal segments dorsally pale grey with very few scattered blackish spots; tubercles on postero-median points black-marked, less distinct than in male; 10th transverse, carinated, apex straight. Cerci short, rounded, exposed a little beyond lateral corners of the rounded ends of 10th segment.

Preopercular organ black, conical and spine like. Proximal half of operculum white patched and laterally compressed; distal half flat boat form, carinated, apex conical, reaches the end of the 10th segment.

Material examined: Allotype female, Bamboo Teri near Ferrargunj in South Andaman, 12.12.2013, 11.72 N, 92.65 E, 109 mts, 12.xii.2013, coll. G. Srinivasan. Egg from the female came out in the alcohol tube.

Measurements: Total length 95; antenna 44; head 2.8; prothorax 3.8; mesothorax 16; metathorax 12.2;



**Fig. 6**



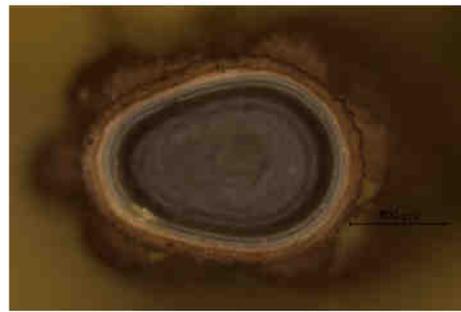
**Fig. 7**



**Fig. 8**



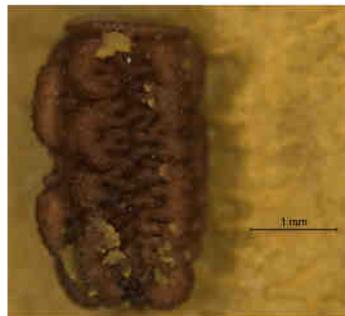
**Fig. 9**



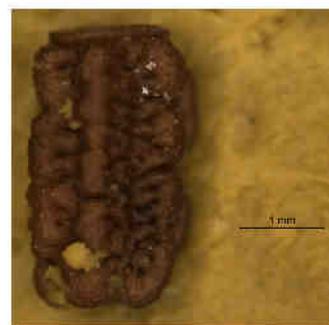
**Fig. 10**



**Fig. 11**



**Fig. 12**



**Fig. 13**

- Fig. 6: Head and thorax of allotype female.  
Fig. 7: Fore and hind wings of allotype female.  
Fig. 8: Abdomen of allotype female.  
Fig. 9: Operculum of allotype female.  
Fig. 10-13. Egg of allotype female.

median segment 7; elytra 4.5; hind wing 46; fore leg 20.5+20.5+6.8; middle leg 15+18+5.5; hind leg 18+16+6. Abdominal segments 70.

#### *Egg* (Figs 10-13)

The description is based on the terminology of Clark-Sellick (1997). Capsule brown, rectangular, irregularly sculptured by ridges. Its height and maximum width are 3.18 mm and 1.947 mm respectively. Dorsal surface at middle bears a rounded excavated micropylar plate (0.502 mm x 0.443 mm); posteriorly the plate has a short triangular funnel (micropylar cup) which has a very short posterior ridge (median line); the latter is in continuation with the mid-posterior swollen ridge; a similar ridge on the antero-median of the micropylar plate. The two lateral surfaces are irregularly and differently sculptured by swollen ridges and their less swollen branches of ridges. Operculum oval, surface smooth and flat, narrowed towards dorsal face; its rim whitish and outer capsular wall is finely tuberculated. The operculum height (=length) and width are 1.394 mm and 1.077 mm respectively. Capitulum is oval, brown, finely tuberculated, with two anterior and one posterior big rounded elevation and at center with a small irregular less swollen area.

#### *Host plant* (Fig 5)

Ferrargunj is located 13 kms northwards from Port Blair [N 11°44'27.9" N & E 092°39'14.7" E]. Red ants were the main predators feeding on the legs of the female stick insect. The collection was done when the individuals were mating on the forest floor. The soil was damp. The forest type is tropical evergreen forests. The forest was covered with tall trees and underneath there were Cane, Palm and shrubs. The stick insects were located below the shrubs which were of 5 to 10 feet height. The forest floor was totally covered with debris mainly of the dried twigs and leaves of the phasmid host plants and was a good place to camouflage.

The host plant belongs to the species *Drypetes afzelii* (Pax) Hutch. It seems that this plant was not previously recorded from India. The genus *Drypetes* Vahl belongs to the family Putranjivaceae Meisn. and both are distributed along entire equatorial regions of the globe. In India, the genus is distributed in North Eastern region and southernmost region including Andaman and Nicobar islands and also known from adjoining oceanic islands and Australia. *Drypetes afzelii* (Pax) Hutch is known to extend from Sierra Leone to Ghana only.

#### *Comparison*

The new genus differs from the genus *Sosibia* Stål, 1875, to which it shows some affinities, by the presence of ocelli and the spiniform apex of operculum. It has some affinities with the genus *Hemisosibia* Redtenbacher, 1908, from which it differs by the presence of globose head, longer anterior femur than the mesothorax and spiniform apex of operculum. The genus *Sosibia* is widely distributed in India, Malaysia, Borneo, Sri Lanka and some other places and the genus *Hemisosibia* is known from Malaysia, Borneo, China, Kalimantan (Redtenbacher 1908, Bragg 2001, Brock 2002, Brock et al. 2017). The species is distinctly different by the peculiar white colour of all tarsal segments on all legs.

#### *Etymology*

The species name refers to the white tarsi on all legs.

### **Acknowledgement**

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# Ecology and Diversity of Stick Insects (Insecta: Phasmida) from the Virgin Islands

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## Key words

West Indies, Puerto Rico, Guana Island, walkingstick, host plant, phenology, habitat partitioning, biogeography, *Agamemnon*, *Bacteria*, *Clonistria*, *Haplopus*

## Abstract

All five known species of stick insects (Insecta: Phasmida) from the Virgin Islands were systematically studied for the first time: *Bacteria yersiniana* Saussure, 1868, *Clonistria calamus* (Fabricius, 1793), *Clonistria modesta* (Redtenbacher, 1908), *Haplopus micropterus* (St. Fargeau and Serville, 1828), and *Agamemnon cornutus* (Burmeister, 1838). The morphology of *C. calamus* and *C. modesta* males and eggs of all five species are described for the first time. The winged male of *C. modesta* represents the first report of wings in the genus *Clonistria* Stål, 1875. The following new synonymy is proposed: *Dyme krugiana* Brunner, 1907, is a new synonym of *Bacteria yersiniana*; *Bacunculus bradypus* Werner, 1929, is a new synonym of *Clonistria calamus*. In nature, we found *B. yersiniana* feeding on one host plant in Rubiaceae and two in Flacourtiaceae, *C. calamus* being active on two host plants in Fabaceae and confirmed feeding only by tests, *C. modesta* feeding only on *Eugenia cordata* in Myrtaceae, *H. micropterus* feeding on two host plants in Fabaceae, and *A. cornutus* feeding on five different host plants in Boraginaceae, Commelinaceae, Malpighiaceae, Rhamnaceae, and Sapindaceae. In the laboratory, *B. yersiniana* accepted a range of host plants across several families; *A. cornutus* was polyphagous on >15 species in >10 families of plants; all other three stick insects were either monophagous or oligophagous. The classic relationship of species increase with island area size in biogeography was not yet confirmed, but big islands like Tortola 18 times larger in size had all five species, while small islands like Guana had four. Low numbers of species within each genus, sharing mostly the same species with Puerto Rico (except *C. modesta*), and distant relationships among genera or species indicate that the Virgin Island phasmid fauna is a subset of that of the Greater Puerto Rico Bank, either by vicariant or over-water dispersal. The monthly number caught by Malaise traps on Guana Island during a 5-yr period suggests that egg hatch synchronized with the spring rainfall for at least three species, abundance differed between the windward and leeward sides, and habitat partitioning occurred among species. Heterogeneity of phasmid abundance between the leeward and windward sides provides indirect evidence for rainfall pattern and plant diversity even within small and low altitude islands like Guana. Additional morphology, life history, defensive behavior, oviposition, feeding preferences, distribution among different islands, and a key to species provide a firm basis for further research on phasmids from the Virgin Islands and their relationship with those from Puerto Rico.

## Introduction

The mainly nocturnal stick insects (or walkingsticks) are extremely elongate stick-like insects in the order Phasmida (=Phasmatodea), an ordinal name with a long history (Brock and Marshall, 2011). Phasmids not only look like twigs but, when disturbed, some species mimic the swaying of a twig, perhaps to confuse potential predators. The name is derived from the Greek phasm, meaning an

apparition or a phantom, and refers to the cryptic appearance and mimetic behaviour of these insects. The earliest fossil record of phasmids is from the Triassic (Nel et al., 2004). With 3,075 species worldwide documented by the Phasmida Species File Online database (Brock et al., 2015), phasmids are considered to be orthopteroids, related to cockroaches, grasshoppers, and praying mantids. Possession of dorsolateral defensive glands on the prothorax, a vomer in males (a ventral modification of abdominal segment 10 to clasp the female during copulation), and the lid-like operculum of eggs supports the monophyly of the order (Grimaldi and Engel, 2005). This order includes the longest insect in the world, measuring up to 356 mm in body length or 567 mm to include the outstretched legs (Hennemann and Conle, 2008). Stick insects are important herbivores in tropical and sub-tropical ecosystems in addition to being popular pets, but the majority have been poorly investigated in their natural environment (Blüthgen et al., 2006). We report herein the phasmid ecology and diversity of the Virgin Islands systematically in terms of abundance, species number, morphological variation, life history, behaviour, host plants, and biogeography.

Geologically the Virgin Islands (except St. Croix) are part of the Greater Puerto Rico Bank (Fig. 1), and were united with mainland Puerto Rico and the Passage Islands until about 10,000 years ago (Lazell, 2005). Politically the Virgin Islands are divided into the British Virgin Islands (BVI) and the United States Virgin Islands (USVI). Although part of USVI politically, St. Croix geologically forms a separate unit south of the Greater Puerto Rico Bank. The phasmid fauna of St. Croix and other Virgin Islands on the Greater Puerto Rico Bank was overall understudied. The classical view of island biogeography is that land area ( $A$ ) determines the number of species ( $S$ ) or the number of species increases in proportion to the size of a given land area ( $S=CA^Z$ ) where  $C$  and  $Z$  are both constants. This theory has been questioned by many (summarized in Lazell, 2005) and has never been tested with phasmids. To test the hypothesis that species number increases with island size, we set out to document the number of phasmid species on the Virgin Islands since 1992. Furthermore, synthetic work on diversity of the Virgin Island phasmids and their relationships with those of Puerto Rico was greatly needed in comparison to various papers on ecology and taxonomy of mainland Puerto Rican phasmids result-

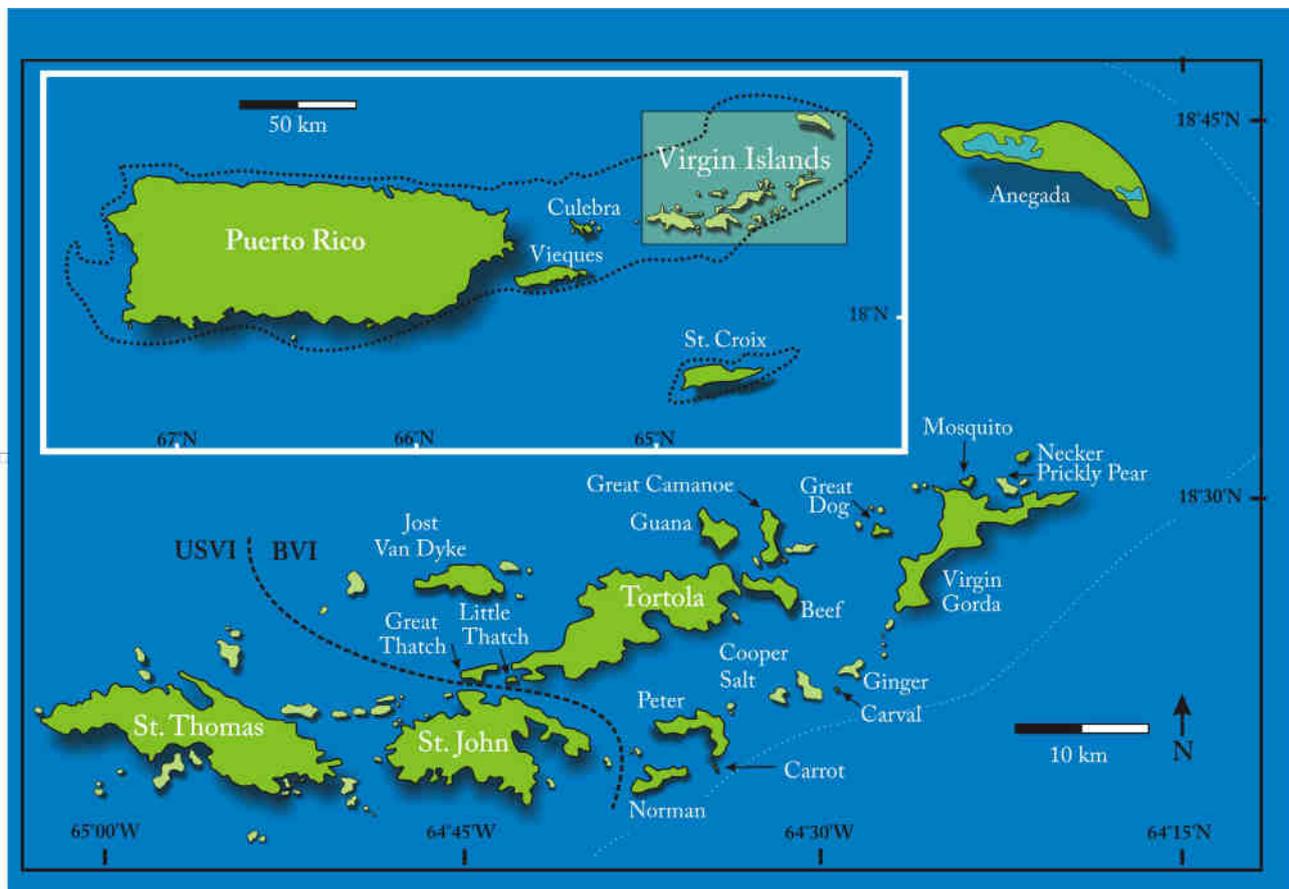


Figure 1. British (BVI) and United States (USVI) Virgin Islands with inset indicating relationships with Puerto Rico and St. Croix.

ing from long-term ecological studies (e.g., Tilgner et al., 2000), or on phasmid faunas of Dominica, Guadeloupe, Martinique, and St. Lucia resulting recently from expeditions of the Association pour la Systématique des Phasmes et l'Etude de leur Répartition (<http://www.asper.org>). We thus studied the abundance of the phasmids from the Virgin Islands over a 5-yr period from 2009 to 2014 in reference with rainfall pattern using Malaise traps.

Albeit unpublished, Moxey (1972) provides a comprehensive taxonomic source on the West Indian phasmids. The earliest stick insect recorded from the Virgin Islands was *Mantis calamus*, described by Fabricius in 1793 from St. Croix. Later, *Acanthoderus cornutus* and *Bacteria modesta* were described from St. Thomas by Burmeister in 1838 and Redtenbacher in 1908, respectively. These are the three species originally from the Virgin Islands and all were subsequently transferred to different genera as *Clonistria calamus* (Fabricius) by Kirby (1904), *Agamemnon cornutus* (Burmeister) by Otte and Brock (2005), and *Clonistria modesta* (Redtenbacher) by Zompro (2005b, without comment on change of status). Kirby (1904) first reported the fourth species from St. Thomas, *Haplopus micropterus* (St. Fargeau and Serville), a name replacement in 1828 for a species mistaken for being from Indonesia. Redtenbacher (1908) described *Haplopus obtusus* from “Santa Cruz,” but it was synonymised with *H. micropterus* by Hennemann et al. (2016). Langlois et al. (2006) summarized known distribution of species from various West Indian isles, including seven species from St. Thomas and *C. calamus* for the first time from St. Croix. However, three of these eight species listed are synonyms and another, *Ocnophila illegitima* Brunner, was described from Cuba in 1907. Their record of *O. illegitima* from St. Thomas is presumably based on Moxey (1972), who treated it as synonym of *A. cornutus*. Whilst these species are similar in appearance, further research is required to confirm the synonymy of *O. illegitima* with *A. cornutus*. *Bacteria yersiniana* was described by Saussure from Puerto Rico in 1868; it is known to have been in culture with a stock from Tortola Island since 2003; hence, the fifth species from the Virgin Islands was reported in an online annotated but unpublished record by Lelong (2008). However, the first published note of *B. yersiniana* on the Virgin Islands was by Harman (2013). In summary, there are a total of five species from the Virgin Islands on the Greater Puerto Rico Bank (*A. cornutus*, *B. yersiniana*, *C. calamus*, *C. modesta*, and *H. micropterus*) and two of them (*C. calamus* and *H. micropterus*) from St. Croix.

To add to the confusion, Beatty (1944) listed a record of *Clonistria* sp. from St. Croix, and Miskimen and Bond (1970) added two more records from St. Croix: *Dyme* sp. and *Diapherodes* sp., who listed the later undetermined species as probably *D. longiscapha* Redtenbacher, 1908, from Puerto Rico. Unfortunately, vouchers for their 1970 records have not been found, although they could still be in the United States National Museum (USMN), where the identifications were made. Their *Dyme* sp., said to be the commonest species on St. Croix, is therefore likely the phasmid described by Fabricius in 1793, and herein placed with the Beatty record under *Clonistria calamus*. Their *Diapherodes* sp. prob. *longiscapha*, said to be the largest and least common species, is therefore provisionally herein placed under the other species known from St. Croix, the large *Haplopus micropterus*. Other than all this taxonomic information, little else about these five species was known.

This paper reviews current taxonomy and adds *Dyme krugiana* Brunner as a new synonym of *Bacteria yersiniana* Saussure, also *Bacunculus bradypus* Werner, 1929, as a new synonym of *Clonistria calamus* (Fabricius). The males of *Clonistria calamus* and *C. modesta* are described for the first time. Because early species descriptions were simplistic for current understanding of a species, we also describe each species in further detail in addition to diagnostic characters. Sexual dimorphism in size and color are often the norm in stick-like phasmids; the size difference and color variation in relation to developmental stages and environments of all five species are reported for the first time. A key to species is given and eggs are figured to assist field identification. Our work contributes further to the knowledge of ecology, life history, behaviour, host plants, distribution, and biogeography of all five species.

## Methods and Materials

Guana Island is a small privately owned island in the BVI (Fig. 1), located off north of the main island Tortola, at 18°28'N by 64°35'W. Its rugged topography of 297 hectares features a well-preserved subtropical dry forest that covers much of the island from sea level to its highest elevation, Sugarloaf Peak at 246 m. One month each year (usually October, rarely July) since 1992, scientists have had the opportunity to collect phasmids on Guana Island at different localities representative of its geography in diurnal and nocturnal forays and, whenever possible, on other islands of the BVI and USVI. To study the species number, habitat, behaviour, and life history, phasmids were collected either with a sweep net from vegetation, handpicked at white or ultraviolet lights, or searched for at night with flashlights. Additionally, a Malaise trap was set up on the leeward Quail Dove Ghut of Guana Island since 1999 (Lu et al., 2014), as well as another one on the windward North Bay since 2009 when we began quantitatively checking for the total number of stick insects every month by species and trap location in five annual periods of XI.2009-X.2010, XI.2010-X.2011, XI.2011-X.2012, XI.2012-X.2013, and XI.2013-X.2014. Separated by Sugarloaf Peak, these two opposite trap sites were both in lowlands (~5 m above sea level) within a forest edge, and set for detecting within-island variation due to rainfall pattern and vegetation. To study their host preferences, we identified plants where these insects were found and used them in feeding tests each October from 2007 to 2012. No-choice feeding with only one plant took 24 hr if a high percentage of individuals ate, or otherwise 48 hr. When >30% of individuals fed on a particular plant in no-choice tests, these plants were used in choice tests for 48 hr with two different host plants supplied, with one insect per plastic bag of 18×15 cm at ambient temperature in a room (average daytime 28°C, night time 22°C). We recorded whether a phasmid ate or refused a specific plant and calculated host plant preference as a) percentage of insects feeding on a specific plant over the total number of insects used in the test for each species, and b) percentage of insects feeding on both plants, pooling data across years. Distributional range of host plants was provided based on Liogier (1985, 1988, 1994, 1995, 1997) and Acevedo-Rodriguez (1996). To examine the relationship of species number to island area, we compared species number on islands within the Greater Puerto Rico Bank and between islands on this Bank and St. Croix, using Guana Island as the research station for the phasmid study exemplary of relatively undisturbed small islands.

Species were identified by comparison with museum material, original descriptions, and taxonomic references downloaded from the Phasmida Species File Online database. Until 2004, most specialists in Phasmida relied on classification by Bradley and Galil (1977), essentially an updated version of Günther (1953). Kevan (1982) suggested some changes without much explanation. Zompro revised the subfamily Diapheromerinae (2001) and proposed several changes in higher classification for part of the order Phasmida (2004b), with priority for phylogenetic relationships controversially based on egg morphology. We follow classification and terminology summarised in Otte and Brock (2005), as updated in the Phasmida Species File Online. The metanotum of most species has a transverse ridge separating it from the first abdominal segment, which is known as the median segment; this ridge is sometimes rather indistinct. The last three abdominal segments (8-10) are often modified in both sexes and termed differently. In males, the subgenital plate is the ventral sclerite of abdominal segment 9, usually swollen and cup-shaped, and referred to as the poculum; the vomer is a moveable ventral sclerite of abdominal segment 10, used during copulation. In females, abdominal dorsal segment 10 is known as the anal segment; abdominal segment 11 is dorsally the supraanal plate, which is usually small (when present), but occasionally elongate and chute-like; the subgenital plate is the last ventral segment (8), elongate, scoop- or keel-shaped, and referred to as the operculum. Specimens were measured from head to abdominal tip, excluding the supraanal plate or operculum if extending beyond the abdominal tip. Length of antennae and forelegs are compared when they are outstretched forward. Eggs of the stick insects are remarkably like seeds, often oval or cylindrical, smooth or rough or heavily sculptured; the truncated anterior pole of the egg is also called the operculum where nymphs emerge, not to be confused with the same term used for the subgenital plate of females; opercula have often a raised structure called a capitulum. Laterally, the eggs have a longitudinal scar-like area called the micropylar plate where sperm enter through the micropyles for fertilization. Eggs were measured and described with standard terminology (Sellick, 1997).

We reported the infraorders Anareolatae and Areolatae phylogenetically but families or species within a family alphabetically. For each species, synonyms were listed chronologically with major taxonomic actions in parentheses and comments in brackets. For specimens examined, reference was made to the depository, number and sex of specimens, locality, date, collector, and collection method, respectively. Some islands do not include that word in their names (e.g., Anegada); for clarity, we have added "Is." to these in our specimen records (e.g., Anegada Is.) except for type specimens. This should avoid confusion of specific sites within islands. Collecting methods were abbreviated as 'beat' for beating vegetation, 'sweep' for sweeping vegetation with net, 'at light' for catching under electrical white light, and 'UV light' for under electrical ultraviolet light. Directions were abbreviated as a single letter, e.g., N or S; the writing "est." on labels was spelled out as estate; Mount Sage National Park on Tortola (BVI) and Gorda Peak National Park on Virgin Gorda (BVI) were consistently abbreviated as Sage Mt. and Gorda Peak, respectively. VIBFP was an acronym for the Virgin Islands Beetle Fauna Project as the collectors. Acronyms for depositories are as follows: BDVC, private collection of B. D. Valentine (to be deposited in the Florida State Collection of Arthropods, Gainesville, FL); BMNH, Natural History Museum, London, United Kingdom; GUANA, Guana Island Natural History Museum, BVI; MAIC, private collection of Michael A. Ivie, Bozeman, MT, USA; MHNG, Muséum d'histoire naturelle, Geneva, Switzerland; MLUH, Wissenschaftsbereich Zoologie, Martin Luther Universität, Halle, Germany; NHMB, Naturhistorisches Museum, Basle, Switzerland; NHMW, Naturhistorisches Museum Wien (Vienna), Austria; UDCC, Entomology Collection, University of Delaware, Newark, DE, USA; USNM, National Museum of Natural History, Washington, DC, USA; ZMHB (ZMB), Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; ZMUC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark; ZMUH, Zoologisches Museum der Universität Hamburg, Hamburg, Germany; VIIS, the Virgin Island National Park, St. John, USVI.

## Results

Both males and females of all five phasmid species in three families previously recorded from the Virgin Islands were found: 3 in Diapheromeridae (*Bacteria yersiniana*, *Clonistria calamus*, *C. modesta*), 1 in Phasmatidae (*Haplopus micropterus*), both families in the infraorder Anareolatae; 1 in Pseudophasmatidae (*Agamemnon cornutus*) in the infraorder Areolatae. On the Virgin Islands, these five species had much smaller males than females; *A. cornutus* was always brown as nymphs and adults, *B. yersiniana* and *C. calamus* were commonly green as nymphs and adults, *C. modesta* was commonly green as young nymphs but always brown as older nymphs and adults, and *H. micropterus* was commonly yellowish brown with green linings. On Guana Island, which we used as research station for >20 years, all species but *B. yersiniana* were found.

Out of >400 adult or nymphal specimens preserved or released, 5% were attracted to lights (mostly winged males), 15% were caught by sweep nets or observation during daylight, and the remaining 80% by searching at night. During the five annual periods of XI.2009-X.2010, XI.2010-X.2011, XI.2011-X.2012, XI.2012-X.2013, and XI.2013-X.2014, Malaise traps on Guana Island captured all four species and these were mostly younger nymphs of instars 1-2, suggesting that eggs hatched from the ground or rain washed either eggs or nymphs to the ground. The number of individuals caught in the Malaise traps was only 56 in total and varied among different months, increasing from April to August with the highest number in May (19.6%), suggesting that egg hatch synchronized with the spring rainfall. The number of individuals and species caught in the Malaise traps varied among different annual periods; the lowest in the second annual period when all species were absent except *Haplopus micropterus*, followed by the third period when both *Clonistria calamus* and *C. modesta* were absent, and by the fifth period when both *Agamemnon cornutus* and *H. micropterus* were absent. The number of individuals caught in the Malaise traps was also different among species; *C. modesta* had the highest (total 24 in 5 years) as compared with *C. calamus*, *H. micropterus*, or *A. cornutus* (total 8, 13, or 11 in 5 years, respectively). The number of individuals caught in the Malaise traps was further different between the leeward and windward sides; *C. calamus* only occurred in the leeward trap; *H. micropterus* only occurred in the windward trap; both *C. modesta* and *A. cornutus* occurred in both traps but the numbers were unbalanced, more *C. modesta* individuals came to the leeward trap, whereas more *A. cornutus* individuals came to the windward trap.

Within the Greater Puerto Rico Bank, the species number on the Virgin Islands <100 ha ranged 1-3, that on islands <1000 ha ranged 1-4, that on islands >2000 ha ranged 1-5 (Table 1). Small islands like Guana had one species fewer than big islands like Tortola, despite the area difference between them (>18 times). These figures reflected past collecting success, not final diversity, but may indicate that the variation in species number among islands cannot be explained by island area alone. The morphological diagnoses, host plants, behaviours, new island records, and phenologies for each species are given as follows:

## Family Diapheromeridae

### 1. *Bacteria yersiniana* Saussure, 1868 (Figs. 2-4)

*Bacteria yersiniana* Saussure, 1868: 65, Puerto Rico; 1870: 158, as *Bacteria (Pseudobacteria) yersiniana*; Zompro and Brock, 2003: 26; Otte and Brock, 2005: 67; Harman, 2013: 12, Tortola.

*Pseudobacteria yersiniana* (Saussure), Kirby, 1904: 346; Van den Bussche et al., 1988: 422, Puerto Rico.

*Heteronemia yersiniana* (Saussure), Rehn, 1904: 53.

*Dyme yersiniana* (Saussure), Brunner, 1907: 327; Langlois et al., 2006: 14, Puerto Rico.

*Dyme krugiana* Brunner, 1907: 324, Porto Rico [Puerto Rico] (new synonym).

*Bacteria krugiana* (Brunner), Langlois et al., 2006: 13, Puerto Rico.

#### *Nomenclature*

This species has been placed in four genera and was named after the collector, Yersin. After comparing the type specimen and the original description, *Dyme krugiana* is found to be a new synonym of *Bacteria yersiniana*, in terms of locality and morphology.



Figure 2. *Bacteria yersiniana* male on Tortola, BVI. T. James.

Island	Area (ha)	Elevation (m)	<i>Bacteria</i> <i>yersiniana</i>	<i>Clonistria</i> <i>calamus</i>	<i>Clonistria</i> <i>modesta</i>	<i>Haplopus</i> <i>micropterus</i>	<i>Agamemnon</i> <i>cornutus</i>	Species total
Little Thatch	23.3	90	-	-	+	+	+	3
Necker	28.5	36	-	+	-	-	+	2
Moskito	51.8	82	-	+	-	+	+	3
Frenchman's Cay	59.6	116	-	+	-	-	-	1
Norman	251.2	131	-	+	-	-	-	1
Guana	297.8	246	-	+	+	+	+	4
Great Camanoe	341.9	166	-	+	+	-	+	3
Peter	429.9	162	-	-	-	-	+	1
Jost Van Dyke	834.0	320	-	+	-	-	+	2
Virgin Gorda	2188.5	414	-	-	-	-	+	1
Anegada	3931.6	9	-	+	-	+	+	3
St. John	5180.0	387	-	+	+	+	+	4
Tortola	5571.1	530	+	+	+	+	+	5
St. Thomas	7660.0	474	+	+	+	+	+	5
St. Croix	21466.0	355	-	+	-	+	-	2
Island absence of a species			13/15	3/15	9/15	7/15	3/15	

Table 1. Relationships of phasmid species number with areas and maximum elevations of 15 islands within the Greater Puerto Rico Bank and between that Bank and St. Croix.

*Adult diagnosis*

This species is sexually dimorphic in size and color, with males mainly brown, females mainly green; both sexes are wingless, elongate, and slender with sparse white granules but no spines or horns. The mesonotum is always  $>6\times$  longer than the pronotum. The median segment is much shorter than the metanotum and about  $1/5$  as long. The antennae are longer than the fore legs.

*Male* (Fig. 2)

72-90 mm, brown with basal femora green, legs appear banded at certain light angles with light and dark brown color; posterior sides of metanotum turned red quickly in ETOH but faded after a period. Head slightly longer than pronotum, with a distinct but shallow depression between antennae, which is slightly divided in center (as two shallow depressions in nymphs), straw color with dark markings: a dark cloud between eyes followed by 5 black stripes on vertex, center and lateral ones thicker and darker than sub-lateral ones. Pronotum with 3 dark stripes: a thick black stripe in the center, a lighter stripe on each side before black lateral margins; mesonotum  $>7\times$  as long as pronotum; metanotum almost  $5\times$  as long as median segment. Last 3 abdominal segments shortened, but 8-9 expanded ventrally, broader than long apically, subequal ( $\leq$ ) in length, combined length  $\leq$  segment 5, which is the longest abdominal segment; anal segment shortest, rounded with a small emargination in center; poculum swollen, triangular with a rounded apex, reaching base of anal segment; vomer visible, slender, pointed; cerci short, stout, curved to overlap each other, with rounded tips, barely extending beyond end of abdomen.

*Female* (Fig. 3)

130 mm, head with a light brown protuberance at base of each antenna; occiput (posterior of head) with 2 smooth, shallow, distinct bumps, which make the head slightly convex; mesonotum  $>7\times$  as long as pronotum; metanotum almost  $5\times$  as long as median segment. Abdomen longer than head and thorax combined, last 3 abdominal segments short, but longer than broad, segment 8 as long as or slightly longer than segments 9-10 combined, combined length  $\leq$  segment 5, which is the longest abdominal segment; anal segment broadly rounded, emarginate in center; supraanal plate visible, rounded; operculum spatulate, barely reaching anal segment apex; cerci short, stout with rounded tips, broader at base.



Figure 3. *Bacteria yersiniana* female on Tortola, BVI. T. James.

*Nymph*

Gender was evident even in young nymphs. Younger nymphs were all green with sparse white granules on thorax; last 3 abdominal segments of males shortened, but longer than broad, segment 8 as long as or slightly shorter than segments 9-10 combined; poculum almost reaching middle of anal segment; last 3 abdominal segments of females also shortened, but operculum only reaching middle of anal segment; otherwise similar to adults. We found nine body length categories corresponding to head width: 23-27, 30-35, 40-45, 50-55, 62-65, 70-73, 90-95, 100-105, and 125 mm, suggesting at least six instars in males and nine instars in females. Both the poculum and operculum were visible and progressively lengthening during the nymphal development. Whether or not abdominal dorsal segment 9 (preceding the anal segment) greatly expanded laterally to cover the poculum and the operculum extends to the apex of the anal segment are the criteria for separating male and female nymphs from adults, respectively.

*Egg* (Fig. 4)

Capsule length 2.4 mm, height 1.8 mm, width 1.4 mm; dark brown to black; surface fairly smooth but with some sculpturing; operculum slightly sloping, with a distinctly raised and paler capitulum. Micropylar plate long and central, not reaching the operculum rim, lighter brown with a darker micropyle posteriorly. Adults did not lay eggs in October when we were usually present on the islands, but eggs were reportedly laid scattered on the ground in captivity (T. James, pers. comm. 20.I.2009).

*Host plant*

All specimens of *Bacteria yersiniana* were found along the track to Sage Mountain of Tortola. On 28.X.2009, a young female nymph was found on a dead twig, a female nymph and a male adult were on *Margaritaria nobilis* (Euphorbiaceae) or *Pseudolmedia spuria* (Moraceae), but no actual feeding activity observed. A female nymph was feeding on *Gonzalagunia hirsuta* (Rubiaceae), an older female nymph was on *Casearia decandra* (Flacourtiaceae), and a large 95-mm female nymph was on *Casearia guianensis* (Flacourtiaceae) and ate a lot during feeding tests, but did not molt after a whole week before we preserved her as a voucher specimen. These three plants are absent from Guana Island (Proctor, 2005), but are native to islands of the Greater Puerto Rico Bank. In October 2011 and 2013 all individuals of *B. yersiniana* were found on *G. hirsuta*. In 2003, a female was found low on deciduous tree suckers (presumably mistletoe in Loranthaceae) and some males coexistent with some *Agamemnon cornutus* (Species 5) males on *G. hirsuta*; in captivity, this species takes *Ligustrum* species (Oleaceae) readily and breeds consecutively (T. James, pers. comm. 20.I.2009). We were not able to collect enough specimens for quantitative feeding tests in the field to draw conclusions, but confirm that the coexistence of *B. yersiniana* and *A. cornutus* on *G. hirsuta* was observed frequently and *B. yersiniana* appeared to have a broad range of host acceptance across several plant families.



Figure 4. *Bacteria yersiniana* egg (dorsal and lateral). P. Brock.

*Variation*

This species perched high on twigs or leaves, was frequently found clinging to vegetation upside down as if hiding under leaves; half of the specimens (larger ones) collected at night in October 2009 were high up on bushes or trees 2-4 m above ground; some were so high up that we lost one individual that played dead and fell into the darkness of the jungle when we climbed the tree simply to reach it.

An older 102-mm female nymph found on 12.X.2013, on *Gonzalagunia hirsuta*, was completely brown with dense, irregular, black mottles scattered on the whole body, but forming bands on all legs. This is the first report of both the green and brown color morphs of *Bacteria yersiniana*. The appearance of the brown form as well as the number of individuals may have something to do with low rainfall in the spring of 2013, when a night hunt in the fall resulted in only this and a released younger green nymph as opposed to >10 of them on each visit of previous years.

*Phenology and habitat*

We have not been able to find *Bacteria yersiniana* from Guana Island or any other islands except Tortola and a MAIC specimen from St. Thomas before our work. In the BVI, *B. yersiniana* only occurs in the cooler, higher, and wetter part of Sage Mt., where tree ferns are still surviving in small pockets. We are not sure where the museum specimen from St. Thomas was collected, but most likely also in the wetter area of Magens Bay. Our infrequent visits to these big islands yielded no phenological data except that the species did not lay eggs but had an array of nymphs in October excluding instars 1-2 by our estimate.

*Distribution*

The type locality is Puerto Rico and the type of *Bacteria yersiniana* is in MHNG. The first association of this species with the island of Tortola (Harman, 2013) was based on material collected in 2003 by T. James (pers. comm. 20.I.2009). Otherwise, our specimens from Tortola and St. Thomas are the first substantiation of its existence in the Virgin Islands since its description from Puerto Rico in 1868.

*Type material examined*

*Dyme krugiana*: ZMHB-1 syntype male/1 syntype male nymph/1 syntype female, Porto Rico [Puerto Rico], Krug.

*Bacteria yersiniana*: MHNG-holotype male, Puerto Rico, Yersin.

*Specimens examined*

BMNH-BVI: 1 female nymph, Tortola Is., Sage Mt., 22.X.2009, S. Valentine-Cooper; 1 male nymph, Tortola Is., Sage Mt., 28.X.2009, W. Lu. USNM-BVI: 1 female nymph, Tortola Is., Sage Mt., 22.X.2009, W. Lu; 2 female nymphs, Tortola Is., Sage Mt., 28.X.2009, T. Willard; 1 male, Tortola Is., Sage Mt., 20.X.2011, S. Valentine-Cooper; 3 female nymphs/2 male nymphs/1 male, Tortola Is., Sage Mt., 26.X.2012, E. Hill/T. Willard/S. Valentine-Copper; 1 female nymph [brown], Tortola Is., Sage Mt., 12.X.2013, S. Darby. MAIC-USVI: 1 male, St. Thomas Is., Magens Bay, 8.VII.1979 [no collector]; 1 male, Tortola Is., Sage Mt., 1600 ft., 7.I.1993, M. A. Ivie & D. H. Chadwick.

**2. *Clonistria calamus* (Fabricius, 1793) (Figs. 5-7)**

*Mantis calamus* Fabricius, 1793: 13, St. Croix; Zimsen, 1964: 616.

*Phasma calamus* (Fabricius), 1798: 187; Lichtenstein, 1802: 10.

*Spectrum calamus* (Fabricius), Lamarck, 1817: 255.

*Bacteria calamus* (Fabricius), Serville, 1831: 64; Gray, 1835: 17, St. Vincent [in error, see Brock (1998: 32)]; Burmeister, 1838: 564; Westwood, 1859: 20; Redtenbacher, 1908: 423; Wolcott, 1951: 49, Puerto Rico.

*Clonistria calamus* (Fabricius), Kirby, 1904: 351; Brock, 1998: 31 (lectotype designation, redescription); Otte and Brock, 2005: 106; Langlois et al., 2006: 14, Puerto Rico, St. Croix.

*Bacunculus bradypus* Werner, 1929: 5, St. Thomas (new synonym).

*Heteronemia bradypus* (Werner), Otte and Brock, 2005: 157 (combination).

*Clonistria bradypus* (Werner), Zompro, 2005b: 256 (combination); Langlois et al., 2006: 14, St. Thomas.

*Clonistria* sp., Beatty, 1944: 117, St. Croix.

*Dyme* sp., Miskimen and Bond, 1970: 19, St. Croix.

*Nomenclature*

This species has been named synonymously in seven genera. After examining the type material of this species, Brock (1998) designated a lectotype (from St. Croix) of *Clonistria calamus* in ZMUC. Although the description of its female dates from 1793, this is the first description of the male and the first note of its color variation of both green and brown color morphs. Examination reveals that a specimen labeled as '*Manomera tenuescens*' at VIIS is clearly a *C. calamus*; *M. tenuescens* (Scudder, 1900) is a species from northern Florida (Rehn and Hebard, 1907: 283). When including *Clonistria bradypus* (Werner) in a checklist of species, Langlois et al. (2006: 14) raised doubts that it may be a synonym of *Bacteria bradypus* Redtenbacher (1908: 421). However, *B. bradypus* is a synonym of *Paraphanocles keratoskeleton* (Olivier, 1792). After comparing the type specimens and the original description, *Bacunculus bradypus* Werner is found to be a new synonym of *Clonistria calamus*.

*Adult diagnosis*

This species is sexually dimorphic in size as usual; both sexes are wingless, elongate, and slender without spines or horns. It is one of the three green species from the Virgin Islands but also has a brown form, like many phasmids. The male is the narrowest and shortest among those from the Virgin Islands. The mesonotum is always  $>6\times$  longer than the pronotum. The median segment is shorter than the metanotum (1:3 in females and 1:2 in males). The antennae are longer than the fore legs.

*Male* (first description, Fig. 5)

51-57 mm, extremely narrow, smooth or with sparse granules, green with lateral black stripes on head and pronotum, and also a dark brown dorsal stripe running from top of head to anal segment; head, pronotum, and mesonotum may be paler dorsally than body color.

Head elongate, smooth, much longer than broad,  $>1.5\times$  length of pronotum; antennae reaching anterior of abdominal segment 4 or before middle of abdomen, basal segment broad, rather flattened, longer than any other segments, nearly twice as long as segment 2, which is narrower distally.

Thorax elongate; pronotum rectangular, about 1.5 as long as wide; mesonotum  $7\times$  length of pronotum; metanotum shorter than mesonotum, but twice as long as median segment.

Abdomen elongate, as long as mesonotum and metanotum combined, last 3 segments greatly shortened, quadrate, subequal, slightly increasing in width, combined length shorter than any other segment alone; posterior of each segment with small blackish central and lateral blotches dorsally; anal segment tapering, truncate, but slightly incised in centre at tip; poculum spatulate, relatively flat, about reaching anterior of anal segment; vomer visible, elongate triangular, pointed at apex; cerci short, thick at base, curved inwards to a rounded tip.

*Female* (Fig. 6)

Green form: 73-85 mm, green with a faint lateral black stripe on head and pronotum; mesonotum  $3\times$  broader than male,  $8\times$  length of pronotum; last 3 abdominal segments short, but longer than broad, with segment 8 shortest, combined length longer than any other abdominal segment; anal segment truncate at tip but with a lateral lobe on each side; supraanal plate visible, triangular; operculum long, tapering to a pointed tip, reaching anal segment apex; ventral surface of abdominal segment 7 with a reddish apical triangular patch when alive, which can be a sexual difference; cerci pale yellowish brown, long, straight but pointing outward,  $2/3$  as long as anal segment, broader at base, tapering to a rounded tip; otherwise similar to males.

Brown form: 84 mm, mottled with black patches. The dark stripes on head and pronotum are more distinct than in the green form; the anal segment is slightly emarginate in center between the lateral lobes; otherwise similar to the green form.

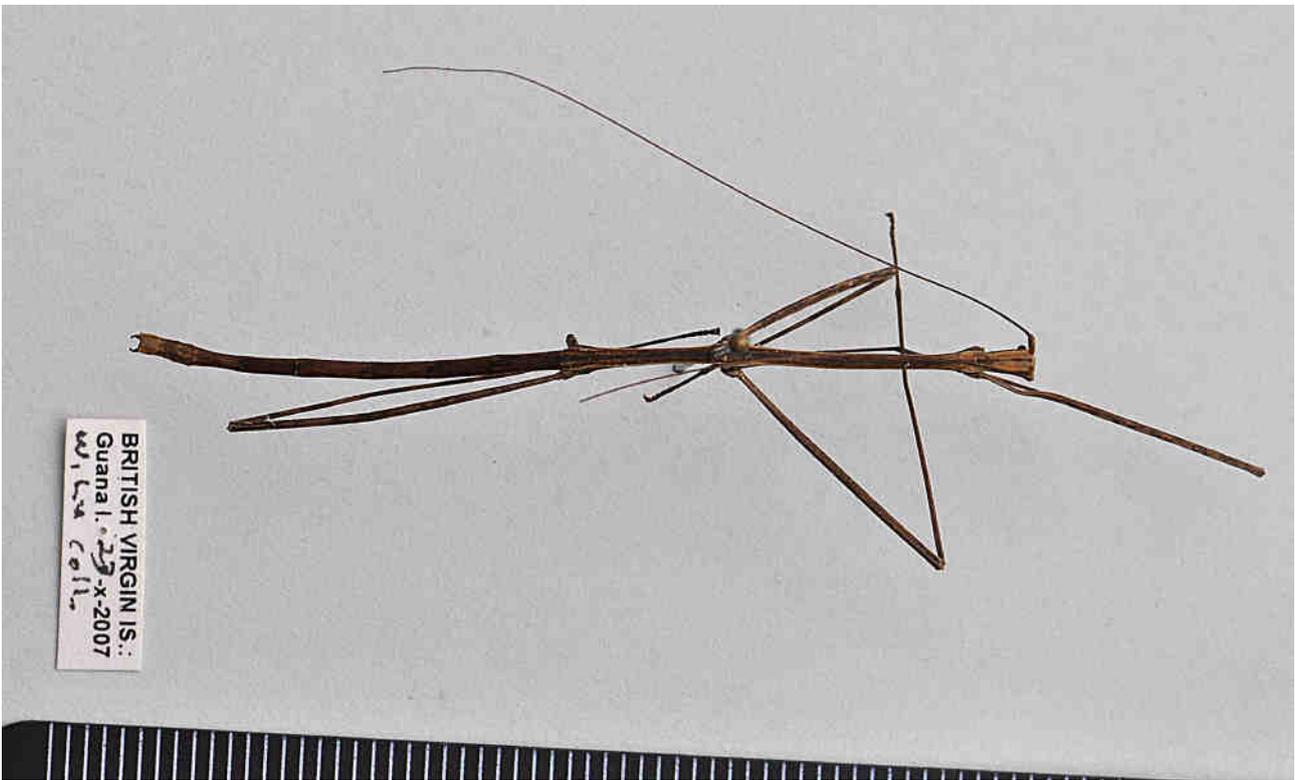


Figure 5A. *Clonistria calamus* male (dorsal). P. Brock.

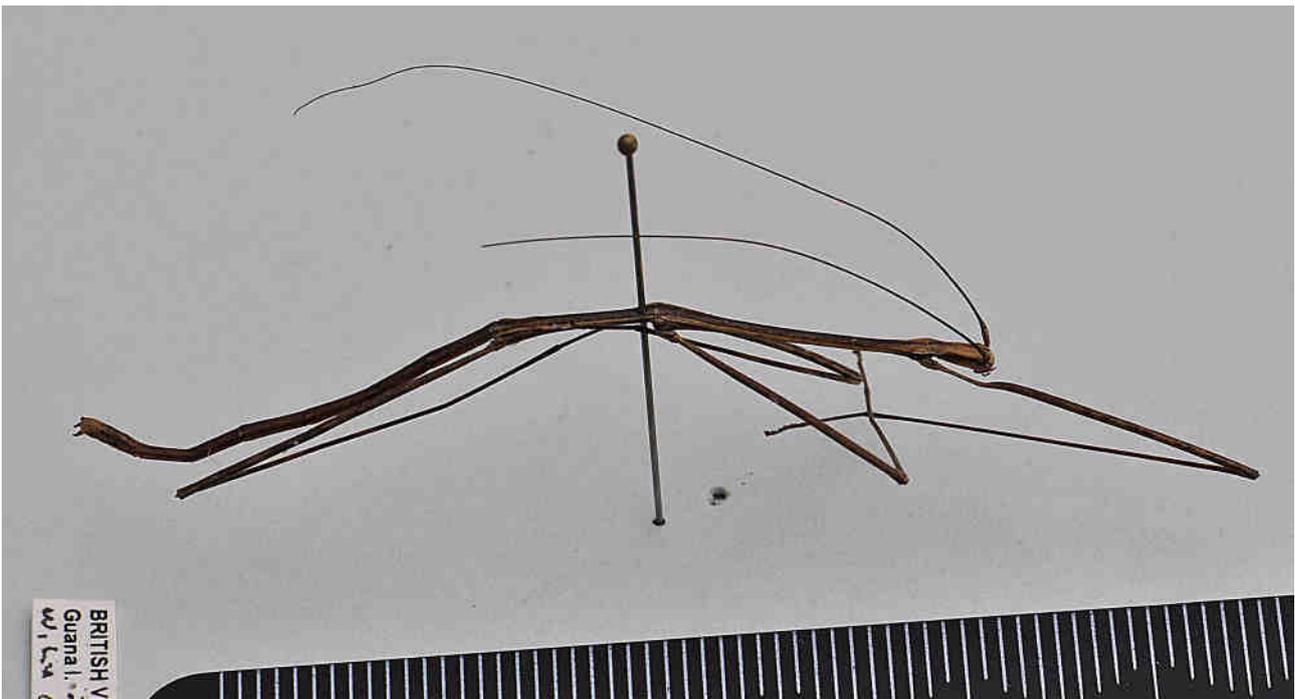


Figure 5B. *Clonistria calamus* male (lateral). P. Brock.

### Nymph

Gender is evident even in young nymphs. A brown form male nymph measured 28 mm, with similar color pattern to the brown female on head and pronotum, but much less black mottling. It lacks the ventral reddish patch of female adults. There are two black spots on metanotum just before the median segment. We found seven body length categories corresponding to head width: 9-10, 24-25, 28-35, 40-50, 55-60, 65-70, and 70-80 mm; between the length categories of 9-10 versus 24-25, there should be another stadium, suggesting at least five male and eight female instars. Regardless of color morph, whether or not the combined length of the last 3 segments is never longer than any other abdominal segment and whether there is a reddish patch before the operculum for live specimens or whether the operculum reaches the base of the cerci for dead specimens are the criteria for separating male and female nymphs from adults, respectively.



Figure 5C. *Clonistria calamus* male (dorsal, end of abdomen). P. Brock.



Figure 5D. *Clonistria calamus* male (ventral, end of abdomen). P. Brock.

#### Egg (Fig. 7)

Capsule length 2.0 mm, height 1.5 mm, width 1.2 mm; dark brown to black; surface smooth and glossy; operculum gently sloping, black with a distinct pale edge ring and a slightly raised, pale brown capitulum. Micropylar plate elongate but not central, reaching the operculum rim, whitish with a pale brown center and a darker micropyle posteriorly. Females of different colors may lay eggs slightly different in color. A green and a brown female laid 5 and 6 eggs, respectively, in a 72-hr period (26-29.X.2009) and again 8 and 9 eggs in a 48-hr period (18-20.X.2010). Eggs were attached to substrates by the micropyle during feeding tests; many were easily dislodged from vegetation when we took out host plant branches from containers and may not be necessarily attached to substrates in the wild. The length ratio of egg to first instar is about 1:5.

#### Host plant

On Anegada, we found *Clonistria calamus* on a whirly spiky *Lantana camara* bush (Verbenaceae), a spiny *Pithecellobium unguis-cati* thicket with bifid leaves (Fabaceae), and an unidentified bush with succulent, oval, toothed leaves. On Necker Island, in addition to *P. unguis-cati*, we also found individuals on *Piscidia carthagenensis* and *Pictetia aculeata* (both Fabaceae). On Guana Island, during preliminary 48-hr feeding with choice between plants where they were found in nature and other plants nearby or related, individuals ate *Lantana camara*, *L. involucrata*, *Pictetia aculeata*, *Pithecellobium unguis-cati*, and *Chromolaena corymbosa* (Asteraceae), but took only small bites of *Colubrina arborescens* (Rhamnaceae) and, surprisingly, did not eat *Piscidia carthagenensis* at all. Refusal of leguminous *P. carthagenensis* made us wonder whether plant preference was different between nymphs and adults or between various parts of the shrub. We were not able to collect enough specimens for quantitative feeding tests in the field to draw conclusions, but *C. calamus* appeared to have a narrow range of host acceptance and strong preference for the legume plants *Pithecellobium unguis-cati* and *Pictetia aculeata*. These two plants are present on Guana (Proctor, 2005, as of Leguminosae) and native to islands of the Greater Puerto Rico Bank.

#### Variation

In addition to the color correspondence between adults and eggs, we found that the frequency of brown color morph was lower than the green form and varied among islands; this may be related to either geographic or environmental effects because color is usually adapted to match surroundings. Both color forms from the same island at the same time were found; a brown female adult and male



Figure 6A. *Clonistria calamus* female (green form, dorsal). P. Brock.



Figure 6B. *Clonistria calamus* female (green form, lateral). P. Brock.

nymph were discovered at night from the island of Anegada on 25.X.2009, along with a green female adult that same night; a green female was mating with a brown male under a leaflet of *Piscidia carthag-enensis* at night on Necker Island on 16.X.2010, a plant that it does not eat in laboratory feeding trials. Both Anegada and Necker are low elevation and remote in the Virgin Islands group, rather flat and arid; no other brown forms have been found from lush areas of other islands that we frequent such as Guana or Moskito. This species in either color form has not been found on the wet and high part of Sage Mt. on the big island of Tortola. Interestingly we have not yet found green males from either Anegada or Necker, suggesting further adaptation to dryer environment. All this indicates that color form appeared to be an ecological adaptation and *C. calamus* may be better adapted to lower elevation, warmer climate, and a dryer environment.



Figure 7. *Clonistria calamus* egg (lateral and dorsal). P. Brock.

Behaviorally, *Clonistria calamus* and *Bacteria yersiniana* (Species 1) are alike in clinging to vegetation upside down as if hiding under leaves. Some green adults of *C. calamus* were found 3 m high above ground, but most brown adults were found close to ground on vegetation on Anegada on 25.X.2009. On 16.X.2010, up to four males and one female were found aggregating on a single branch of *Pictetia aculeata*, high up in bright moonlight on Necker Island.

#### *Phenology and habitat*

The number of individuals of *Clonistria calamus* caught by Malaise traps on Guana Island was very low. During the five annual periods of XI.2009-X.2010, XI.2010-X.2011, XI.2011-X.2012, XI.2012-X.2013, and XI.2013-X.2014, no individuals were ever caught in the second and third periods. All eight individuals were instars 1-2 concentrating only in the spring rainfall season, 50% in May and two each in June and July. All of them appeared from the leeward trap; none came to the windward trap in the 5-yr period. We also observed nymphs of instar 1 in each of the months of VI.2002, VII.2002, and VIII.2007 in the same leeward trap and oviposition during feeding tests in each October. On 16.X.2010 after a wet September and a stormy early October, we swept numerous young nymphs from the brush during the day and found >15 adults or all ages of older nymphs at night on Necker Island; all young nymphs were green but the older ones came in both green and brown. We never found such abundance on the lush Guana Island. These combined data are consistent with the color variation abovementioned and indicate that *C. calamus* may have two generations a year, frequently utilize habitats on the dryer leeward side of Guana Island, or is more abundant on dryer islands like Anegada and Necker, and its egg hatch may synchronize with not only the spring but also the fall rainfall peaks.

#### *Distribution*

Although Gray (1835) listed "*Bacteria calamus*" from St. Vincent, Brock (1998) believed this was a misidentification and later was able to check the specimen collected by Gray in BMNH to confirm this. Therefore we herein exclude the presence of *Clonistria calamus* on St. Vincent from its geographic range for the first time. Langlois et al. (2006) also did not list this species from St. Vincent. It is herein reported for the first time on the islands of Anegada, Frenchman's Cay, Great Camanoe, Guana, Jost Van Dyke, Moskito, Necker, and Norman, all BVI, and St. John, USVI, in addition to the previous records of St. Croix and St. Thomas, USVI, and Puerto Rico. Although it has not been recorded on the big island of Tortola, its presence on big islands like St. John and St. Thomas and on the small island of Frenchman's Cay (off the southwest point of Tortola) call for increased search effort in the future.

*Type material examined*

*Mantis calamus*: ZMUC–lectotype female/1 paralectotype female, West Indies, St. Croix.

*Bacunculus bradypus*: ZMHB–holotype female nymph, Loango, St. Thomas.

*Specimens examined*

BMNH–BVI: 1 female [brown], Anegada Is., 25.X.2009, W. Lu, at night; 1 male, Guana Is., 23.X.2007, W. Lu, UV light; 1 female, Norman Is., 19.X.2004, S. Valentine-Cooper, beat. USNM–BVI: 1 female/1 nymph [brown instar 2], Anegada Is., 25.X.2009, T. Willard; 2 nymphs [instar 1], Guana Is., V.2010, W.-P. Liao, QDG Malaise trap; 2 males/1 female nymph, Moskito Is., 23.X.2012, W. Lu; 4 males/2 brown females/1 green female/3 nymphs [instars 2, 4, 6], Necker Is., 16.X.2010, W. Lu; 1 brown female, Necker Is., 16.X.2014, W. Lu, sweep; 1 brown female nymph [instar 7], Necker Is., 16.X.2014, E. Hill. BDVC–BVI: 2 nymphs [instar 1], Guana Is., 9.VI-9.VII.2000, 23.VIII.2007, W.-P. Liao, QDG Malaise trap; 1 female, Jost Van Dyke [as Pyke] Is., 19.X.2008, W. Lu; 1 female nymph, Moskito Is., VI-VIII.2007, C. Petrovic; 1 male, Norman Is., 19.X.2004, S. Valentine-Cooper, beat. GUANA–BVI: 1 male, Guana Is. (no other data); 1 female, Moskito Is., 25.X.2007, W. Lu. VIIS–USVI: VIIS8991 [female], St. John Is., 8.VI.1968, A. E. Dammann [as *Manomera tenuescens*]. MAIC–BVI: 1 female, Frenchman's Cay, 6.X.1994, M. A. & L. L. Ivie, beat; 1 male/1 female, Great Camanoe Is., Low Bay 0-550 ft, 17.X.1994, M. A. & L. L. Ivie.

**3. *Clonistria modesta* (Redtenbacher, 1908) (Figs. 8-10)**

*Bacteria modesta* Redtenbacher, 1908: 418, St. Thomas [not *Bacteria modesta* (Brunner, 1907) = *Dyme modesta* Brunner, 1907: 324; see Bradley and Galil (1977: 180)].

*Bacteria paramodesta* Otte and Brock, 2005: 65 (replacement name for the preoccupied *Bacteria modesta* Redtenbacher, 1908).

*Clonistria modesta* (Redtenbacher), Zompro, 2005b: 272 (combination without comment); Langlois et al., 2006: 14, St. Thomas.

*Nomenclature*

Although this species has been placed in two different genera, it has never been named synonymously. Bradley and Galil (1977) listed the genus *Dyme* Stål, 1875, as a synonym of the genus *Pseudobacteria* Sausure, 1872, but Brock (1998) later determined *Pseudobacteria* to be a synonym of the genus *Bacteria* Latreille, 1825. The generic description of *Bacteria* also confusingly appears in Latreille and Berthold (1827) and St. Fargeau and Serville (1828). Regardless of this publication year, as a result, the transfer of *Dyme modesta* Brunner, 1907, to *Bacteria* as *B. modesta* (Brunner, 1907) by Bradley and Galil (1977) rendered *Bacteria modesta* Redtenbacher, 1908, homonymic. Otte and Brock (2005) recognized this confusion and used *Bacteria paramodesta* as the replacement name for *Bacteria modesta* Redtenbacher, which was preoccupied by the above mentioned *Dyme modesta* Brunner and later transferred to *Bacteria*. Because the original names for the two different species were *Dyme modesta* Brunner, 1907, and *Bacteria modesta* Redtenbacher, 1908, these are not primary homonyms, but are secondary homonyms when the names were placed in the same genus *Bacteria*. In his listing of phasmid type material in German museums, Zompro (2005b) gave the valid name for Redtenbacher's species as *Clonistria modesta* (Redtenbacher, 1908) but did not cite it as a new combination. Nevertheless, the transfer of this species from *Bacteria* to *Clonistria* Stål, 1875, is justified based on our specimen comparisons and this homonymy is removed. Therefore, the combination of *Clonistria modesta* (Redtenbacher) is correct and the replacement name *Bacteria paramodesta* is no longer valid. The female was described in 1908, but this is the first description of the male, the first report of the discovery of a winged male in the genus *Clonistria*, and the first note of its color variation of both green and brown nymphs.

*Adult diagnosis*

This species is sexually dimorphic not only in size but also in wing form. Males are short-winged, females are wingless but with a distinct protuberance on abdominal segment 4; both are elongate, dark brown, mottled with paler or gray dots, without spines or horns. The mesonotum is always >6× length of the pronotum. The median segment is longer than the metanotum (3:2). The antennae are longer than the forelegs in both sexes.



Figure 8. *Clonistria modesta* male on Guana Island, BVI. S. Valentine-Cooper.

*Male* (first description, Fig. 8)

50-65 mm, more gray than brown in appearance due to hindwings that cover 1/2 of the abdomen. Forewings short, near oval but with tip truncate; hindwings longer, reaching apex of abdominal segment 4 or just beyond.

Head longer than broad, longer than but  $<1.5\times$  length of pronotum, brown with black circular blotches dorsally, dotted with paler tubercles, several black dots almost forming a band between eyes and a short black central stripe posteriorly (these black markings and extent of tubercles can vary slightly and become pale in dry specimens); occiput (posterior of head) with 2 smooth, shallow, distinct bumps, making it slightly convex; antennae long, exceeding apex of hindwings or reaching beyond middle of abdomen; basal segment broad, rather flattened,  $1.5\times$  length of segment 2, which is broad but nearly 1/2 shorter than segment 3.

Thorax elongate, weakly mottled with paler, convex granules, more numerous on mesonotum; pronotum slightly shorter than head, with several black, short stripes both anteriorly and posteriorly; mesonotum  $7\times$  length of pronotum; metanotum much shorter than mesonotum or median segment.

Abdomen elongate, twice as long as thorax (to base of hind leg); last 3 segments considerably shorter than previous segments, combined length equal to segment 5, which is the longest; each segment with several black, short, central stripes posteriorly; anal segment tapering, broadly rounded apically, rather hairy; poculum spatulate, not strongly arched; vomer visible, elongate triangular, pointed at apex; cerci short, fairly stout, narrower on apical 1/3, rounded at tip; legs moderately long, banded, mottled indistinctly.

*Female* (Fig. 9)

64-80 mm, with numerous smaller tubercles and granules and fine median keel; unlike males, black dots and blotches on head and pronotum at times inconspicuous or absent; mesonotum nearly  $5\times$  length of pronotum, not  $>6\times$  as in male,  $3\times$  broader than male width; metanotum short,  $<1/2$  length of median segment; abdomen with a distinct protuberance on segment 4, which is the broadest, last 3 segments narrowed, short, as long as or slightly shorter than preceding 2 segments combined; anal segment truncate at tip; supraanal plate short, barely visible; operculum vaulted, tapering to a rounded tip, extending beyond anal segment, which is unusual in the genus (normally only reaching apex of the anal segment); cerci much shorter and stouter than those of males, without narrowed apical portions.



Figure 9. *Clonistria modesta* female on Guana Island, BVI. D. Dennis.

### *Nymph*

Gender is evident even in young nymphs. Nymphs mottled with many small, weakly swollen, white spots that become convex. The black stripes on pronotum of adults are also present on metanotum of older nymphs posteriorly, extending to the median segment. We found seven body length categories corresponding to head width: 10-14, 18-20, 24-29, 34-39, 42-50, 55-60, and 65-70 mm, indicating five male and seven female instars, two nymphal stadia fewer in males than females. The first 3 instars are green regardless of gender and have similar head width in both sexes; however, older male nymphs begin to change to dull brown during the late stadium of instar 4 and retain slender body; older female nymphs remain green until instar 5 and begin to show visible difference in width from male nymphs, becoming longer and more robust in width of head and body. Wing pads of males begin to develop or become visible in instars 4 and 5, when hindwings reach anterior of the median segment or cover the latter completely, respectively. In October 2009, a 45-mm female nymph had slightly greater head width than a 50-mm male nymph whose wing buds had not completely covered the median segment; both were instar 5 and grayish brown. Whether or not the hindwings reach the apex of abdominal segment 4 and the operculum extends beyond the anal segment are the criteria for separating male and female nymphs from adults, respectively.

### *Egg* (Fig. 10)

Capsule length 2.1 mm, height 1.6 mm, width 1.3 mm; grayish brown; surface smooth but with distinct dark irregular sculpturing; operculum with a distinct edge ring and a large, raised, dark capitulum. Micropylar plate short and central, with a darker micropyle posteriorly and a clear median line beneath. Eggs were attached to substrates by the micropyle during feeding tests; many were easily dislodged from vegetation when we took out host plant branches from containers and may not be necessarily attached to substrates in the wild. During feeding tests, many females laid eggs and the maximum number per female was nine eggs within a period of 48 hours; another laid 17 eggs in 4 nights (23-27.X.2009). The length ratio of egg to first instar is from 1:4 to 1:5.

### *Host plant*

*Eugenia cordata* (Myrtaceae), a tall bush with opposite oval leaves, present on Guana Island (Proctor, 2005) and native to islands of the Greater Puerto Rico Bank, was the only natural host plant of *Clonistria modesta* on the Virgin Islands. Among >100 specimens, >90% were caught on this plant. It was found only once on *Cassine xylocarpa* (Celastraceae), *Jacquemontia pentanthos* (Convolvulaceae), *Pictetia aculeata* and *Rhynchosia reticulata* (both Fabaceae), *Croton astroites* (Euphorbiaceae), *Rondeletia*

*pilosa* (Rubiaceae), *Serjania polyphylla* (Sapindaceae), and *Solanum polygamum* (Solanaceae); all were plants near *E. cordata* at the time. When given a choice between *E. cordata* with seven of these eight other plants (Table 2), individuals feeding on both plants were no higher than 15%. In captivity, this species accepted guava *Psidium guajava* (Myrtaceae) as a food plant when given a wide range of plants



Figure 10. *Clonistria modesta* egg (dorsal and lateral). P. Brock.

cates that *C. modesta* had a very narrow range of host acceptance and strong preference for *E. cordata*.

#### Variation

Behaviorally, *Clonistria modesta* adults often rest dorsal side up on top of vegetation as compared with *C. calamus* (Species 2) and *Bacteria yersiniana* (Species 1) that cling frequently to vegetation upside down. In early October 2007 when the host plant was unknown, five night searches resulted in only 1 adult male. During 5-24.X.2008, once we discovered the host plant, 12 night hunts resulted in 56 male and 29 female individuals, indicating that there is a high male to female ratio (about 2:1) at that time of the year. However, during 2-27.X.2009 when the fall rainy season was delayed until the last week, 14 night hunts resulted in only 2 males and 4 females (1 adult per gender); during X.2013 when the spring rainfall had been low, frequent visits (17 nights) to a host plant site yielded only two nymphs and one male; both observations suggest activity of *C. modesta* may be correlated with rainfall. This is supported by lower tolerance of *C. modesta* to arid environments; extensive searches for this species on the remote and low islands of Anegada and Necker proved negative; we have not found the host plant *Eugenia cordata* on these two islands, which may be evidence for the strict host specificity of *C. modesta*.

#### Phenology and habitat

The number of individuals of *Clonistria modesta* caught by Malaise traps on Guana Island was relatively high. During the five annual periods of XI.2009-X.2010, XI.2010-X.2011, XI.2011-X.2012, XI.2012-X.2013, and XI.2013-X.2014, no individuals were ever caught in the second and third periods and over 70% occurred in the fifth period. All 24 individuals were instars 1-2 appearing in most months except VI-VII and IX-X, nearly 35% in August and over 15% each in January and April. Individuals were caught from both traps in the 5-yr period, but nearly 85% appeared in the leeward trap and only four came to the windward trap. We also observed all ages from young nymphs to adults in nature and oviposition during feeding tests in each October. These combined data indicate that *C. modesta* may have two generations a year, is more abundant and frequently utilize habitats on the dryer leeward side of Guana Island, and its egg hatch may peak in the dry months after the spring rainfall and secondarily after the fall rainfall.

#### Distribution

The type locality of this species is St. Thomas and the type is in ZMHB. It is herein reported for the first time on the islands of Great Camanoe (found on host plant *Eugenia cordata* on 20.X.2008 and molted to adult next day, but specimen was lost), Guana, Little Thatch, and Tortola, all BVI, and St. John, USVI, in addition to the previous record of St. Thomas, USVI. Because the host plant *E. cordata*

is also present on Puerto Rico, it will be a matter of going through species names recorded from Puerto Rico to confirm *Clonistria modesta* on that big island.

*Type material examined*

*Bacteria modesta*: ZMHB–holotype female, St. Thomas, Moritz.

*Specimens examined*

BMNH–BVI: 3 males/2 females, Guana Is., 19.X.2008, W. Lu; 1 male, Little Thatch Is., 18.X.2004, S. Valentine-Cooper; 1 female, Little Thatch Is., 13.X.2007, W. Lu. USNM–BVI: 1 male/1 female, Guana Is., 9.X.2008, W. Lu; 6 nymphs (instars 2-5), Guana Is., 7-11.X.2008, W. Lu; 1 female/1 female nymph (instar 4), Guana Is., X.2010, W. Lu; 1 nymph (instar 1), Guana Is., QDG Malaise trap, IV.2010, W.-P. Liao. BDVC–BVI: 1 male, Guana Is., 25.X.2003, B. D. Valentine & S. Valentine-Cooper; 1 nymph, Guana Is., 22.X.2007, W. Lu; 2 males, Guana Is., 8/14.X.2008, W. Lu; 1 female, Tortola Is., Sage Mt., 18.X.2008, W. Lu. UDCC–BVI: 1 male, Guana Is., Palm Ghut, 6.X.1994, C. R. Bartlett; 1 male [badly damaged], Tortola Is., 28.X.1997, C. R. Bartlett. VIIS–USVI: VIIS9278 [female], St. John Is., Reef Bay, XII.1970, R. William. MAIC–BVI: 1 male, Guana Is., Grenada House to Sugar Loaf, 400-806 ft., 24.X.1992, M. A. Ivie, beat; 1 male nymph, Tortola Is., Sage Mt., 1600 ft., 30.X.1992, M. A. Ivie.

## Family Phasmatidae

### 4. *Haplopus micropterus* (St. Fargeau and Serville, 1828) (Figs. 11-13)

*Phasma angulata* Stoll, 1813: 61, plate 21-77, Amboina [Indonesia, but presumably in error; non *Mantis angulata* Fabricius, 1793].

*Cyphocrana microptera* St. Fargeau and Serville, 1828: 445 (replacement name for the preoccupied *Phasma angulata* Stoll, 1813); Serville, 1831: 61.

*Aplopus micropterus* (St. Fargeau and Serville), Gray, 1835: 34; Wolcott, 1951: 50, Puerto Rico; Langlois et al., 2006: 14, St. Thomas [as *Aplopus micropterus* (Gray, 1835)].

*Haplopus spinipes* Gray, 1835: 34 [no data]; Hennemann et al., 2016:122 (synonymy).

*Phasma (Haplopus) micropterus* (St. Fargeau and Serville), Haan, 1842: 128.

*Haplopus cytherea* Westwood, 1859: 86, Dominican Republic [Hispaniola]; Hennemann et al., 2016: 121 (synonymy).

*Haplopus ligia* Westwood, 1859: 89, Dominican Republic [Hispaniola]; Hennemann et al., 2016: 122 (synonymy).

*Haplopus micropterus* (St. Fargeau and Serville), Westwood, 1859: 87 (female redescription); Kirby, 1904: 363, St. Thomas; Redtenbacher, 1908: 431; Otte and Brock, 2005: 152; Hennemann et al., 2016: 121 (synonymy).

*Haplopus ligiolus* Redtenbacher, 1908: 432, Mona Island [Puerto Rico]; Moxey, 1972: 107; Hennemann et al., 2016: 121.

*Haplopus obtusus* Redtenbacher, 1908: 429, Santa Kruz [St. Croix]; Moxey, 1972: 107; Hennemann et al., 2016: 121 (synonymy).

*Aplopus ligiolus* (Redtenbacher), Langlois et al., 2006: 13, Mona Island [Puerto Rico] (combination).

*Diapherodes* sp. prob[ably] *longiscapha*, Miskimen and Bond, 1970: 19, St. Croix.

### *Nomenclature*

This species has been placed in four different genera and named synonymously three times, not counting the tentative identification by Miskimen and Bond (1970). *Phasma angulata* Stoll, 1813, is a homonym of *Mantis angulata* Fabricius, 1793, because Fabricius (1798) transferred the latter species from *Mantis* to *Phasma*. *Cyphocrana microptera* was the replacement name by St. Fargeau and Serville (1828) for the preoccupied *Phasma angulata* Stoll. We could not examine Stoll's female type specimen(s) of *Phasma angulata* because it is lost. The published year for *Haplopus micropterus* (St. Fargeau and Serville) is somewhat confusing. It turns out that St. Fargeau and Serville wrote some sections in "Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire Naturelle des Crustacés, des Arachnides et des Insectes." This Encyclopédie Méthodique is part of volume 10 of a much larger series of Encyclopédie Méthodique, ou par ordre de matières, par un société de gens de

Species	Plant family	Plant I	Plant II	Feeding on I/II	% feeding on both	N
1	Rhamnaceae/Boraginaceae	<i>Colubrina arborescens</i>	<i>Cordia polycephala</i>	2/2	66.7	3
1	Rhamnaceae/Celastraceae	<i>Colubrina arborescens</i>	<i>Cassine xylocarpa</i>	12/0	0.00	15
1	Rhamnaceae/Euphorbiaceae	<i>Colubrina arborescens</i>	<i>Croton astroites</i>	13/10	71.4	14
1	Rhamnaceae/Euphorbiaceae	<i>Colubrina arborescens</i>	<i>Croton flavens</i>	16/8	47.1	17
1	Rhamnaceae/Fabaceae	<i>Colubrina arborescens</i>	<i>Rhynchosia reticulata</i>	16/14	63.2	19
1	Rhamnaceae/Fabaceae	<i>Colubrina arborescens</i>	<i>Pictetia aculeata</i>	13/11	56.3	16
1	Rhamnaceae/Malpighiaceae	<i>Colubrina arborescens</i>	<i>Stigmaphyllon emarginata</i>	17/7	33.3	18
1	Rhamnaceae/Moraceae	<i>Colubrina arborescens</i>	<i>Ficus microcarpa</i>	9/5	14.3	14
1	Rhamnaceae/Myrtaceae	<i>Colubrina arborescens</i>	<i>Eugenia procera</i>	11/5	45.5	11
1	Rhamnaceae/Nyctaginaceae	<i>Colubrina arborescens</i>	<i>Guapira fragrans</i>	11/8	53.9	13
1	Rhamnaceae/Polygonaceae	<i>Colubrina arborescens</i>	<i>Antigonon leptopus</i>	8/9	33.3	15
1	Rhamnaceae/Rubiaceae	<i>Colubrina arborescens</i>	<i>Randia aculeata</i>	15/3	11.8	17
1	Rhamnaceae/Rubiaceae	<i>Colubrina arborescens</i>	<i>Rondeletia pilosa</i>	16/5	31.3	16
1	Rhamnaceae/Sapindaceae	<i>Colubrina arborescens</i>	<i>Serjania polyphylla</i>	13/5	25.0	16
1	Rhamnaceae/Verbenaceae	<i>Colubrina arborescens</i>	<i>Citharexylum fruticosum</i>	12/0	0.00	17
1	Myrtaceae/Convolvulaceae	<i>Eugenia cordata</i>	<i>Jacquemontia pentanithos</i>	6/2	0.00	15
1	Myrtaceae/Euphorbiaceae	<i>Eugenia cordata</i>	<i>Croton astroites</i>	1/3	0.00	5
1	Myrtaceae/Euphorbiaceae	<i>Eugenia cordata</i>	<i>Croton flavens</i>	0/3	0.00	7
2	Myrtaceae/Celastraceae	<i>Eugenia cordata</i>	<i>Cassine xylocarpa</i>	14/0	0.00	16
2	Myrtaceae/Convolvulaceae	<i>Eugenia cordata</i>	<i>Jacquemontia pentanithos</i>	13/2	10.0	20
2	Myrtaceae/Euphorbiaceae	<i>Eugenia cordata</i>	<i>Croton astroites</i>	7/1	0.00	13
2	Myrtaceae/Fabaceae	<i>Eugenia cordata</i>	<i>Rhynchosia reticulata</i>	19/0	0.00	21
2	Myrtaceae/Fabaceae	<i>Eugenia cordata</i>	<i>Pictetia aculeata</i>	16/2	12.5	16
2	Myrtaceae/Rhamnaceae	<i>Eugenia cordata</i>	<i>Colubrina arborescens</i>	26/5	12.8	39
2	Myrtaceae/Rubiaceae	<i>Eugenia cordata</i>	<i>Rondeletia pilosa</i>	16/0	0.00	18
2	Myrtaceae/Solanaceae	<i>Eugenia cordata</i>	<i>Solanum polygamum</i>	10/0	0.00	10

Table 2. Choice feeding when given two plants simultaneously at ambient temperature and light by *Agamemnon cornutus* (Species 1) and *Clonistria modesta* (Species 2) on various plants where they were captured on British Virgin Islands during Octobers of 2007, 2008, and 2009, with data pooled across years (N = total number of individuals).

lettres, de savans et d'artistes, Zoology, in multiple volumes. Volume 10 has two parts and four editors involved. Part 1 is published in 1825 as the title page of volume 10 indicates, but part 2 is published in 1828 as stated by Sherborn and Woodward (1899). Therefore, the published year for the replacement name as *Haplopus micropterus* should be 1828, not 1825 as recorded inaccurately in several previous publications.

Moxey (1972) indicated that *Haplopus obtusus* and *H. ligiolus* were synonyms, first published though by Hennemann et al. (2016); Zompro (2005a) clarified that *Haplopus* Burmeister (1838) is the valid generic name for the homonymic *Aplopus* Gray (1835). Miskimen and Bond (1970) reported that the largest and least common species on St. Croix was probably *Diapherodes longiscapha* Redtenbacher, 1908, a different species from Puerto Rico (Wolcott, 1951); we therefore place it under the large species already known from the island, *Haplopus micropterus*. Examination also reveals that a specimen at VIIS is clearly a *H. micropterus* but labeled as *Aplopus mayeri*, which is a different species from Florida (Werner, 1929; Otte and Brock, 2005) now known as *Haplopus mayeri* (Caudell, 1905).

#### *Adult diagnosis*

This species is not only sexually dimorphic in size as usual, but also in color and wing form. Males are yellowish brown dorsally and greenish at least ventrally but females are duller, pale brown all over. Both sexes have short forewings, but males have much longer hindwings than females, likely facilitating dispersal in search of females. The mesonotum is always  $>3\times$  longer than the pronotum. The median segment is slightly shorter than the metanotum. The antennae are longer than the fore legs. The head has a pair of stout, swollen spines behind eyes on vertex.



*Male* (Fig. 11)

85-90 mm, robust, yellowish with green lining underside and green edges along legs; head convex, broader than long, but as long as pronotum or slightly longer; antennae almost reaching middle of abdomen. Thorax with a pair of small tubercles (at times spinose) on anterior pronotum; mesonotum  $5\times$  as long as pronotum, with 4-8 unevenly paired, black-tipped conical tubercles; forewings as long as head and pronotum combined, not covering metanotum completely, with a large conical, discal protuberance that partly harbors the base of hindwings; hindwings pink at basal portion when alive, long, reaching beyond middle of abdomen. Last 3 abdominal segments short, but longer than broad, each  $1/4$  shorter than previous segment, combined length longer than any other segment alone; anal segment rounded, slightly bilobed; poculum strongly arched, scoop-shaped, tapering apically but rounded at tip; vomer visible, heart-shaped at base, narrowed abruptly for apical  $1/3$ ; cerci stout, as long as anal segment, rounded at tips.

*Female* (Fig. 12)

173-175 mm, 222 mm with legs outstretched, brown with black mottling; head broad, 8 mm between eyes, strongly convex; antennae as long as head, pronotum, and mesonotum combined; forewings similar to male but with raised dark veins; hindwings unusually short (as implied by the spe-

Figure 11. *Haplopus micropterus* male on Tortola, BVI. T. James.



Figure 12. *Haplopus micropterus* female on Tortola, BVI. T. James.

cies name *micropterus*), reaching posterior median segment, exposed part grayish brown, folded part in striking contrast: anal vein black, membrane yellow basally and transparent distally; abdominal segment 7 with lateral flanges; anal segment elongate, rounded at tip; supraanal plate short, almost invisible; operculum like a chute, reaching well beyond abdomen to a combined length of last 3 segments.

#### *Nymph*

Gender is evident even in young nymphs. In instars 1-4, the mesonotum is barely 3× as long as the pronotum, the median segment is distinctly shorter than the metanotum (2:3 in instar 1), and the antennae are shorter than forelegs; all three characters are in contrast to adults and grow proportionately longer as the nymphs mature. Live nymphs were yellowish overall, but the legs were green basally with a greenish lining underside, particularly among the younger ones. In alcohol all ages of nymphs turned brown. We found nine body length categories corresponding to head width: 13-14, 16-18, 20-25, 30-35, 40-50, 55-60, 65-75, 110-120, and 135-145 mm, suggesting seven male and nine female instars, two nymphal stadia fewer in males than females.

Female nymphs had a longer and broader body than males; their wing pad development lagged behind that of male nymphs; their size leapt from the seventh stadium (65-75) to the eighth (110-120) for >30 mm when the male adult could obtain only 85-90 mm body length. For example, a female nymph collected on Guana Island on 20.X.2007 measured 75 mm long; its forewing pads were a pair of laterally extended lobes on the apex of mesonotum, barely recognizable, with a pointed tip; the hindwing buds were small but readily visible; her body length reached 110 mm after molting. But on 23.X.2012 on Guana, a male nymph of 40 mm long already had forewing pads shorter than hindwing pads, and a female nymph of 55 mm long was an older instar, as indicated by her much greater head width, and had no wing pad development. Among different nymphs that had visible wing pads, those of the hindwings remained more distinctly developed than those of the forewings, regardless of gender. At the last two stadia, the forewing pads were quite wing-like, but had not partly covered the hindwing base as in adults. Whether or not the hindwings reach the apex of abdominal segment 5 is the criterion for separating male nymphs from adults. The best character distinguishing older female nymphs from adults is the opercular chute, which does not extend beyond the anal segment by 20 mm if it is a nymph and always goes beyond 20 mm if it is an adult.

#### *Egg* (Fig. 13)

Capsule length 4.7 mm, height 2.8 mm, width 2.4 mm; brown, elongate; surface coarse with irregular dark mottling, without any sculpturing; operculum of similar color, without a distinct rim, but with a small, raised, and highly sculptured capitulum. Micropylar plate broad, Y-shaped, and smooth, with micropyle at meeting point of two short arms of the 'Y'. Eggs were observed being dropped to the ground by females high up on branches of host plants. The length ratio of egg to first instar is about 1:3.

#### *Host plant*



Figure 13. *Haplopus micropterus* egg (dorsal and lateral with capitulum off). P. Brock.

We only found *Haplopus micropterus* feeding on legumes, commonly *Piscidia carthagenensis* (Fabaceae) from islands of Guana and Moskito, locally called Fish Poison Tree, and rarely on *Pictetia aculeata* (Fabaceae), locally called Fustic. *Pithecellobium unguis-cati* (Fabaceae), a spiny bush with bifid leaves, is the most abundant plant on Anegada, where we found all our *H. micropterus* specimens. Like *Pictetia aculeata* and *Pithecellobium unguis-cati*, *Piscidia carthagenensis* is also present on Guana Island (Proctor, 2005) and native to islands of the Greater Puerto Rico Bank. We were not able to collect enough specimens for quantitative feeding tests in the field to draw conclusions; of five specimens kept alive in 2008, the third instar did not eat at all; the rest fed on this three legume plants in no-choice tests, and when given a choice, refused all other plants where individuals were occasionally found like *Colubrina arborescens* (Rhamnaceae). In captivity, adults of this species initially accepted guava *Psidium guajava* (Myrtaceae) and *Rosa* sp. (Rosaceae) as food plants but developed only for three generations with high attrition rates (T. James, pers. comm. 20.I.2009). All this indicates that *H. micropterus* has a narrow range of both host acceptance and plant preference. However, its natural diet appears to be broader to include Malpighiaceae and Asteraceae in addition to Fabaceae on Hispaniola (Hennemann et al., 2016).

#### Variation

Compared with other species from the Virgin Islands, *Haplopus micropterus* used a startle display in defense against possible predators; the brightly colored hindwings are readily flashed open and may remain open for several seconds. Additionally, the adult female and older female nymphs curved their abdomens upwards, rather like a scorpion, and pushed their bodies up and down, not swaying sideways or back and forth like the other wingless phasmids did in the Virgin Islands. These defensive strategies are common in phasmids (Brock, 1999). This nocturnal species perched on twigs or branches 2-3 m high, unlike *Clonistria modesta* (Species 3), which utilized also leguminous plants but rested on lower vegetation. Most male adults were collected at UV or white lights, further collaborating that the hindwings are used for dispersal. We tethered the only adult female collected so far with a thread spool and found she moved very little over a 72-hr period, and was always on distal parts of a branch within 1 m of her original position.

#### Phenology and habitat

The number of individuals of *Haplopus micropterus* caught by Malaise traps on Guana Island was relatively low. During the five annual periods of XI.2009-X.2010, XI.2010-X.2011, XI.2011-X.2012, XI.2012-X.2013, and XI.2013-X.2014, no individuals were ever caught in the fifth period. All 13

nymphs were mostly instars 1-2 appearing in the months of III, V, VI, VII, and XI (instar 4), nearly 40% in June and <25% each in May and July. Individuals were caught from only the windward trap; none came to the leeward trap in the 5-yr period. We also observed different ages from older nymphs to adults in nature and oviposition during feeding tests in each October. These combined data indicate that *H. micropterus* may have only one generation a year, is more abundant and frequently utilized habitats on the wetter windward side of Guana Island, and its egg hatch may be coincident with the spring rainfall season.

#### *Distribution*

The type locality of Stoll's *Phasma angulata* is Amboina, i.e., now the Ambon Island of Indonesia, but is believed really to be from the West Indies by Burmeister (1838) and subsequent authors. A pair of *Haplopus micropterus* was caught at the Belmont Estate at the end of Long Bay on Tortola in 2003 (Figs. 11-12), but no specimens were preserved (T. James, pers. comm. 20.I.2009); this is our sole basis for its occurrence on Tortola. This species is widely distributed throughout Hispaniola, Mona Island, and Puerto Rico (Hennemann et al., 2016), and herein reported for the first time on the islands of Anegada, Guana, Little Thatch, Moskito, and Tortola, all BVI, and St. John, USVI, in addition to the previous records from St. Croix and St. Thomas, both USVI.

#### *Type material examined*

*Haplopus ligiolus*: ZMUH-1 syntype male/1 syntype female, Mona Island [Puerto Rico]. NHMB-1 syntype female, West Indies.

*Haplopus obtusus*: NHMW-holotype female, Santa Kruz [presumably St. Croix].

#### *Specimens examined*

BMNH-BVI: 1 female nymph [instar 4], Guana Is., XI.2010, W.-P. Liao, North Bay Malaise trap; 1 male nymph [instar 1], Guana Is., V.2011, W.-P. Liao, North Bay Malaise trap; 1 male nymph [instar 2], Guana Is., VI 2011, W.-P. Liao, North Bay Malaise trap; 1 male, Little Thatch Is., 18.X.2004, S. Valentine-Cooper, at light. USNM-BVI: 1 male nymph [instar 4], Anegada Is., 25.X.2009, T. Willard; 4 nymphs [instar 1], Guana Is., 1-30.VI/VII.2010, W.-P. Liao, North Bay Malaise trap; 1 male/1 female, Guana Is., X.2010, W. Lu; 1 male nymph [instar 5], Moskito Is., 23.X.2012, W. Lu. BDVC-BVI: 1 male, Guana Is., 23-25.X.2000, B. & B. Valentine, UV light; 1 male, Guana Is., 4.X.2004, B. D. & S. C. Valentine-Cooper, UV light; 1 male, Guana Is., 14.X.2006, B. D. Valentine family. GUANA-BVI: 1 female nymph [instar 7], Moskito Is., 23.X.2008, S. C. Valentine-Cooper; 1 nymph [instar 3], Moskito Is., 23.X.2008, W. Lu, beat. VIIS-USVI: VIIS8990 [male], St. John Is., 28.VI.1968, A. E. Dammann [as *Aplopus mayeri*]; VIIS8993 [female nymph], St. John Is., Lameshur Ranger Station, 28.IX.1963, J. Riddle. MAIC-USVI: 1 male, St. Thomas Is., Frenchman's Bay Estate, 750 ft., 23.I.1979 [no collector]; 1 male, St. Thomas Is., Estate Nazareth, 1.I.1993-6.VII.1994, M. A. Ivie, flight intercept trap.

## **Family Pseudophasmatidae**

### **5. *Agamemnon cornutus* (Burmeister, 1838) (Figs. 14-16)**

*Acanthoderus cornutus* Burmeister, 1838: 569, St. Thomas; Westwood, 1859: 56.

*Pygirhynchus thomae* Saussure, 1868: 64, St. Thomas.

*Bacteria cornuta* (Burmeister), Saussure, 1868: 65; 1870: 161; Langlois et al., 2006: 14, St. Thomas [as *Bacteria cornuta* Saussure, 1868].

*Ceroys cornutus* (Burmeister), Kirby, 1904: 354.

*Canuleius cornutus* (Burmeister), Redtenbacher, 1906: 67; Wolcott, 1951: 50, Puerto Rico.

*Agamemnon thomae* (Saussure), Moxey, 1971: 80; Otte and Brock, 2005: 41 (synonymy); Langlois et al., 2006: 13, Puerto Rico; 14, St. Thomas.

*Agamemnon cornutus* (Burmeister), Otte and Brock, 2005: 41; Zompro, 2005b: 258 (type data); Langlois et al., 2006: 13, Puerto Rico; 14, St. Thomas; Lelong 2008: 6, Tortola.

#### *Nomenclature*

This species has been placed in six different genera and named synonymously, which reflects confu-



Figure 14. *Agamemnon cornutus* male in nature. P. Brock.



Figure 15. *Agamemnon cornutus* female in nature. P. Brock.

sion in taxonomy and perhaps, the great morphological variation of *Agamemnon cornutus*. Moxey (1971) is the first who established a new genus *Agamemnon* and transferred *Pygirhynchus thomae* to it at the same time. This species name of 1868 by Saussure was surprisingly omitted by Brunner (1907) and Redtenbacher (1906, 1908). The type(s) of *P. thomae* from St. Thomas has not been traced in MHNG and is probably lost, but we agree with its synonymy with *Acanthoderus cornutus* by Otte and Brock (2005), who reached the conclusion that the descriptions clearly represented a single species.

They gave priority to Burmeister's *A. cornutus* of 1838, and transferred it from the genus *Canuleius* Stål, 1875, to *Agamemnon* Moxey, 1971.

#### *Adult diagnosis*

This species is sexually dimorphic in size and morphology; both sexes are wingless, brown, and spiny on head and pronotum (most spines variable in development and some are frequently reduced to granules, or occasionally absent). The mesonotum is always  $>3\times$  length of the pronotum; the median segment is shorter than the metanotum (1:2). The antennae are slightly longer than (males) or as long as (females) the fore legs. The head consistently has two spines between eyes on vertex. Females often have a pair of large, swollen, conical tubercles in middle of the mesonotum.

#### *Male* (Fig. 14)

41-60 mm (usually within range 50-60 mm), slender; head longer than broad, slightly longer than pronotum, with 3-4 pairs of conical spines: anterior pair between eyes largest, posterior pairs close to each other just before pronotum (2 pairs dorsal, 1 pair lateral). Thorax with a pair of conical spines on posterior pronotum just before mesonotum, another pair on posterior mesonotum just before metanotum, and another pair on metanotum that is just before and demarcates the median segment; mesonotum  $5-6\times$  length of pronotum. Well spread, sparse tubercles also present on head and thorax. Abdominal dorsal segment 6 usually with a pair of often low ridges; last segments short with 8-9 broader apically, combined length longer than any other segment alone; poculum strongly arched, scoop-shaped; vomer visible, heart-shaped; cerci short, rounded at tip, extending just beyond end of abdomen.

#### *Female* (Fig. 15)

70-80 mm, robust, covered with not only dark blotches and markings that are absent in males, but also more conspicuous tubercles on whole of body (ventrally tubercles are small and sparse). Head broad, as long as pronotum, often with lateral black stripes crossing from anterior of eyes to apex; anterior pair of conical spines between eyes stouter than those of males, horn-like. Mesonotum  $5\times$  length of pronotum, centrally with another pair of large spine clusters that can develop into a pair of large, swollen, conical tubercles, in addition to those present in males. Legs irregularly banded with darker brown; mid and hind femora with 6 leaf-like protuberances towards apex. Anal segment short, supraanal plate narrow and long, twice as long as anal segment, beak-like with a pointed tip; operculum long, which is well beyond the anal segment and slightly longer than the long supraanal plate, tapering to a pointed tip. Each abdominal segment with a pair of short spines posteriorly, except segment 6, which has instead a pair of raised, leaf-like protuberances; segments 4-6 broadened with a small leaf-like lateral lobe on each side posteriorly, which occasionally is reduced or completely absent.

#### *Nymph*

Gender is evident even in young nymphs. In young female nymphs the operculum is less elongated and thus does not extend beyond the supraanal plate; otherwise similar to adults. Although the spines on the mesonotum, metanotum, and abdomen are smaller in male than female adults (and rarely obsolete), male and female nymphs are always spinier than adults. The pair of leafy protuberances on abdominal segment 6 is better developed in older female nymphs, but occasionally reduced or absent. Males are consistently narrower than females; in male nymphs there are five body length categories corresponding to head width: 15, 25-30, 35-38, 40-45, and 50-55 mm; in female nymphs, seven body length categories: 15-17, 25-30, 33-38, 40-47, 50-58, 60-67, and 70-72 mm; this indicates five male and seven female instars, two nymphal stadia fewer in males than females. Whether or not the poculum is in the form of a characteristic bump and the operculum extends beyond the long supraanal plate are the criteria for separating male and female nymphs from adults, respectively.

#### *Egg* (Fig. 16)

Capsule length 4.1 mm, height 2 mm, width 1.7 mm; dark brown, elongate, about twice as long as broad; surface coarse with darker hairy lines; operculum flat, indistinct but hairy, capitulum minimal. Micropylar plate short and central, arrow-shaped, where the arrowhead is slightly emarginate to ac-



Figure 16. *Agamemnon cornutus* egg (capitulum, dorsal, and lateral). P. Brock.

commodate a darker micropyle. Although the eggs were injected into various substrates quite forcibly with the strong ovipositor in captivity (T. James, pers. comm. 20.I.2009), we found that they were easily dislodged from vegetation when we checked feeding tests by taking out plant branches from the containers and may not necessarily attach to any vegetation or substrates. During feeding tests, many females laid eggs and the maximum number per female was nine eggs within a 48-hr period. The length ratio of egg to first instar is from 1:3 to 1:4.

#### Host plant

We found *Agamemnon cornutus* in nature resting or mating on >35 plants in 21 families [number of plant species: names] of Apocynaceae [1: *Nerium oleander*], Asteraceae [1: *Chromolaena corymbosa*], Bignoniaceae [2: *Macfadyeana unguis-cati*, *Tecoma stans*], Boraginaceae [4: *Bourreria succulenta*, *Cordia alliodora*, *Cordia polycephala*, *Tournefortia hirsutissima*], Celastraceae [2: *Cassine xylocarpa*, *Crossopetalum rhacoma*], Commelinaceae [1: *Commelina diffusa*], Convolvulaceae [1: *Jacquemontia pentanthos*], Euphorbiaceae [2: *Croton astroites*, *Croton flavens*], Fabaceae [2: *Pictetia aculeata*, *Rhynchosia reticulata*], Malpighiaceae [3: *Heteropterys purpurea*, *Malpighia woodburyana*, *Stigmaphyllon dichotomum*], Moraceae [1: *Ficus microcarpa*], Myrtaceae [3: *Eugenia cordata*, *Eugenia procera*, *Myrcia splendens*], Nyctaginaceae [2: *Guapira fragrans*, *Pisonia subcordata*], Polygonaceae [1: *Antigonon leptopus*], Rhamnaceae [1: *Colubrina arborescens*], Rubiaceae [4: *Gonzalagunia hirsuta*, *Ixora coccinea*, *Randia aculeata*, *Rondeletia pilosa*], Sapindaceae [1: *Serjania polyphylla*], Sterculiaceae [1: *Melochia tomentosa*], Solanaceae [1: *Solanum polygamum*], Verbenaceae [2: *Citharexylum fruticosum*, *Lantana involucrata*], and Vitaceae [1: *Cissus verticillata*].

We observed *Agamemnon cornutus* feeding in nature only on five plants in five families. On the night of 8.X.2003 on Guana Island, a herpetologist reported a story of a strange looking insect during his night hunt for snakes; it was the chewing noise that first caught his attention. We immediately found it: a female feeding along the trail in the North Bay woods at about 2 m above sea level. The plant was

later identified as Maubi Bark, *Colubrina arborescens* (Rhamnaceae), a broad-leaved perennial shrub or small tree attaining 20 m, widely distributed over the Greater Puerto Rico Bank, Florida, Mexico, and Central America. The plant was recorded from Guana but no ecological data provided (Proctor, 2005). We found it quite common on the island at sea level up to the peak (246 m), usually in damp coastal conditions and occasionally in forested areas. It is one of the two species in this genus used in Puerto Rico and other islands to make a popular fermented drink called Maubi. The insect damage was quite obvious; the phasmid fed on mature leaves at about midlevel of the young tree. The damaged leaves had large sections missing but sometimes thicker veins remained. On 19.X.2003 in Grand Ghut, northern side of Guana Island ca. 100 m above sea level, we found a male adult in daytime on a different plant with damaged leaves: *Malpighia woodburyana* (Malpighiaceae), a perennial shrub attaining 5 m with small needlelike leaf hairs. This plant is distributed throughout the Greater Puerto Rico Bank, although uncommon, and usually found in dry coastal woodlands. It is much less common than *Colubrina arborescens* is on Guana, only found above 50 m (Proctor, 2005), and is related to, but distinct from, the Barbados or West Indian Cherry, *Malpighia emarginata*, one of the best sources of vitamin C. On 22.X.2009, in a grassy area on the lower section of the trail to Sage Mt. National Park, Tortola, BVI, we observed a congregation of four males on *Cordia polycephala* (Boraginaceae) with heavily damaged leaves, a shrub vine with many flower buds, native to islands of the Greater Puerto Rico Bank. This plant was not listed on Guana (Proctor, 2005). A few nights later, on 28.X.2009, three mating pairs were found on the same plant; subsequent feeding tests confirmed it was a host plant (Table 2). On 11.X.2010 a female fifth instar nymph was found feeding on *Commelina diffusa* (Commelinaceae), a forb naturally widespread in southeastern United States and the Caribbean, along the roadside of Little Thatch Island, BVI; it continued feeding overnight on the same plant. This plant family was not listed on Guana (Proctor, 2005) but we found it common along trails. On 15.X.2011, a female older nymph was found feeding at night on Guana Island on *Serjania polyphylla* (Sapindaceae), a vine with succulent, saw-toothed leaves, native to islands of the Greater Puerto Rico Bank. This plant was listed on Guana (Proctor, 2005).

In addition to these five natural host plants, we tested in laboratory all plants where *Agamemnon cornutus* was found in no-choice feeding tests. When given no choice, 100% fed on *Colubrina arborescens* (Rhamnaceae, N=13) and *Cordia polycephala* (Boraginaceae, N=10) voraciously. When given choices, individuals ate 16 plant species in 13 families (Table 2); the number of individuals feeding on *Colubrina arborescens* was greater than any other plant; >50% of individuals fed on both *Colubrina arborescens* and each of *Cordia polycephala*, *Rhynchosia reticulata* (Fabaceae), *Pictetia aculeata* (Fabaceae), *Croton astroites* (Euphorbiaceae), and *Guapira fragrans* (Nyctaginaceae). In captivity, this species accepted guava *Psidium guajava* (Myrtaceae) and bramble *Rubus* (Rosaceae) as food plants and can develop continuously for generations (T. James, pers. comm. 20.I.2009); both are native plants to the Lesser Antilles, but not recorded from the Virgin Islands. All this indicates that individuals may have simply been resting or trespassing on vegetation near host plants for nearly half of the plants, and *A. cornutus* likely had a wide range of host acceptance and high adaptability, but a narrower range of plant preference.

#### Variation

This species is highly variable in the development of spines, lobes, and ridges; some of which are frequently reduced to granules, or occasionally absent, in adult females. The striation pattern with gray, black, and green colors, which are striking in some females, is also highly variable. All stages we have are grayish brown, but an adult male found on Jost Van Dyke on 18.X.2010 had bright green under the femora and the abdominal underside; this is the first report of green color in this species.

In addition to morphological variation, there may be geographic variation in size and development; a "dwarf" 41-mm adult male was discovered on Anegada Island on 25.X.2009 and a 42-mm on 23.X.2012. Anegada is the most remote of the island group, much dryer and lower in elevation than Guana and Tortola. This environmental condition may cause early maturity as in the dwarf male who may have skipped one nymphal stadium to become adult; it may also delay developmental growth be-

cause we were unable to find adult females but only nymphs on Anegada in late October of both years, while on the lush islands of Guana and Tortola adult females were abundant.

Night searches (number in parentheses) during the following periods produced 15 males and 6 females in October 2007 (5), 39 males and 22 females on 5-24.X.2008 (12), and 24 males and 14 females on 2-28.X.2009 (17), indicating that there is a high male to female ratio (about 3:1, 3:2, and 2:1, respectively) at least at that time of the year. Similar to *Clonistria modesta* (Species 3), this species rested on lower vegetation, seldom dangling under leaflets or branches.

#### *Phenology and habitat*

The number of individuals of *Agamemnon cornutus* caught by Malaise traps on Guana Island was relatively low. During the five annual periods of XI.2009-X.2010, XI.2010-X.2011, XI.2011-X.2012, XI.2012-X.2013, and XI.2013-X.2014, no individuals were ever caught in the second and fifth periods. All 11 nymphs were mostly instars 1-2 concentrating in the months of III-V and IX-X in the 5-yr period, 70% occurred in the spring rainfall, 30% in the fall rainfall. Individuals were caught >80% in the windward trap and <20% in leeward trap. We also observed different ages from older nymphs to adults in nature and oviposition during feeding tests in each October. These combined data indicate that *A. cornutus* may have two generations a year, is more abundant and frequently utilized habitats on the wetter windward side of Guana Island, and its egg hatch may be preceding and concordant with each of the spring and fall rainfall peaks.

#### *Distribution*

The type locality of this species is St. Thomas and the types are in ZMHB and MLUH. Burmeister (1838) referred to a likely nymph of this species from Puerto Rico, almost certainly the source of the Puerto Rico record for this species in Wolcott (1951) and in turn in Langlois et al. (2006). Therefore, all records on Puerto Rico require further confirmation. It is herein reported for the first time on the islands of Anegada, Great Camanoe, Guana, Jost Van Dyke, Little Thatch, Mosquito, Peter, Necker, and Virgin Gorda, all BVI, and St. John, USVI, in addition to the previous records of Tortola and St. Thomas.

#### *Type material examined*

*Acanthoderus cornutus*: ZMHB-2 syntype females, St. Thomas; 1 female nymph, St. Thom. [Thomas], Poeschke Mor. MLUH-1 syntype female, St. Thomas [damaged].

#### *Specimens examined*

BMNH-BVI: 1 male, Guana Is., 20-22.X.2000, B. & B. Valentine, UV light; 1 female, Guana Is., 5.X.2003, B. & B. Valentine, beat & sweep; 1 male, Guana Is., Pyramid, 16.X.2007, B. & B. Valentine, sweep; USNM-BVI: 2 males, Anegada Is., 25.X.2009, T. Willard; 1 male, Anegada Is., 23.X.2012, W. Lu; 3 males/1 female/1 female nymph [instar 2], Guana Is., 11.X.2008, W. Lu; 1 female, Guana Is., X.2010, W. Lu; 2 nymphs [male/female, instar 1], Guana Is., IX.2012, North Bay Malaise trap, W.-P. Liao; 1 female nymph [instar 1], Guana Is., X.2012, North Bay Malaise trap, W. Lu; 1 male/2 female nymphs [instar 6], Jost Van Dyke Is., 18.X.2010, E. Wright; 1 female nymph [instar 6], Little Thatch Is., 11.X.2010, E. Wright; 1 male/1 female, Necker Is., 16.X.2014, E. Hill; 1 female nymph, Tortola Is., Sage Mt., 22.X.2009, W. Lu; 1 male/2 female nymphs [instars 2, 6, 7]/1 male nymph [instar 5], Tortola Is., Sage Mt., 22.X.2009, T. Willard; 1 male, Virgin Gorda Is., Gorda Peak, 23.X.2011, S. Valentine-Cooper. BDVC-BVI: 1 female nymph, Great Camanoe Is., 20.X.2008, Lu & S. Valentine-Cooper, at night; 1 male, Guana Is., 20-22.X.2000, B. & B. Valentine, UV light; 1 female nymph, Guana Is., 9-15.X.2002, B. & B. Valentine; 5 male nymphs, Guana Is., 9-15/16-22/23-30.X.2002, B. & B. Valentine, beat & sweep; 1 female, Guana Is., 5.X.2005, B. & B. Valentine, beat & sweep; 1 male nymph, Guana Is., 20.X.2003, B. D. Valentine & S. Valentine-Cooper, sweep; 2 males, Guana Is., 6-15.X.2005, B. D. & B. S. Valentine; 1 female nymph, Guana Is., 10.X.2007, B. D. Valentine family, sweep; 1 male nymph, Guana Is., 10.X.2007, B. D. Valentine, sweep; 1 female nymph, Guana Is., 12.X.2007, W. Lu; 2 males, Guana Is., Pyramid, 16.X.2007 [no collector], sweep; 1 male, Guana Is., 22.X.2007, W. Lu; 1 male nymph, Little Thatch Is., 13.X.2007, W. Lu; 1 male, Little Thatch Is., 23.X.2008, W. Lu; 1 male nymph, Peter Is., 7.X.2003, B. S. Valentine; 1 male/1 male nymph/1 female nymph, Tortola Is., Sage Mt., 1600-1700 ft., 6.X.2001, B.

& B. Valentine; 1 male nymph, Tortola Is., Sage Mt., 750 m, 24.X.2002, B. & B. Valentine, beat; 1 male/1 female, Tortola Is., Sage Mt., 18.X.2008, W. Lu. UDCC–BVI: 2 female nymphs, Guana Is., X.1997, C. R. Bartlett, beat & sweep; 2 males, Guana Is., 22/27.X.1997, C. R. Bartlett, beat & sweep; 1 female nymph, Tortola Is., 28.X.1997, C. R. Bartlett. VIIS–USVI: VIIS9699 [male], St. John Is., VIERS, 31.I.1986, W. B. Muchmore; VIIS8992 [male], St. John Is., Great Lameshur Bay, 15.II.1970, L. L. Curry; VIIS8995 [female], St. John Is., Lameshur Bay Camp, 25.VIII.1970, R. Philibosian & J. Yntema; VIIS8994 [male], St. John Is., Great Lameshur Bay, 9.XI.1970, C. Richards. MAIC–BVI: 1 male, Anegada Is., The Creek, at bridge, salt flat, 8.X.1994, M. A. & L. L. Ivie; 1 male, Guana Is.; 15–25.X.1992; J. Krececk & M. A. Ivie, at night; 1 male, Guana Is.; North Beach, 10.VII.1994, M. A. Ivie, on beach, at night; 1 male, Jost Van Dyke Is., Great Harbour, 23.VII.1993, M. A. Ivie, beat; 1 male, Tortola Is., Balast Bay, 530 ft., 6.X.1994, M. A. & L. L. Ivie, beat; 1 male, Virgin Gorda Is., Gorda Peak, 1000–1300 ft., 6.I.1993, M. Ivie & D. Chadwick; 1 male, Virgin Gorda Is., Gorda Peak, 1000–1250 ft., south entrance trail, 11.X.1994, M. A. & L. L. Ivie; 1 male, Virgin Gorda Is., Gorda Peak, 16.X.1994, M. A. Ivie; 1 male, Virgin Gorda Is., Gorda Peak, 16.VII.1994, M. A. & L. L. Ivie, beat. USVI: 1 male, St. John Is., Estate Caneel Bay, Caneel Hill Trail, 580–600 ft., 02.XI.1992, M. A. Ivie; 2 males, St. John Is., Cinnamon Bay, 3.I.1993, VIBFP, at light; 1 male, St. John Is., Estate Hope, Bordeaux Mt. Rd., 980 ft., 14.X.1994, M. A. & L. L. Ivie, under bark, dead log; 1 male, St. Thomas Is., Estate Bovoni, 15.V.1978, M. A. Ivie; 1 male, St. Thomas Is., Estate Lilliendahl, 1000 ft., 12.X.1978, M. A. Ivie; 1 female, St. Thomas Is., Estate Hope, 25.I.1979; 1 male, St. Thomas Is., Estate Enighed, Magen’s Bay Arboretum, 1.I.1993, VIBFP.

## Discussion

### *Taxonomy*

The information in the present paper covers unpublished data on distributional range, life history, food plants, and habits, and provides minor taxonomic changes as follows: the first male descriptions for *Clonistria calamus* and *C. modesta*, the first egg descriptions for all five species, the elimination of *Clonistria calamus* presence from St. Vincent, and new synonymy. Whilst our description of male wings for *C. modesta* is the first instance of wings to be reported in the genus *Clonistria* Stål, the presence of wings in genera of mainly wingless species is not unique. Conle et al. (2008) present a recent example in the genus *Malacomorpha* Rehn (1906: 113) and *Clonistria* is a genus in need of revision. Based on our work and previous faunal studies, it is likely that out of the currently valid 3,075 phasmid species worldwide (<http://phasmida.speciesfile.org>), there are still several hundred synonyms yet to be reported, balanced by hundreds of as yet undescribed species in major museum collections, let alone those species awaiting discovery in nature.

Typically Pseudophasmatidae have a sunken areola (triangular notch) on the underside of the mid and hind tibiae, separating them from other families of the Anareolatae. Without explanation, Zompro (2004a) omitted reference to *Agamemnon* and four other genera still allocated in the tribe Hesperophasmatini (Subfamily Xerosomatinae, Family Pseudophasmatidae), and listed only four genera: *Hesperophasma*, *Lamponius*, *Rhynchacris*, and *Taraxippus*. Indeed, Zompro goes on to state that “With high probability all members of the Anareolatae could be incorporated within the Areolatae.” Confusingly different terms (some with invalid names) are being proposed for higher classification in phasmids and these are summarized in the Phasmida Species File Online. Considerably more research would be necessary before making such a drastic change to higher classification.

Sexual dimorphism is common in size, wing form, and the number of nymphal stadia among the Virgin Island phasmid fauna. As expected; all males of the five Virgin Islands species are smaller than females; males of two species have wings that are either lacking or shortened in females; all males have fewer nymphal stadia than females. Color form may be a morphological adaptation not only environmentally but also behaviorally; most young nymphs are green, but many turn brown as they develop older, perhaps beneficial to dispersal; coloration often differs between nymphs and adults, and varies between islands in terms of frequency or between windward and leeward sides of an island due to host plant abundance and microclimatic differences. We are in process collecting data on within and between island variation in body size and color form due to island ecology and host plant abundance.

### *Biogeography*

The distributional range of each species in the Virgin isles sheds light on relationships and dispersal ways of these species among different islands. All five species recorded here from the Virgin Islands are sporadically listed for various other isles in the West Indies, and all but *Clonistria modesta* have been recorded from Puerto Rico (Lelong, 2008), even though some of these species are not substantiated by recent records. Because the host plant of *C. modesta* also occurs in Puerto Rico, further search effort may prove its presence. Even within the genus *Clonistria* the differences in morphology and host plant range between *C. calamus* and *C. modesta* are considerable, indicating distant phylogenetic relationship and that speciation elsewhere on the Greater Puerto Rico Bank occurred long before the last glacial maximum when the islands were connected with Puerto Rico by land. Therefore, the low number of species within each genus, occurrence of the same species on Puerto Rico, and distant relationships among genera or among species within the same genus imply that the phasmid fauna of the Virgin Islands is a subset of the Greater Puerto Rico Bank. Most populations may be vicariantly separated by the most recent postglacial sea level rise.

However, these five species do not occur sympatrically anywhere else in the West Indies except the Greater Puerto Rico Bank. Occurrence of only two species (*Clonistria calamus* and *Haplopus micropterus*) on St. Croix is notable because this big island is on its own separate bank and never had a terrestrial connection to the other Virgin Islands. The former species is wingless and the latter is long-winged in males but short-winged in females; it is likely they had colonized St. Croix across water, probably dispersing on rafting vegetation, quite possibly at the Wurm glacial maximum (ca. 15,000 yBP) when the water gap was much smaller (Lazell, 2005). There is no significant differentiation between populations on St. Croix and the other Virgin Islands on the Puerto Rico Bank, suggesting recent or continuing colonization of St. Croix from populations on the Greater Puerto Rico Bank. By far the wingless *Agamemnon cornutus* is the most common species within the Greater Puerto Rico Bank, but it is not found on St. Croix. Because of its polyphagy and presence on the most remote Anegada Island, its absence from St. Croix calls for further search effort. Assuming over-water dispersal for phasmid species to establish on St. Croix, we suggest that wings even only in male would increase the probability of successful colonization. Future molecular studies should be undertaken to reveal the relationships and timing of separation or dispersal of these species.

Species diversity has more to do with altitude and habitat differences than just island size (Lazell, 2005). Tortola is 5,571 hectares with a maximum BVI elevation of 530 m on Sage Mountain and a suggestion of a unique cloud forest; St. Thomas is 7,660 hectares and attains a maximum USVI elevation of 474 m at Crown Mountain -- not a national park; St. John is 5,180 hectares with a height of 387 m on Bordeaux Mountain -- lower than St. Thomas but within the USVI national park; and Guana is 297 hectares with a height of 246 m. The Virgin Islands have been extensively degraded by human activity; Sage Mountain on Tortola and Bordeaux Mountain on St. John were designated national parks not long ago. However, nearby Guana was only partially cleared a century ago (Lazell, 2005) and has been protected for many years and recovering. Tortola is 18 times larger than Guana and nearly twice the altitude, but is less well-protected. We refrain currently from drawing quantitative conclusions of comparison to the classic island biogeography where number of species increases with area because of infrequent visits to other Virgin Islands other than Guana Island. However, big islands like Tortola or St. Thomas have all five species, only one species more than small islands like Guana. This indicates that other factors like altitude or plant distribution may be involved in a successful colonization by either vicariant or over-water dispersal.

#### *Host plant acceptance and abundance*

All five species are most likely nocturnal as they are seldom found during daytime (as is typical in phasmids). Our feeding experiments confirm results by Blüthgen et al. (2006) that phasmids feed on most plant species where they are collected. During night hunts, individuals usually stopped feeding at our lights, and sometimes would freeze or sway their bodies instead. It was unusual that we observed actual feeding for four of the five species.

Abundance seems to be related to the range of host plant acceptance and the rainfall pattern between windward and leeward sides of an island. *Agamemnon cornutus* is the commonest phasmid from the Virgin Islands; it feeds on a broad spectrum of plant families and can be considered polyphagous. Three other species are much less abundant and have a largely restricted diet; they are likely monophagous or oligophagous: *Clonistria calamus* feeds mainly on *Pithecellobium unguis-cati* and *Pictetia aculeata* (both Fabaceae), *C. modesta* only feeds on *Eugenia cordata* (Myrtaceae), and *Haplopus micropterus* on legumes like *Piscidia carthagenensis* and *Pithecellobium unguis-cati* (both Fabaceae). Although *Bacteria yersiniana* accepts plants across several families and is likely polyphagous as well, its cool and wet habitat is only present on the windward side of Sage Mountain and rather restricted on the Virgin Islands; thus it is unlikely to be as abundant as *A. cornutus* and this may explain its absence from small islands like Guana or Moskito. The allopatric distribution of more *Clonistria calamus* on the leeward and more *Haplopus micropterus* on the windward traps indicates habitat partitioning. Rainfall pattern may have affected the distribution and abundance of the host plants and thus these phasmids. The mutual host plant preference of these two species for legume plants supports habitat partitioning and evolutionary convergence due to distant phylogenetic relationships between the two families of Diapheromeridae and Phasmatidae, respectively. The lopsided abundance of more *A. cornutus* on the windward and more *C. modesta* on the leeward traps also reveals the host plant distribution heterogeneity. It is amazing that a small island like Guana at only 246 m altitude and 297 hectares can have such obvious within-island variation in rainfall pattern and plants, but our phasmid abundance data support this. The impact of rainfall on abundance varies among phasmid species; long term surveillance is required before drawing conclusions at this point. Nevertheless, significant habitat partitioning among phasmids of the Virgin Islands may have ensured their long term survival since their separation from Puerto Rico by sea level rise.

### Keys to Adult Phasmids from the Virgin Islands

- |   |   |  |
|---|---|--|
| 1 | Head with distinct sharp or conical spines<br>Head without spines   | 2<br>3   |
| 2 | At least a pair of sharp spines between eyes; wingless, abdominal apex with a long chute dorsally in female<br><br>Only a pair of large conical hump-like spines behind eyes; forewings short; hindwings microp-<br>terous (small wings) in female, long in male; abdominal apex with a long chute ventrally in<br>female | <br><br><i>Agamemnon cornutus</i><br><br><i>Haplopus micropterus</i>   |
| 3 | Head broad, as long as pronotum, median segment shorter than metanotum (1:2)<br>Head elongate, always longer than pronotum  | <br><i>Agamemnon cornutus</i><br>4                                     |
| 4 | Head elongate, nearly twice as long as pronotum; wingless, median segment shorter than<br>metanotum (1:3)<br>Head rectangular, less than 1.5× as long as pronotum; winged or wingless   | <br><i>Clonistria calamus</i><br>5                                     |
| 5 | Wingless, median segment much shorter than metanotum (1:5)<br>Winged or wingless, median segment longer than metanotum  | <br><i>Bacteria yersiniana</i><br>6                                    |
| 6 | Wings long, covering most abdomen<br>Wingless, abdominal segment 4 with a raised protuberance   | <br>Male <i>Clonistria modesta</i><br>Female <i>Clonistria modesta</i> |

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# Resolving the synonymy of *Paraphanocles keratoskeleton* (Olivier, 1792) (Phasmida: Diapheromerinae)

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## Introduction

*Paraphanocles keratoskeleton* was originally described by Stoll in 1788, although he did not use binominal nomenclature. The first valid publication of a name for this species, *Mantis keratoskeleton*, was published in Olivier 1792. Lichtenstein, presumably unaware of the work of Olivier, described *Phasma cornutum* Lichtenstein 1802 as an objective synonym. Stoll's later work was edited and published posthumously in 1813, with the same species bearing the binominal *Phasma bicornis* Stoll 1813. The objective synonyms resulting from the work of Stoll, Lichtenstein and Olivier are discussed by Bragg 1995.

The genus *Paraphanocles* was erected by Zompro 2001 containing the single species *Mantis keratoskeleton* Olivier 1792. The genus is differentiated from *Phanocles* Stål 1875 in the male by a dilating tergite X that is wider than tergite IX, in females by the lack of lateral lobes on tergite VI. In the same publication Zompro synonymised *Bacteria bellangeri* Redtenbacher 1908, *Bacteria bradypus* Redtenbacher 1908, *Bacteria integra* Redtenbacher 1908 and *Bacteria maxwelli* Redtenbacher 1908 with *Pa. keratoskeleton*. Prior to this Redtenbacher 1908 made *Phanocles curvipes* Redtenbacher, 1892 a junior synonym of *Phasma bicornis* Stoll 1813. *Dyme mutica* Brunner von Wattenwyl, 1907 was subsequently synonymised with *Pa. keratoskeleton* by Bellanger et al. 2012. Otte & Brock 2005 later synonymised *Bacteria cyphus* Westwood, 1859 under *Pa. keratoskeleton*.

Examination of type material of the species currently synonymised under *Pa. keratoskeleton* has revealed errors in prior works. In this paper we demonstrate that *Dyme mutica* and *Bacteria integra* form a distinct species from *Pa. keratoskeleton* and transfer them to the genus *Phanocles* sensu Zompro 2001. This species is believed to be endemic to Trinidad and Tobago. *Bacteria maxwelli* Redtenbacher 1908 has its abdominal segment X as widened as the posterior half of abdominal tergite IX in the male, excluding it from membership of *Paraphanocles* sensu Zompro, 2001 even though it was this author who synonymised the species. We remove *B. maxwelli* from synonymy under *Pa. keratoskeleton* and transfer it to the genus *Bacteria*.



Figure 1. Adult male corresponding to the type of *Dyme mutica* collected by Baker in Tobago, January 2016.

## Materials and methods

A male phasmid, corresponding to the type of *Dyme mutica* collected by Baker in Tobago (Fig. 1), was found by the authors to differ significantly from males from the type series of various species currently synonymised under *Pa. keratoskeleton*. Further research using the Phasmida Species File (Brock et al. 2016) and original type material confirmed that *Dyme mutica* should be considered a valid species in the genus *Phanocles* and that *B. maxwelli* does not belong to the genus *Paraphanocles*. Further investigation of the current nine synonyms of *Paraphanolces keratoskeleton* revealed that *Bacteria maxwelli* and *Bacteria bellangeri* are conspecific with each other, but not with *Pa. keratoskeleton*.

## Specimen Repositories

MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum, London, United Kingdom
NMW	Naturhistorisches Museum, Vienna, Austria

## Material Examined

HOLOTYPE: *Bacteria cyphus*. BMNH(E):#844538. West Indies. SYNTYPE x3: *Phanocles curvipes*. BMNH(E):#844539,#844540,#844541. St Vincent. HOLOTYPE: *Dyme mutica*. NMW. Trinidad. HOLOTYPE: *Bacteria integra*. NMW, Trinidad. LECTOTYPE, PARALECTOTYPE. *Bacteria maxwelli*. MNHN-EO-PHAS571.

## Taxon Treatments

### *Paraphanocles keratoskeleton* (Olivier, 1792)

- = *Phasma cornutum* Lichtenstein, 1796 (objective synonym)
- = *Phasma bicornis* Stoll, 1813 (objective synonym)
- = *Bacteria bradypus* Redtenbacher, 1908 (junior synonym)

### Diagnosis

Male: Protrusions on the head. Tergite X wider than the posterior of tergite IX. Last tergite strongly curved. Cerci protruding longer than anal segment. Setose.

### *Phanocles mutica* (Brunner von Wattenwyl, 1907) n. comb.

- Dyme mutica* Brunner von Wattenwyl 1907
- = *Bacteria integra* Redtenbacher, 1908 (junior synonym)

*Dyme mutica* is removed from synonymy under *Paraphanocles keratoskeleton* and transferred to the genus *Phanocles*.

### New specimens examined

1 Male; Mary's Hill Lodge, Tobago 14m. 11.20N,60.75W. 2017.i.27. Coll. E. Baker.

### Diagnosis (Figs 2, 3)

Male: lack of protrusions on the head and tergite X of the male being as wide as the posterior of tergite IX. Anal segment straight and flat, narrowing distally.

Female: subgenital plate more than 1.5x the length of the last tergite. Cerci protude past anal segment.

### Distribution

Currently considered to be endemic to the islands of Trinidad and Tobago (Bellanger et al. 2012, Langlois and Bellanger 2012 ).

### Ecology

A common species of xerophilic environments on the islands. Specimen collected by Baker found in close proximity to Glory Cedar (*Gliricidia sepium*, Fabaceae), on which it also fed on for a few days in



Figure 2A. Holotype of *Dyme mutica* end of abdomen (ventral) NMW



Figure 2B. Holotype of *Dyme mutica* metathorax (lateral) NMW

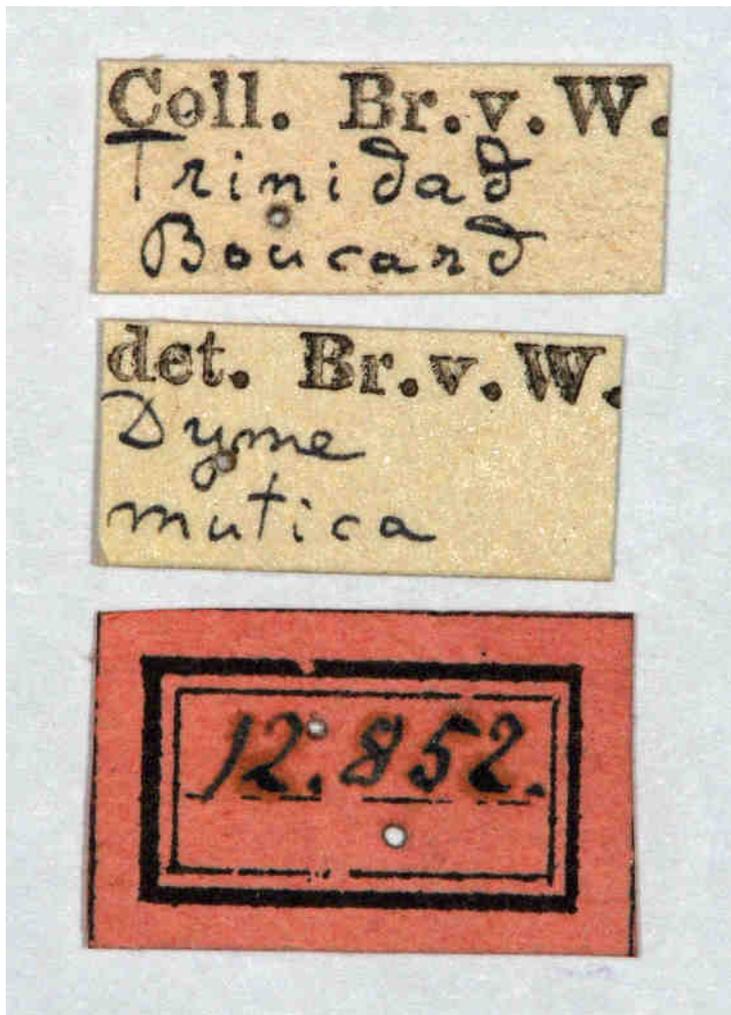


Figure 2C. Holotype of *Dyme mutica* (specimen labels) NMW



Figure 2D. *Phanocles mutica* end of abdomen.

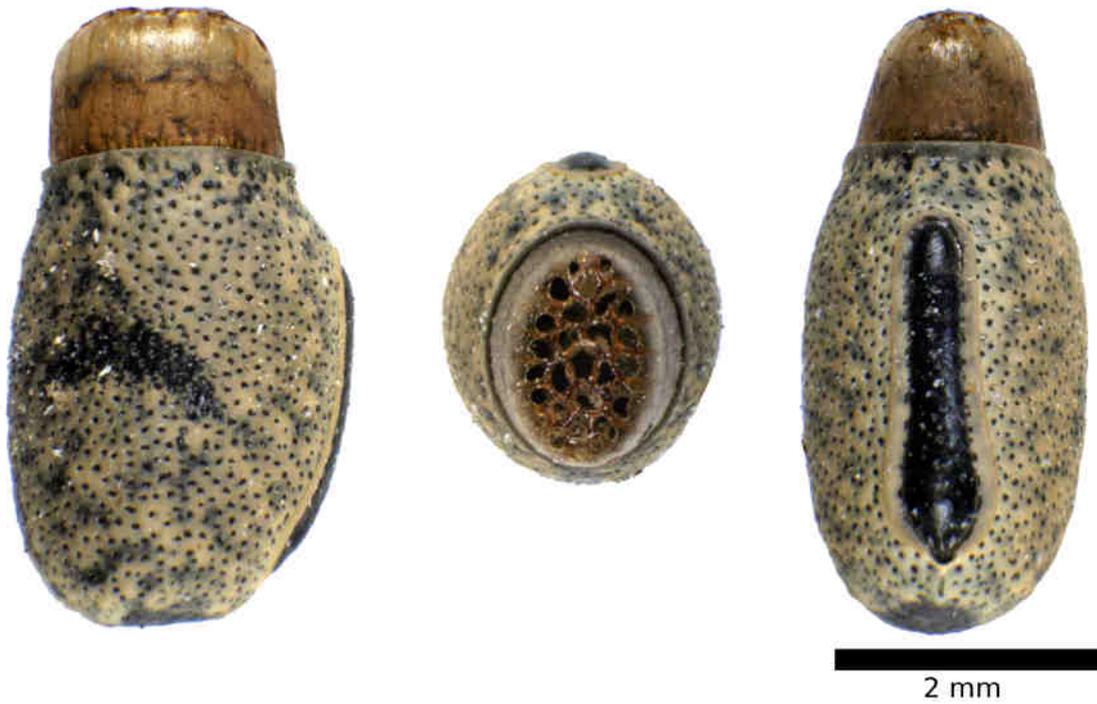


Figure 2E. *Phanocles mutica* eggs descendants of a female from Trinidad (leg. Y. Bellanger).  
F. Tetraert.



Figure 3A. Holotype of *Bacteria integra* abdomen (dorsal)



Figure 3B. Holotype of *Bacteria integra* metathorax (dorsal)



Figure 3C. Holotype of *Bacteria integra* (specimen labels)

captivity. This tree species is introduced to the island. Bellanger et al. (2012) report the species to feed on *Chamaecrista nictitans* (Fabaceae) and a species of *Cecropia* (Urticaceae). It is likely to be highly polyphagous, and in captivity accepts several species from the Rosaceae and Fabaceae (Bellanger et al. 2012, Langlois and Bellanger 2012 ).

*Taxon discussion*

*Dyme mutica* and *Bacteria integra* were both described using single specimens of differing sexes from Trinidad and Tobago. The work of Bellanger et al. (2012) and Langlois & Bellanger (2012) found only a single species of the *Phanocles* group sensu Zompro (2001) on the islands. This single species matches the type material of both *Dyme mutica* and *Bacteria integra*, and these two species are considered here to be synonymous. It is supposed by that the habitus of specimens from Trinidad and Tobago examined by Bellanger et al. 2012 and Langlois and Bellanger (2012) differ from the continental american populations of *Pa. keratoskeleton* and might be a different species. As the type specimen of *Pa. keratoskeleton* belongs to a continental population and originated from Suriname, this leads to the assumption that the, morphological different, specimen described as *D. mutica* is not synonym of *Pa. keratoskeleton*, contrary to the synonymisation by Langlois and Bellanger (2012).

***Bacteria maxwelli* (Redtenbacher, 1908) n. comb.**

*Bacteria maxwelli* Redtenbacher, 1908

= *Bacteria bellangeri* Redtenbacher, 1908 (junior synonym)

*Diagnosis* (Figs 4-8)

Male: protrusions on the head. Tergite X as wide as the posterior of tergite IX. Cerci protruding past anal segment.

Female: subgenital plate protrudes last tergite more than 1.5x the length of the last tergite. Cerci protruding past anal segment.

*Distribution*

Martinique.

***Phanocles curvipes* Redtenbacher, 1892 n. comb.**

*Phanocles curvipes* Redtenbacher, 1892

*Bacteria cyphus* is removed from synonymy under *Paraphanocles keratoskeleton* and transferred to the genus *Phanocles* .

*Diagnosis*

Male: protrusions on the head. Anal segment broadened. Long cerci.

Female: protrusions on the head. Subgenital plate protrudes anal segment only shortly. Cerci not reaching over the anal segment.

***Dyme cyphus* (Westwood, 1859) n. comb. Nomenclature**

*Bacteria cyphus* Westwood, 1859

*Bacteria cyphus* is removed from synonymy under *Paraphanocles keratoskeleton* and transferred to the genus *Dyme*.

*Diagnosis*

Male: head with protrusions. Cerci short, not exceeding the last tergite. Last tergite broadened distally.

*Egg*

As defined for *Dyme*, the ovae of *D. cyphus* lack a capitulum (Sellick 1997, Sellick 1988 ).



Figure 4A. Lectotype of *Bacteria maxwelli*. MNHN.



Figure 4B. Lectotype of *Bacteria maxwelli*. MNHN.

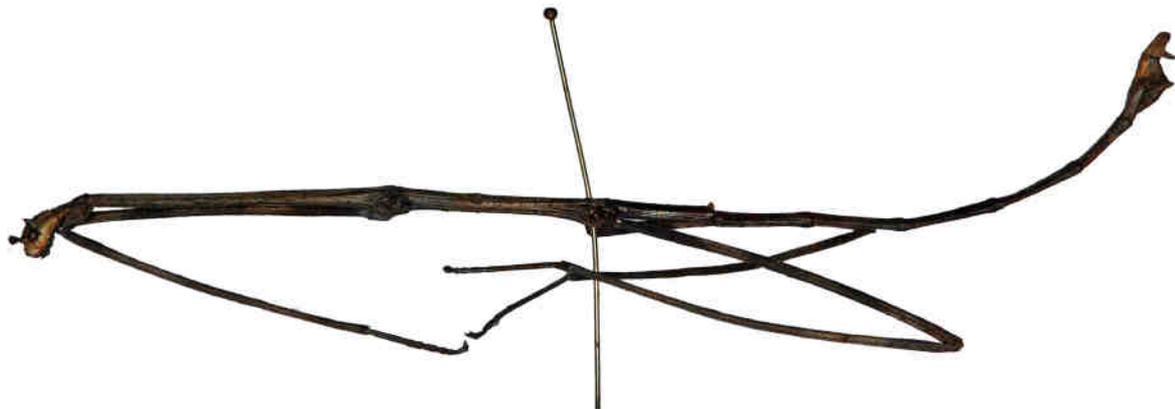


Figure 5A. Paralectotype *Bacteria maxwelli* (NMW)



Figure 5B. Paralectotype *Bacteria maxwelli* (NMW)



Figure 6A. *Bacteria maxwelli* male (NMW)



Figure 6B. *Bacteria maxwelli* male (NMW)

**Identification key to the males of the species hitherto confunded under the name of *Paraphanocles keratosqueleton***

- |   |  |                                      |
|---|--|--------------------------------------|
| 1 | Head with protrusions                            | 2                                    |
|   | Head without protrusions                         | <i>Phanocles mutica</i>              |
| 2 | Cerci long, extending beyond anal segment        | 3                                    |
|   | Cerci short, not extending beyond anal segment   | <i>Dyme cyphus</i>                   |
| 3 | Tergite X as wide as the posterior of tergite IX | 4                                    |
|   | Tergite X wider than the posterior of tergite IX | <i>Paraphanocles keratosqueleton</i> |
| 4 | Last tergite broadened                           | <i>Phanocles curvipes</i>            |
|   | Last tergite not broadened                       | <i>Bacteria maxwelli</i>             |

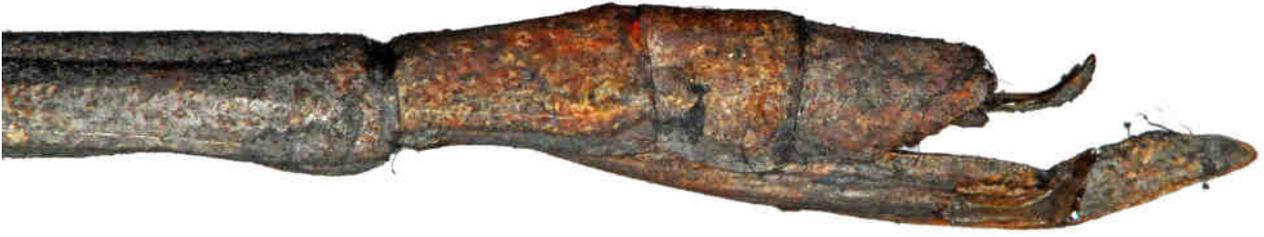


Figure 7A. *Bacteria maxwelli* female (NMW) abdomen (lateral)



Figure 7B. *Bacteria maxwelli* female (NMW) metathorax (lateral)



Figure 7C. *Bacteria maxwelli* female (NMW) label

## Discussion

### *Biogeography*

While culturally being part of the Caribbean the islands of Trinidad and Tobago, close to the north eastern coast of Venezuela, are on the South American continental plate, and a large proportion of their fauna is South American in origin. The distribution of several notable species, in particular the White-tailed Sabrewing *Campylopterus ensipennis* (Swainson, 1822), reflects this geological history. In contrast the remainder of the Lesser Antilles belong to the Caribbean plate. The fact that *Phanocles mutica* is found on Trinidad and Tobago reflects this history, with *Phanocles* having a mainland Central and South American distribution (Brock et al., 2016).

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