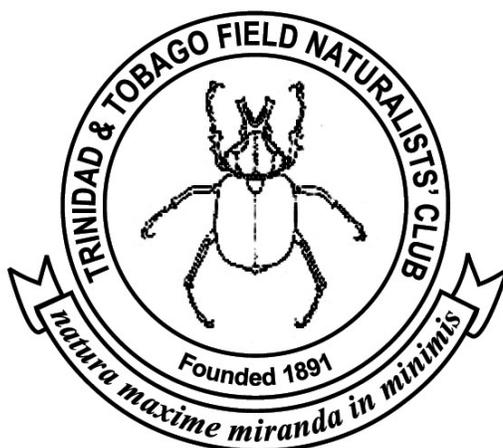


# LIVING WORLD

Journal of The Trinidad and Tobago Field Naturalists' Club



2014



## THE TRINIDAD AND TOBAGO FIELD NATURALISTS' CLUB

The Trinidad and Tobago Field Naturalists' Club was founded on 10 July, 1891. Its name was incorporated by an Act of Parliament (Act 17 of 1991). The objects of the Club are to bring together persons interested in the study of natural history, the diffusion of knowledge thereof and the conservation of nature.

Monthly meetings are held at St. Mary's College on the second Thursday of every month except December.

Membership is open to all persons of at least fifteen years of age who subscribe to the objects of the Club.

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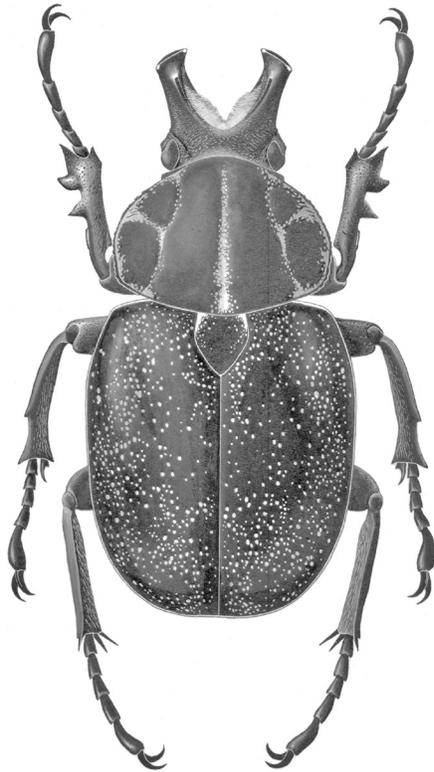
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# LIVING WORLD

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Field Naturalists' Club  
2014



*Inca clathrata quesneli* Boos and Ratcliffe

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## Editorial

The 2014 issue of Living World represents a change in Editor and new additions to the editorial team. Dr Elisha Tikasingh has retired after 15 years serving as the Editor as described in the Editorial of the 2013 issue. We thank Dr Tikasingh for his hard work in getting the Living World to its current standard. The editorial team now includes Graham White (Editor), Yasmin Comeau, Bill Murphy and Palaash Narase. While the team has changed, our vision for the Journal has not. We will continue to encourage the publication of studies and observations on the natural history of Trinidad and Tobago and the wider region. We will continue to encourage Nature Notes so that rare occurrences or observations are recorded and not forgotten and we will continue to honour those naturalists with outstanding contributions to our knowledge of our natural history. This year we have instituted a new section containing reviews. This section will be by invitation only and address subjects for which we consider a review timely or which might encourage further work.

To create wider circulation and accessibility, we plan to be on-line by the next issue with the backlog of past issues becoming available on-line in a searchable format soon after.

This, the 2014 issue contains six research papers, eight Nature Notes, the report of the bird records committee, a review of our knowledge, or lack thereof, of Social Insects in the West Indies and two of our Notable Naturalists are highlighted.

Matthew Cock has completed his mammoth task of cataloguing the butterflies of the family Hesperidae, which was published over the last 23 years. This year he has provided us with an account of the biology of several of the skipper butterflies of Trinidad.

A team of authors, Ryan Mohammed, Shiva Manickchan, Stevland Charles and John Murphy, has given an account of the herpetofauna of southeast Trinidad, bringing together past studies and collected specimens.

We have two papers on amphibians. Roger Downie and M. Nokhbatolfoghahai tell us how to separate tad-

poles of *Mannophryne trinitatis* from *M. olmonae* but generally advise us to read the collection location off the label! Roger, this time working with N.J. Barron and Mark Greener, describes the nesting of the Gladiator Frog.

Studies on the Trinidad Motmot in Tobago have demonstrated for the first time the use of an anvil by that species for feeding on snails and other hard prey. We thank Mike Rutherford and Giovanni Bianco for this interesting study and encourage readers to see a video of this for themselves on the TTFNC webpage at [www.ttfnc.org](http://www.ttfnc.org)

All naturalists are familiar with and most have some affinity for praying mantises. In this issue Mark Greener and Mike Rutherford provide us with an account of the mantids of Trinidad and Tobago together with a well-illustrated key to help us identify those species which we may come across.

The Nature Notes section includes observations of opilionids and spiders, a leucistic hummingbird and a pod of Atlantic Spotted Dolphins in Tobago, new records of mantids, scorpions and bats from Huevos Island and an account of a location in Tobago well-stocked with invasive species.

We have our regular report from the Trinidad and Tobago Bird Status and Distribution Committee. This report includes 90 observations and tells us that the checklist for Trinidad and Tobago at the end of 2013 stood at 473 species.

Two of our Notable Naturalists are highlighted. It is fitting that one of these is our outgoing Editor, Dr Elisha Tikasingh. The other, A.M. Adamson, was of an earlier vintage.

Our new review section contains an account of our knowledge, or lack thereof, of Social Insects in the West Indies. We thank Chris Starr for this review.

**GW, June 2014**

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### Cover Photograph

This Atlantic Spotted Dolphin (*Stenella frontalis*) was one of a group of dolphins seen off the South East Coast of Trinidad and was photographed by Kerrie T. Naranjit. The Atlantic spotted dolphin is one of 19 species of cetacean known to inhabit the waters around Trinidad and Tobago. See Nature Note on page 51 which reports a sighting of this species among a large school of dolphins off the coast of Charlotteville, Tobago in 2012.

Special thanks to Michael E. Tikasingh  
for the design and layout of the front and back covers.

# Observations on the Biology of Skipper Butterflies in Trinidad, Trinidad and Tobago: *Phocides*, *Chioides*, *Typhedanus*, and *Polythrix* (Hesperiidae: Eudaminae)

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## ABSTRACT

Observations are provided on the early stages and food plants of *Phocides polybius polybius* (Fabricius), *P. pigmalion pigmalion* (Cramer), *Chioides catillus catillus* (Cramer), *Typhedanus undulatus* (Hewitson), *Polythrix auginus* (Hewitson), *P. caunus* (Herrich-Schäffer), *P. metallescens* (Mabille), *P. octomaculata* (Sepp), *Polythrix roma* Evans from Trinidad, supplemented with observations on *Phocides polybius lilea* (Reakirt) and *Polythrix octomaculata* in Mexico.

**Key words** (not in title): egg, caterpillar, larva, pupa, leaf shelter, parasitoid, Mexico, guava.

## INTRODUCTION

In 1981, I started to publish a series of papers in *Living World* to document the butterfly family Hesperiidae in Trinidad (Cock 1981), which at that time was only documented with lists of recorded species (Kaye 1921, 1940; Barcant 1970). In 2013, the final, twentieth part was published in *Living World* (Cock 2013), “an integral part of the building of a knowledge base on the biodiversity of the country,” (Kenny 2007).

However, the classification used in the early parts, including the checklist (Cock 1982), is now out of date. Some names have changed and much new information and new records are available on biology and distribution. In a separate publication I have prepared a new checklist, including new records, which brings the total known species from Trinidad to 307 (Cock 2014).

An earlier paper (Cock 2008) described two life histories in the Pyrrhopygini (Pyrginae). Here, I document partial life histories of some Trinidad species of several genera in the subfamily Eudaminae (Warren *et al.* 2009), which were either unknown, or could not be illustrated in the earlier parts (Cock 1984, 1986).

Further papers will follow. I hope they will encourage *Field Naturalists* to seek out and document the early stages of other species, as yet unknown from the island. I recently published a full description of the methods that I used to rear and document skipper life-histories, which may provide useful advice as to how to go about this (Cock 2010).

### *Phocides polybius polybius* (Fabricius)

Figs. 1-6.

This species in Trinidad was treated in Cock (1984). Mielke (2004) follows Evans (1952) in recognising three subspecies: nominate *polybius* from Panama to the Guianas, ssp. *lilea* (Reakirt) from Central America, and ssp.

*phanias* (Burmeister) from southern Brazil to Argentina. The biology of ssp. *phanias* on guava (*Psidium guajava*; Myrtaceae) was documented more than 100 years ago (Jones 1882-3, as *Pyrrhopyga palemon* (Cramer), a synonym), and more recently by Moss (1949). Other reported food plants for *P. polybius phanias* include *Eucalyptus*, *Eugenia*, and *Myrciaria* spp. (all Myrtaceae) in Argentina and Brazil (Beccaloni *et al.* 2008).

The early stages of ssp. *polybius* on guava have been described from Trinidad (Cock 1984). It is not a difficult species to find as a caterpillar, although seldom seen as an adult. To supplement the earlier account which lacked illustrations, these are now provided for the shelters (Fig. 1), n-2 instar (Fig. 2), newly moulted final instar (Fig. 3), before it acquires the white body colouring (Fig. 4), pupa (Fig. 5) and living adult (Fig. 6). It has also been reared from *Myrcia tomentosa* (Myrtaceae) in Trinidad (S. Alston-Smith in Beccaloni *et al.* 2008).



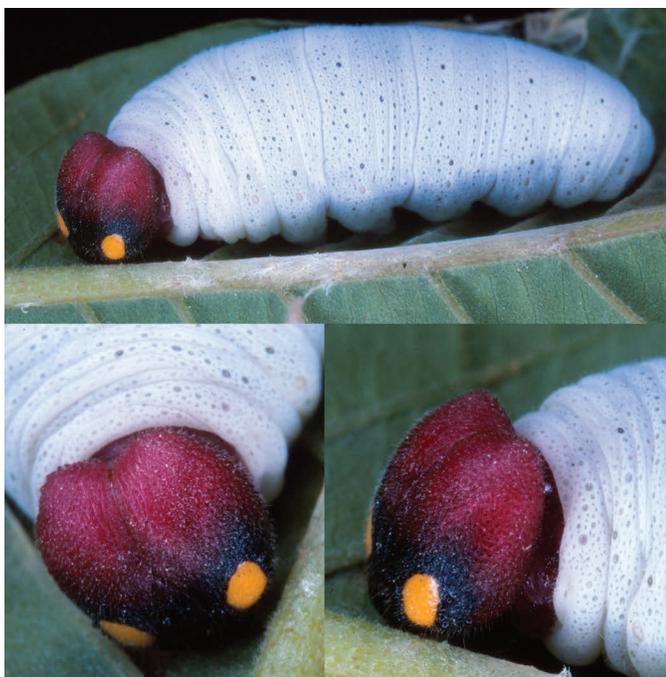
**Fig. 1.** Leaf shelters of *Phocides polybius polybius* on guava tree of 1m, St. Benedict's, 2 May, 1995; 95/8.



**Fig. 2.** Instar n-2 caterpillar of *Phocides polybius polybius* collected on guava, St. Benedict's, 12 October, 1993; 95/8.



**Fig. 3.** Newly moulted final instar caterpillar of *Phocides polybius polybius* collected on guava, St. Benedict's, 12 October, 1993; moulted and photographed 21 October, 1993; 95/8.



**Fig. 4.** Final instar caterpillar of *Phocides polybius polybius* collected on guava, St. Benedict's, 2 May, 1995; 95/8.



**Fig. 5.** Pupa of *Phocides polybius polybius* collected as caterpillar on guava, St. Benedict's, 12 October, 1993; pupated 14 November; photographed 16 November; emerged 7 December; 93/13.



**Fig. 6.** Adult *Phocides polybius polybius* collected as caterpillar on guava, St. Benedict's, 12 October, 1993; emerged 7 December; 93/13.

The early stages are very similar to those of the Central American ssp. *lilea* (which is sometimes referred to as *P. lilea*). Adults of the two subspecies are similar but ssp. *lilea* lacks the orange cilia at tornus hindwing of ssp. *polybius* (Fig. 6). Subspecies *lilea* has also been reported from guava (Comstock and Vázquez 1961; Kendall and McGuire 1975), and Janzen and Hallwachs (2013) have

reared it from at least eight species of *Eugenia*, *Psidium* and *Syzygium* (Myrtaceae) in Costa Rica, although the great majority were found on *P. guajava*. The author found caterpillars on *Terminalia catappa* (Combretaceae) in Mexico (Tapachula, Chiapas, 98/102) (Beccaloni *et al.* 2008). The early stages apart from the egg are comprehensively documented by Janzen and Hallwachs (2013) as *Phocides lilea*.

### ***Phocides pigmalion pigmalion* (Cramer)**

Mielke (2004) accepts six subspecies of *P. pigmalion*, including nominate *pigmalion* found from Guatemala to Ecuador and Trinidad, and ssp. *okeechobee* (Worthington) in Florida.

Stoll (1787-91) purportedly illustrates the caterpillar and pupa of this species, but his figures and description are of a Hesperinae, Calpodini, e.g. *Calpodes ethlius* (Stoll).

Red mangrove (*Rhizophora mangle*; Rhizophoraceae) is widely reported as the food plant, but most records refer to ssp. *okeechobee* in Florida (Dyar 1890; Minno *et al.* 2005; Wagner 2005); the caterpillars are similar to those of *P. polybius* (Figs. 2-4). Farnsworth and Ellison (1991) list *P. pigmalion pigmalion* as a common herbivore of red mangrove in Belize, and Ellison and Farnsworth (1996) report an outbreak there which reached densities of more than 7 per sapling in May-June 1993, leading to many saplings losing >50% of their leaf area, compared typically to about 10% due to all defoliators. Hernández *et al.* (1998) state that ssp. *batabano* (Lucas) in Cuba also feeds on red mangrove.

Janzen *et al.* (2011) and Janzen and Hallwachs (2013) indicate that at least two cryptic species occur under this name in Costa Rica, one feeding primarily on *Terminalia catappa* (Combretaceae) and Sapindaceae (*Melicoccus* and *Nephelium*) and the other primarily on *Trichospermum* spp. (Malvaceae).

When caterpillars resembling *P. polybius* were found on *T. catappa* in Trinidad (Maracas Bay, 22 March, 2003; 03/216), I expected them to be *P. polybius polybius*, having found *P. polybius lilea* on this species in Mexico (above), but S. Alston-Smith reared one out and it was *P. pigmalion pigmalion*. This is the only food plant record from Trinidad, but given that *T. catappa* is introduced, it seems likely that one or more related indigenous plants are also food plants. The penultimate and earlier instars of *P. pigmalion* are superficially similar in colour and markings to those of *Pyrrhopyge amyclas amyclas* (Cramer), which also feeds on *T. catappa* in Trinidad (Cock 2008), but the latter are conspicuously hairy, whereas those of *P. pigmalion* are smooth. The possibility of a second species breeding on red mangrove in Trinidad

merits investigation.

### ***Chioides catillus catillus* (Cramer)**

Figs. 7-11.

Although Evans (1952) recognised eight subspecies for *C. catillus*, several of these are now considered valid species, and Mielke (2004) lists only three subspecies: nominate *catillus* found throughout most of South America, *albius* Evans from Panama and Costa Rica, and *jethira* (Butler) from north Peru and Ecuador.

In Suriname, the early stages of *C. catillus* were first documented by Sepp (1843-7, pl. 90) as *Papilio longicauda*, a synonym (Mielke 2004), on what they refer to as a *Mimosa* sp., but their plate shows a species of Faboideae. Subsequently, Hayward (1927) described the caterpillar and pupa on *Rhynchosia senna* (Faboideae) in Argentina.

Cock (1986) briefly described the early stages on *Pueraria phaseoloides*, and it has since been recorded in Trinidad from *P. montana* (= *P. lobata*) (S. Alston-Smith in Beccaloni *et al.* 2008), *Galactia striata* and *Dioclea guianensis* (all Faboideae) (M.J.W. Cock in Beccaloni *et al.* 2008). Most food plant records are from Faboideae (*Calopogonium*, *Glycine*, *Phaseolus*, *Rhynchosia*, *Tephrosia*), but there are also records from Caesalpinoideae (*Senna*), Lamiaceae (*Hyptis*, *Monarda*, *Origanum*) and Asteraceae (*Lindheimera*) (Beccaloni *et al.* 2008).

Janzen and Hallwachs (2013) list nearly 600 rearings in Costa Rica, all from Fabaceae, including *Calopogonium*, *Centrosema*, *Dioclea*, *Eriosema*, *Galactia*, *Phaseolus*, *Rhynchosia* and *Teramnus*, of which *Rhynchosia* spp. and *Teramnus uncinatus* dominated. Since this massive rearing programme yielded no observations from Lamiaceae or Asteraceae, these records are likely to represent errors, misidentifications or cryptic species.

To supplement the information already provided in Cock (1986), figures are provided here of caterpillar instars 3, 4 and 5 (Figs. 7-9), the pupa (Fig. 10) and living adult (Fig. 11).



**Fig. 7.** Instar 3 caterpillar of *Chioides catillus*, collected on *Galactia striata*, Manzanilla Beach, 14 November, 1995; 13mm; 95/72.



**Fig. 8.** Instar 4 caterpillar of *Chioides catillus*, collected on *Galactia striata*, Manzanilla Beach, 14 November, 1995; 29mm; 95/71B.



**Fig. 9.** Instar 5 caterpillar of *Chioides catillus*, anterodorsolateral view of anterior portion; collected on *Galactia striata*, Manzanilla Beach, 14 November, 1995; moulted to final instar 14 November; photographed 19 November; pupated 30 November; 33mm; 95/71A.



**Fig. 10.** Pupa of *Chioides catillus*, lateral view; collected as instar 4 on *Galactia striata*, Manzanilla Beach, 14 November, 1995; pupated 30 November; photographed 3 December; adult 23 December; 21mm; 95/71A.

As can be seen at Janzen and Hallwachs (2013), and the author will document in a future contribution, some *Urbanus* spp. caterpillars are superficially similar to the earlier instars, but the final instar of *C. catillus* seems distinct in Trinidad.

The pupa is covered with a dense particulate layer of white waxy powder which, in Fig. 10, has been abraded on the wings by rubbing against the Y-shaped silk girdle.

This is one of the more frequently photographed skipper-poppers in Trinidad, due to the striking tails and fondness for flowers (Fig. 11).



**Fig. 11.** Adult *Chioides catillus* feeding at flowers of *Austro-eupatorium inulifolium*, Rio Claro-Guayaguayare Road, 11 October, 1993.

### *Typhedanus undulatus* (Hewitson)

Fig. 12.

Cock (1986) provided a brief description of the caterpillar of this species which he found on *Senna obtusifolia* (as *Cassia obtusifolia*). A figure of this caterpillar is now provided (Fig. 12). It seems to be a specialist on *Senna* spp. (Beccaloni *et al.* 2008).



**Fig. 12.** Final instar caterpillar of *Typhedanus undulatus*, anterior view of head and lateral view of body; collected on *Senna obtusifolia*, Piarco, 19 November, 1981; photographed 19 November; 20mm; 81/21C.

### *Polythrix auginus* (Hewitson)

Figs. 13-14.

Cock (1986) considered the life history of this species to be unknown. However, this overlooked that Moss

(1949) reported that he reared it from *Tanaecium pyramidatum* (as *Tabebuia pyramidatum*) (Bignoniaceae), although in a footnote W.H. Evans notes that Moss's series of *P. auginus* included some *P. caunus* (Herrich-Schäffer), which also feeds on Bignoniaceae (below). Since then, S. Alston-Smith (in Beccaloni *et al.* 2008) also reared this species from *T. pyramidatum* (as *Paragonia pyramidatum*) in Trinidad. Janzen and Hallwachs 2013 reared it from four genera of Bignoniaceae (*Anemopaegma*, *Fridericia* as *Arrabidaea*, *Lundia*, *Macfadyena*) in Costa Rica.

I reared this species from a field collected pupa, with associated signs of earlier stages of two individuals on *Fridericia patellifera* (MJWC273), Moruga East, 24 March, 2003 (03/221). The egg associated with the pupa was laid on the edge of the upper surface of a leaf used in the pupal shelter; it had 13 strong ribs. On an adjacent leaf, a hatched egg was partially eaten and had 12 strong ribs. Leaf shelter 1 associated with the second egg was almost quadrate in shape, cut from the leaf margin, 8 x 6mm. Shelter 2 was adjacent, also folded from the edge of the leaf, but the distal margin of the 20 x 10mm shelter had been irregularly eaten. This may have been due to caterpillar feeding before the shelter was made, but could have been done during shelter construction. The pupa was formed in a shelter made from two leaves, one on top of the other; it was attached upside down to the upper leaf by the cremaster and held with a Y-shaped silk girdle.

Unfortunately, the final instar cast skin and head capsule was dropped and lost as the pupa was collected, but the head was observed to be similar to that of *P. caunus* (Fig. 15), but plain brown. The pupa (Fig. 13) measured 23mm; frontal spike blunt, laterally flattened and slightly upturned; scattered similar, but less pronounced protuberances on head and thorax: one above the frontal spike, one each side of this but lower, two small ones at front of eye and two at the back; subdorsal on T1; two small ones at the base of the forewing, one on dorsum forewing, laterally on T2-3 above last, and one subdorsally on T3 at the highest point; abdomen wider at posterior margin of each segment than anterior margin of the following segment; ground colour grey-green white on head, thorax and appendages, bone white on abdomen; extensive brown markings including: heavier spot anterior to eye, two above each eye, spiracle T1, dorsal to spiracle T1, several spots on abdomen just above forewing dorsum, laterally on A5; basal part of antennae pale brown; scattered pale brown dots notably on head, anterior margin T1, dorsum T2-3, wings, posterior margin abdominal segments etc.; cremaster elongate, lateral margin ridged dorsally, apex black.



**Fig. 13.** Pupa of *Polythrix auginus*, collected on *Fridericia patellifera*, Moruga East, 24 March, 2003; 23mm; 03/221.



**Fig. 14.** Adult male *Polythrix auginus*, collected as pupa on *Fridericia patellifera*, Moruga East, 24 March, 2003; adult 3 April; 03/221.

### *Polythrix caunus* (Herrich-Schäffer)

Fig. 15.

Cock (1986) stated that the life history of this species was unknown. Since then, S. Alston-Smith (in Beccaloni *et al.* 2008) has reared this species from *Fridericia patellifera* (as *Arrabidaea patellifera*; Bignoniaceae) in Trinidad. Janzen and Hallwachs (2013) have reared it from several genera of Bignoniaceae of which the most frequent were *Fridericia* (as *Arrabidaea*) and *Cerato-phytum*.

Now that the early stages are known, we can see that *P. caunus* is the species that Moss (1949, Pl. IV, f. 5) illustrated as *P. asine*. However, his text makes it clear that the caterpillar of *asine* resembles that of *P. metallescens* and *P. octomaculata* (both treated below), so this is an error of association in Moss's material.



**Fig. 15.** Final instar caterpillar of *Polythrix caunus*, collected on *Tanaecium tetragonolobum* (MJWC217) on Mt. Tamana, 14 October, 1995; photographed 14 October; subsequently died; MJWC 95/55.

I found and documented a caterpillar on *Tanaecium tetragonolobum* (= *Ceratophytum tobagense*) (MJWC217) on Mt. Tamana, 14 October, 1995 (95/55), but was not able to rear it through. My identification of this individual as *P. caunus* is by comparison with Janzen and Hallwachs (2013). The final instar caterpillar (Fig. 15) measured 19mm and was found in a shelter formed between two partially overlapping leaves. Head chordate, broadly indented at vertex; shiny, slightly rugose, no obvious setae; light chestnut; small diffuse spot in middle of anterior-facing epicranium; small dark spot over stemmata. T1 light chestnut. Body smooth, no obvious setae; dorsally and laterally dull maroon, patterned with narrow yellow-white lines; dorsolateral line well marked. Dorsal to the dorsolateral line there are narrow transverse lines as follows: T2 and T3 on anterior margin and mid segment, with a mid-dorsal spot between the two lines; A1 anterior margin and near posterior margin; A2 anterior margin, near posterior margin and a partial narrow line on posterior margin, interrupted dorsally; A3-A7 behind anterior margin, near posterior margin, and a narrower

line on posterior margin; A8 anterior margin and posterior margin, the area adjacent to the margins slightly paler maroon. Below the dorsolateral line: A2-A7 a small triangle and three vertical lines posterior to this, the pattern breaking up T1-A1 and A8. Ground colour from just dorsal to ventrolateral flange to below it reddish brown, the flange paler. Legs T1 light chestnut; legs T2-T3 reddish brown; prolegs concolorous; gonads faintly visible.

### *Polythrix metallescens* (Mabille)

Figs. 16-17.

Moss (1949) found the caterpillars and pupae of this species similar in all respects to those of *P. asine* and found on the same food plants: *Pterocarpus santalinoides* (= *P. amazonicus*), *P. officinalis* (= *P. draco*) and *Lonchocarpus monilis* (= *Muellera moniliformis*), as well as on *Lonchocarpus* sp. and *Machaerium floribundum* (all Fabaceae, Faboideae).

S. Alston-Smith (in Beccaloni *et al.* 2008) reared this species from *Lonchocarpus heptaphyllus* (= *L. pentaphyllus*) and *Platymiscium trinitatis* (Fabaceae, Faboideae) in Trinidad.

I found a penultimate caterpillar on an unidentified sapling at Inness Field, 2 October, 1994 (94/52), which subsequently fed on *Lonchocarpus* sp. in captivity, but died in the final instar. This caterpillar closely resembles that of *P. kanshul* Shuey from Central America (Janzen and Hallwachs 2013). *P. kanshul* is most closely related to *P. metallescens*, so this caterpillar is likely to be that species. Janzen and Hallwachs (2013) have reared *P. kanshul* from several similar genera: *Dioclea*, *Erythrina*, *Lonchocarpus*, *Machaerium* and *Pterocarpus* (all Fabaceae, Faboideae).

The egg base remains associated with this caterpillar were found on the leaf upper surface, adjacent to the midrib. The shelter of the penultimate instar caterpillar was an irregular two-cut oval folded over upwards adjacent to the midrib of a mature leaf. The caterpillar measured 15mm two days before moulting to the final instar (Fig. 16); head rounded, chordate, semiprognathous; ground colour brown; posterior margin black, extending in a broad lateral stripe to mouthparts; anterior to this a narrow orange line, wider dorsally; just below vertex, an oval black spot on each epicranium, the basal 80% joined at the epicranial suture. T1 concolorous with body. Body dull, dark green, covered with a network of short, fine, white longitudinal lines; dorsal line narrowly clear; narrow, white dorsolateral line; spiracles pale, inconspicuous; all legs concolorous.



**Fig. 16.** Dorsolateral view of penultimate instar caterpillar of *Polythrix metallescens* collected and photographed on unidentified Faboideae, Inniss Field, 2 October, 1994; 94/52.

The final instar caterpillar was similar (Fig. 17), but no detailed description was prepared. The lateral stripe on the head is yellow-brown rather than orange, and the two spots dorsally on the face are separated at the epicranial suture, rather than joined.



**Fig. 17.** Dorsolateral view of final instar caterpillar of *Polythrix metallescens* collected on unidentified Faboideae, Inniss Field, 2 October, 1994; photographed 8 October; died in final instar; 94/52.

### *Polythrix octomaculata* (Sepp)

Figs. 18-22.

This species was treated as *P. octomaculata octomaculata* in Evans (1952) and Cock (1982, 1986), but this species is now considered monotypic and the former subspecies treated as synonyms (Mielke 2004).

Sepp (1843-7, pl 58) described this species from Suriname and illustrated the early stages which were found on *Pterocarpus indicus*. Moss (1949) illustrates a similar caterpillar which he also found on species of Faboideae near Belem, Brazil: *P. santalinoides* (= *P. amazonicus*), *P. officinalis* (= *P. draco*) and *Lonchocarpus monilis* (= *Muellera moniliformis*).

In Trinidad, S. Alston-Smith (in Beccaloni *et al.* 2008) reared this species from *Dalbergia ecastaphyllum* (Faboideae). Most of Janzen and Hallwachs' (2013) material was reared in Costa Rica from *Andira inermis* and *Acosmium panamense*, but they also reared it from seven other genera of Faboideae as well as *Ceiba pentandra* (Malvaceae) and *Karwinskia calderonii* (Rhamnaceae). Beccaloni *et al.* (2008) include further records from

Fabaceae (Faboideae, Caesalpinioideae), Bignoniaceae and Sapindaceae.

I have reared this species from Trinidad from a pupa collected on *Lonchocarpus benthamianus* (MJWC264) at Point Gourde, 22 March, 2003 (Fig. 18). The food plant was a young roadside tree that had been cut back and was regrowing. The remains of the egg and first larval shelter were associated. The egg was laid on the leaf upper surface and had 11 strong ribs, similar to that of *P. roma* (Fig. 23). The stage 1 shelter was a two-cut triangle from the edge of a leaf and hinged on a vein. The stage two shelter was not found. The stage 3 shelter was formed from two leaves, one on top of the other. The pupa (Fig. 18) was attached by its cremaster to a bar of silk across one leaf and supported by a Y-shaped silk girdle. It measured 20mm; the frontal spike was 1mm, blunt, widened at the base; tubercles on the anterior and dorsal aspects of the head and the eyes; abdomen segments wider at anterior and posterior margins; cremaster elongate. Ground colour white with small brown markings: a pair of spots each side just above and just below frontal spike, spiracle T1, a spot just dorsal to spiracle T1, a subdorsal spot on posterior margin of T1, spot on base of forewing, irregular markings on basal part of wing, on T3, A1 and A2 just posterior to dorsum of forewing, a conspicuous spot laterally on A5; tip of cremaster black.



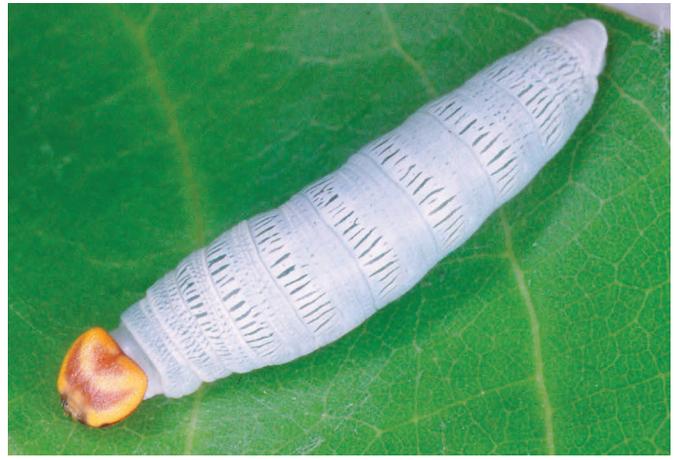
**Fig. 18.** Pupa of *Polythrix octomaculata* collected on *Lonchocarpus benthamianus*, Point Gourde, 22 March, 2003, 20mm; 03/205.



**Fig. 19.** Adult male of *Polythrix octomaculata* collected as pupa on *Lonchocarpus benthamianus*, Point Gourde, 22 March, 2003; adult 26 March, 2003; 03/205.

I have not seen the caterpillar from Trinidad, but have found caterpillars near Tapachula, Mexico on an unidentified Faboideae (3 April, 1998; 98/106). The Central American population of *P. octomaculatus* was treated as subsp. *alciphron* (Godman and Salvin) (Evans 1952) but as noted above, the species is now considered monotypic. The Mexican caterpillar matched those illustrated by Sepp (1843-7) and Moss (1949), and therefore provides a good indication of what the caterpillar in Trinidad should look like. Instar n-3 measured 7mm about mid-way through the instar; head brown with a dark posterior margin, and an indistinct black patch on face below vertex. Instar n-2 measured 14mm a day before moulting; head flattened dorsally, only slightly indent at vertex; shiny, rugose; brown with a weakly differentiated, diffuse black rectangle on face below vertex; T1 as body; body dull translucent pale green; dorsally and laterally a series of longitudinal, irregular, pale lines on anterior part of A2-A7; small irregular dots on T1 and A1, and posterior half of A2-A9; legs concolorous; spiracles pale, inconspicuous. Penultimate instar photographed (Fig. 20), but not described.

The final instar (Fig. 21) was similar to the penultimate instar, although the head markings are paler. Head flattened dorsally; slightly, but broadly indent at vertex; colour dark yellow with pink-brown markings: an arc across face (concave side up), the ends reaching to just below apices, and the central area across clypeus (which is yellow centrally), an oval area above this arc below vertex, and the posterior margin of the head; black spot around the stemmata. Body white; T1-T3 and A8-A9 uniform, unmarked; anterior half of A1-A7 with a band of about 20 longitudinal slightly darker lines, some of which bifurcate anteriorly or posteriorly; posterior half of A1-A7 with shallow transverse ridges. Spiracles



**Fig. 20.** Penultimate instar caterpillar of *Polythrix octomaculata* collected on unidentified Faboideae, Tapachula, Mexico, 3 April, 1998; photographed 6 April; moulted 8 April; 25mm; 98/106A.



**Fig. 21.** Final instar caterpillar of *Polythrix octomaculata* collected on unidentified Faboideae, Tapachula, Mexico, 3 April, 1998; moulted 8 April; photographed 9 April; pupated 28 April; 26mm; 98/106A.

paler, inconspicuous; legs, prolegs and venter with a green tinge; anal plate slightly pointed posteriorly with a brighter white margin.

The female pupa from Mexico (Fig. 22) was similar to the male pupa from Trinidad (Fig. 18) but noticeably more heavily and extensively marked in darker brown. More material would be needed to assess the significance of the colour differences.

### *Polythrix roma* Evans

Figs. 23-27.

Moss (1949) treated this species as *P. asine* (Hewitson), which is a very similar Central American species. Near Belem, he reared it from the same food plants as *P. octomaculata*: i.e. the Fabaceae, Faboideae, *Pterocarpus santalinoides*, *P. officinalis* and *Lonchocarpus monilis*. In Trinidad, this species has also been reared from three other Faboideae: *Coursetia ferruginea* (M.J.W. Cock in Beccaloni *et al.* 2008), *Dalbergia ecastaphyllum* and *L. punctatus* (S. Alston-Smith in Beccaloni *et al.* 2008).



**Fig. 22.** Female pupa of *Polythrix octomaculata* collected as caterpillar on unidentified Faboideae, Tapachula, Mexico, 3 April, 1998; pupated 28 April; photographed 2 May; emerged 11 May; 24mm; 98/106A.

The following observations are based on material the author collected on *C. ferruginea* (93/24, 94/21, 95/4, and 96/1, although only the last of these was successfully reared through).

The eggs (Fig. 23) are laid on the upper surface of a leaflet, near the midrib; as tall as wide, top flattened, with micropyle slightly indent; 12-13 strong narrow ribs, with a connecting bar at the edge of the flattened top; contents reddish through translucent egg, contrasting with the pale ribs.



**Fig. 23.** Egg of *Polythrix roma* collected on *Coursetia ferruginea*, behind St. Benedict's, 15 October, 1993; photographed 21 October; 93/24E.



**Fig. 24.** Final instar caterpillar of *Polythrix roma* collected on *Coursetia ferruginea*, behind St. Benedict's, 3 July, 1996; photographed 10 July; pupated 15 July; 26mm; 96/1.



**Fig. 25.** Final instar caterpillar of *Polythrix roma* dorsolateral view of anterior portion; collected on *Coursetia ferruginea*, behind St. Benedict's, 13 October, 1993; photographed 13 October; died; 25mm; 93/24A.

Leaf shelter 1 was made on a single leaflet, normally the same leaflet on which the egg is laid, by making an oval two-cut flap which is folded over upwards; feeding was noted in an irregular patch from the edge of the leaf margin, basal to the shelter (93/24B). Larger caterpillars make a shelter between two leaves (93/24A).

The earliest instars have a plain brown head. The following description of the final instar caterpillar is based on individual 93/24A which died (Fig. 25), but seemed identical to individual 91/6 from the same food plant and locality which was reared through (Fig. 24). The caterpillar measured 25mm when described but grew to 31mm; head flattened dorsally, the vertex widely and shallowly indent; semiprognathous; ground colour pale green-brown; face with a narrow yellow-orange rim, except at vertex and mouthparts; a thin black line posterior to this, but separated by a gap of comparable width of ground colour. T1 concolorous with body. Body transparent and shiny; dark green internal colouring visible;

cuticle covered with very fine, short white longitudinal lines, less dense along dorsal line and increasing heavy laterally; small orange spot laterally near anterior margin of A1-A8, joined by a slightly heavier white line com-



**Fig. 26.** Pupa of *Polythrix roma*, dorsolateral view; collected as final instar caterpillar on *Coursetia ferruginea*, behind St. Benedict's, 3 July, 1996; pupated 15 July; photographed 18 July; adult 30 July; 20mm; 96/1.



**Fig. 27.** Adult male *Polythrix roma* collected as final instar caterpillar on *Coursetia ferruginea*, behind St. Benedict's, 3 July, 1996; adult 30 July; 96/1.

pared to rest of body. All legs concolorous; developing gonads small and pale, near posterior margin A5.

The pupa of 91/6 measured 20mm; short, stout frontal spike; head covered with scattered tubercles except down centre of eye; ground colour blue-green, abdomen white-green; scattered small brown dots with larger speckles laterally on anterior margin T2, and on front of head.

Small caterpillars are probably parasitised by an unidentified species of euplectrine wasp. In March, 2003, two stage 1 leaf shelters were found on *C. ferruginea* at Point Gourde, with caterpillars remains which appeared to be this species, and a single euplectrine pupa (03/208D, E).

### ***Polythrix* discussion**

The caterpillars of *Polythrix auginus* and *P. caunus* are very different from those of the other *Polythrix* spp. treated here. Similarly, the food plants are Bignoniaceae for *P. auginus* and *P. caunus*, and Fabaceae, Faboideae for the other species. Burns (1996) is surely correct, when he suggests that *P. auginus* and *P. caunus* belong in a separate genus.

### **ACKNOWLEDGEMENTS**

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# The Herpetofauna of Southeast Trinidad, Trinidad and Tobago

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## ABSTRACT

The Rio Claro-Mayaro area of southeast Trinidad contains a variety of lowland habitats. Because access to much of the area is restricted, its herpetofauna has been poorly explored, resulting in few publications on its herpetofauna. Reported here are results of fieldwork conducted in the Rio Claro-Mayaro area between November 2009 and April 2014. Documented here is the presence in southeast Trinidad of 77 of the 106 known (excluding questionable) species that inhabit the island. Included are records from published literature, our own fieldwork, and museum specimens.

## INTRODUCTION

Herpetofauna (particularly anurans) are good indicators of ecosystem health and diversity. They serve as both predators and prey for a large number of other organisms. They can contribute as much as one tenth of the total faunal biomass and have importance in the transference of energy within food webs (Cushman 2006).

Trinidad's herpetofauna is largely derived from South America (Kenny 1969; Williams 1989; Murphy 1997). Murphy (1997) categorised Trinidad's herpetofauna into seven major distribution categories: widespread taxa extending from Trinidad into Middle or North America; Amazonian taxa; Caribbean coastal range taxa (associated with a montane complex that extends from the Santa Marta region of Colombia across northern Venezuela and Trinidad); lowland Guiana endemic species (at elevations below 1000m on the Guiana Shield and on Trinidad); Orinoco Basin taxa; Lesser Antillean taxa; and Cosmopolitan taxa with distributions extending to the other hemisphere. Taxa from each of these categories have been found in the southeast portion of Trinidad.

The Rio Claro-Mayaro area of southeast Trinidad contains a variety of lowland habitats. Because access to much of the area is restricted, its herpetofauna has been poorly explored, resulting in few publications on its herpetofauna. The area is prone to continual colonising events from the Orinoco River delta (Charles 2013).

## MATERIALS AND METHODS

Our most intensive and structured surveys were conducted during 30 days in November 2009 and 30 days in April 2010. Both wet and dry season conditions were

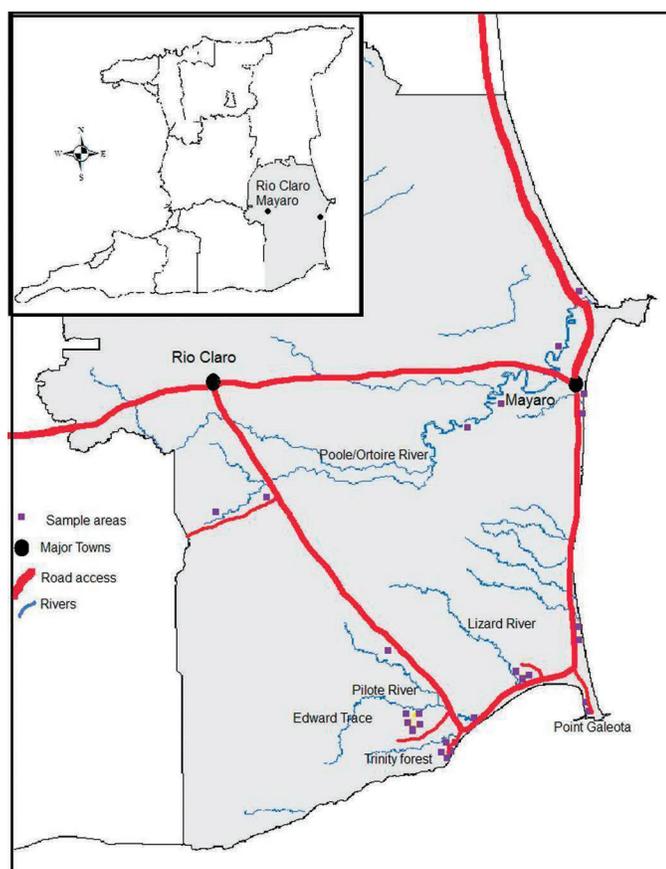
experienced during the sampling periods. We revisited some sites for three days in late September 2013. In April 2014, we made observations along Cedar Grove Road.

Standard visual encounter surveys (Heyer *et al.* 1994) were used for monitoring reptiles. Visual searching was conducted along transects and trails throughout the sample area. Ponds and streams were sampled by use of seines and dip nets. Live specimens were collected, photographed, and released. Hunters' trails were used as sampling transects and to locate sampling points. Sampling was conducted systematically at: morning 0430 to 0900 h, daytime 0900 to 1600 h, sunset 1600 to 1930 h, and nighttime 1900 to 2330 h. Early mornings, sunset, and nighttime searches were most productive for monitoring snakes; daytime, especially sunny days, was most productive for monitoring lizards and turtles. Anurans were monitored by use of audio strip transect and audio point counts (Manickchan 2004; Heyer *et al.* 1994). Occasionally recordings were made on site and later compared to a database of the calls of Trinidad frogs to confirm identifications. Anurans were monitored during sunset and nighttime hours. Audio identifications were made along trails and transect lines. Visual encounters were often for too short a period for photographs to be taken, but GPS locations of sightings were recorded and photographs taken when possible.

The study area included several core areas (Figure 1):

- along Trinity Road,
- Guayaguayare, along the coast, towards the Trinity Hills,
- along the St. Hilaire River,
- at the pond at the end of Trinity Road,

- north of the pond at the north end of Trinity Road,
- along Edward Trace,
- Guayaguayare and northward into the forest towards Pilote River,
- along the Mayaro-Guayaguayare Road towards Manzanilla,
- along the Mayaro-Guayaguayare Road in the vicinity of Baywatch Boulevard,
- Point Galeota mangroves,
- Lizard River wetlands,
- Rio Claro-Guayaguayare Road,
- banks of the Ortoire River along Cedar Grove Road.



**Fig. 1.** Map showing the Rio Claro-Mayaro Municipality (inset) and the sample areas within the region.

Incidental sampling of herpetofauna was conducted at the Lizard River wetlands during daylight hours over a one-year period for two consecutive days at three-month intervals. Incidental sightings were recorded for the Rio Claro Forest (2008 to 2012), Point Galeota (2009 to 2013), and Trinity Hills Wildlife Sanctuary (July 2008). Additionally, a short period of drift fence-pitfall trap sampling was conducted 15-21 August, 2010 near the beach edge of a small coconut (*Cocos nucifera*) plantation near Baywatch Boulevard along the Mayaro-Guayaguayare Road in Mayaro Bay. One straight 10m long, 0.5m high

drift fence equipped with four 5-gallon (18.9-litre) plastic bucket pitfalls was installed in the plantation parallel to and about 7m from the beach. Traps were checked four times per day during daylight hours. Some incidental observations also were made in two nearby areas along the Mayaro-Guayaguayare Road; a very small area of second-growth forest surrounding a small stream near Baywatch Boulevard, and the roadside grass about 600m south of Baywatch Boulevard.

In addition to field survey results, museum records were examined by use of Herpnet (Spencer 2013) and Vertnet (Bloom 2013), by onsite visits to museums, and by examination of specimens borrowed from collections. Some of the specimens were examined by the authors; in other instances we relied on the collector, museum curators, and other authors for identification (i.e. the specimens had been reported in published systematic or taxonomic reviews). Habitats at collection or observation locations were then classified as swamp forest, seasonal evergreen, littoral woodland, forest edge, and palm forest (categories modified from Beard 1946).

## RESULTS AND DISCUSSION

Results from field surveys and museum records are summarised in Table 1. We documented 23 anurans in 17 genera and ten families, one crocodylian species, six species of chelonians in six genera and five families, 19 species of saurians in 15 genera and ten families, and 28 serpents in 20 genera and six families, for a total of 77 species. Murphy (1997) listed 106 species of amphibians and reptiles from Trinidad (excluding questionable records). Our survey documented that 72.6% of the total number of species present on Trinidad were present in the southeast portion of the island.

The species represented on this list are primarily habitat generalists, lowland forest species, or savanna species. The one unexpected species discovered during our survey was the Trinidad stream frog, *Mannophryne trinitatis*. Previously this species was considered to be restricted to the Northern and Central Ranges (Kenny 1969; Murphy 1997; Jowers *et al.* 2011). To our knowledge this is the first record of *Mannophryne* from the Southern Range.

Kenny (1969) considered the highly aquatic frog *Pipa pipa* to be common in Nariva Swamp and also to be present in Rio Claro, Mayaro, and Cedros. One of us (JCM) observed them on the Icos peninsula in the 1980s, but the record presented here is based on a specimen collected in 1947 as well as on the Aitken *et al.* (1973) report from Bush Bush, which was documented with a Trinidad Regional Virus Lab (TRVL) specimen. Two individuals were found in 1990 in the Bush Bush area (G. White, per-

Table.

TAXA/SPECIES	VOUCHER/OBSERVER	LOCATION	HABITAT
<b>AMPHIBIANS</b>			
<b>Family Bufonidae - True Toads</b>			
<i>Rhinella marina</i>	JCM, RSM	Trinity Pond, Bush Bush	Forest edge, littoral woodland
<b>Family Hemiphractidae - Marsupial Frogs</b>			
<i>Flectonotus fitzgeraldi</i>	SAM	Edward Trace	Littoral woodland, swamp forest
<b>Family Hylidae</b>			
<i>Dendropsophus microcephalus misera</i>	CAS 245080-83, SAM	Rio Claro-Mayaro Corp., Trinity Road, Edward Trace	Littoral woodland, swamp forest
<i>Dendropsophus minutus</i>	SAM	Edward Trace	Pond edge
<i>Hypsiboas boans</i>	CAS 245077, RSM	Rio Claro-Mayaro Corp., Trinity Road, Edward Trace	Littoral woodland, swamp forest
<i>Hypsiboas geographicus</i>	Photo	Trinity Pond, Edward Trace	Littoral woodland, swamp forest
<i>Hypsiboas punctatus</i>	CAS 245078	Rio Claro-Mayaro Municipality, Edward Trace	Littoral woodland, swamp forest, seasonal evergreen
<i>Phyllomedusa trinitatis</i>	Kenny 1969, SAM	Mayaro, Edward Trace	Littoral woodland, swamp forest
<i>Pseudis paradoxa caribensis</i>	USNM 306120	Nariva Swamp, on Manzanilla-Mayaro Road near milepost 45.5, 0.15 km S of Bailey bridge over Nariva River, 15.0 km S of junction with Eastern Main Road, Bush Bush	Swamp forest
<i>Scarthyla vigilans</i>	Vic. Trinity Pond (JCM)		Pond edge
<i>Scinax ruber (Laurenti)</i>	USNM 306115, RSM	Nariva Swamp, on Manzanilla-Mayaro Road, near milepost 45.5, 0.15 km S of Bailey bridge over Nariva River, 15.0 km S of junction with Eastern Main Road	Littoral woodland, swamp forest
<i>Sphaenorhynchus lacteus</i>	JCM, SAM	Trinity Pond, Edward Trace, Bush Bush	Pond edge, swamp forest
<i>Trachycephalus typhonius</i>	Photos, JCM	Trinity Pond, Bush Bush	Pond edge
<b>Family Aromobatidae</b>			
<i>Mannophryne trinitatis</i>	SAM	Trinity Pond, Edward Trace	Pond edge
<b>Family Leiuperidae</b>			
<i>Engystomops pustulosus</i>	SAM	Trinity Hills, Edward Trace	Seasonal evergreen
<b>Family Craugastoridae</b>			
<i>Pristimantis urichi</i>	SAM	Edward Trace	Seasonal evergreen
<b>Family Leptodactylidae</b>			
<i>Leptodactylus fuscus</i>	USNM 166621, RSM, SAM	Manzanilla-Mayaro Road, near milepost 44, Trinity Road, Edward Trace	Seasonal evergreen
<i>Leptodactylus insularum</i>			
<i>Leptodactylus validus</i>	MCZ A-11777	Mayaro, Edward Trace	Seasonal evergreen
<b>Family Microhylidae</b>			
<i>Elachistocleis ovalis</i>	TRVL 68	Aitken <i>et al.</i> 1973	
<i>Elachistocleis surinamensis</i>	Mayaro Forest ROM 9746, 9752, SAM	Kenny 1969, Mayaro, Maloney Road, Guayaguayare Road, Edward Trace	Seasonal evergreen
<b>Family Pipidae</b>			
<i>Pipa pipa</i>	FMNH 49601, TRVL 36	Mayaro, Bush Bush	Swamp evergreen
<b>Family Ranidae</b>			
<i>Lithobates palmipes</i>	FMNH 49773, SAM, GW and SA (2009)	Mayaro, Edward Trace	Seasonal evergreen

TAXA/SPECIES	VOUCHER/OBSERVER	LOCATION	HABITAT
<b>TURTLES</b>			
<b>Family Cheloniidae</b>			
<i>Chelonia mydas</i>	RSM	Guayaguayare Bay	Coastal near shore, open water
<i>Eretmochelys imbricata</i>	RSM	Guayaguayare Bay	Coastal near shore, open water
<b>Family Chelidae</b>			
<i>Mesoclemmys gibba</i>	TRVL 301	Bush Bush	Swamp forest
<b>Family Dermochelyidae</b>			
<i>Dermochelys coriacea</i>	Photos, RSM	Mayaro, Trinity Road	Coastal near shore, open water
<b>Family Geoemydidae</b>			
<i>Rhinoclemmys punctularia</i>	USNM 166103, RSM	Rio Claro, Edward Trace, Poole River	Seasonal evergreen, swamp forest, rivers
<b>Family Kinosternidae</b>			
<i>Kinosternon scorpioides</i>	RSM	Rio Claro, St. Hilaire River, Edward Trace, Poole River	Seasonal evergreen, swamp forest, rivers
<b>Family Testudinidae</b>			
<i>Chelonoidis denticulata</i>	RSM, TRVL 301	Rio Claro, Trinity Forest, Edward Trace, Bush Bush, Cedar Grove Road	Littoral woodland, seasonal evergreen, swamp forest
<b>CROCODILIAN</b>			
<b>Family Alligatoridae</b>			
<i>Caiman crocodilus</i>	RSM, TRVL 422	Rio Claro, Mayaro, Trinity Road, Edward Trace, Manzanilla, Bush Bush, Ortoire River, Poole River	Swamp forest, estuary, rivers
<b>LIZARDS</b>			
<b>Family Amphisbaenidae</b>			
<i>Amphisbaena fuliginosa</i>	RSM, TRVL 314	Rio Claro, Trinity Road, Bush Bush	Seasonal evergreen, swamp forest
<i>Amphisbaena alba</i>	GW	Edward Trace	Seasonal forest
<b>Family Gekkonidae</b>			
<i>Hemidactylus mabouia</i>	UWIZM.2012.1.2	Mayaro, Trinity Road, Edward Trace, Cedar Grove Road	Seasonal evergreen
<b>Family Phyllodactylidae</b>			
<i>Thecadactylus rapicauda</i>	SAM, TRVL 438	Trinity Road forest, Bush Bush	Seasonal evergreen
<b>Family Sphaerodactylidae</b>			
<i>Gonatodes ceciliae</i>	SPC	Trinity Hills Wildlife Sanctuary forest	Seasonal evergreen
<i>Gonatodes humeralis</i>	SPC, TRVL 377	Trinity Hills Wildlife Sanctuary forest, Mayaro-Guayaguayare Road, Bush Bush	Seasonal evergreen, second-growth forest edge
<i>Gonatodes vittatus</i>	USNM 166164	Mayaro-Guayaguayare Road, near milepost 5, Edward Trace, Cedar Grove Road	Seasonal evergreen
<i>Sphaerodactylus molei</i>	SAM	Trinity Road, Edwards Trace	Littoral woodland, palm forest
<b>Family Gymnophthalmidae</b>			
<i>Gymnophthalmus underwoodi</i>	RSM, SAM	Trinity Forest, Edward Trace	Littoral woodland
<b>Family Hoplocercidae</b>			
<i>Polychrus marmoratus</i>	TRVL 378	Bush Bush, Cedar Grove Road	Swamp forest
<b>Family Iguanidae</b>			
<i>Iguana iguana</i>	Photo, RSM, TRVL 380	Guayaguayare Forest, Point Galeota, Edward Trace, Trinity Road, Bush Bush, Cedar Grove Road, Ortoire River banks	Littoral woodland, swamp forest

TAXA/SPECIES	VOUCHER/OBSERVER	LOCATION	HABITAT
<b>LIZARDS</b>			
<b>Family Dactyloidae</b>			
<i>Anolis planiceps</i>	Photo, RSM, SAM, TRVL 181	Guayaguayare, Trinity Forest, Edward Trace, Bush Bush, Cedar Grove Road	Littoral woodland, palm forest, swamp forest
<b>Family Scincidae</b>			
<i>Copeoglossum aurae</i>	RSM, SAM	Trinity Forest, Edward Trace	Littoral woodland
<i>Marisora aurulae</i>	SPC	Mayaro Bay (near Baywatch Boulevard)	Coastal coconut plantation
<b>Family Teiidae</b>			
<i>Ameiva atrigularis</i>	JCM, RSM, TRVL 180	Point Galeota, Edward Trace, Bush Bush, Cedar Grove Road	Littoral woodland, swamp forest edge
<i>Cnemidophorus lemniscatus</i>	MCZ R- 39685-88	Guayaguayare Bay and main road, Bush Bush	Forest edge
<i>Kentropyx striata</i>	RSM	Point Galeota, Guayaguayare Road	Forest edge
<i>Tupinambis teguixin</i>	UWI skin, RSM, TRVL 227	Guayaguayare Road, Edward Trace, Bush Bush, Cedar Grove Road, Point Galeota	Forest edge, littoral woodland
<b>Family Tropiduridae</b>			
<i>Plica caribaeana</i>	AMNH 72816-17; TRVL 221	Mayaro, Bush Bush	Forest edge, littoral woodland, swamp forest
<b>SNAKES</b>			
<b>Family Leptotyphlopidae</b>			
<i>Epictia tenella</i>	MCZ R-60801, TRVL 399	Parrylands, Trintoc Well no. 32A, Bush Bush	Forest edge, littoral woodland
<b>Family Boidae</b>			
<i>Boa constrictor</i>	DOR, RSM	Trinity Road, Guayaguayare, Manzanilla, Ortoire River, Cedar Grove Road	Forest edge, littoral woodland
<i>Corallus ruschenbergerii</i>	SAM, JCM, RSM	Trinity Road, Guayaguayare, Manzanilla, Bush Bush, Ortoire River	Forest edge, littoral woodland, swamp forest, palm forest
<i>Epicrates maurus</i>	Photos	Edward Trace, Trinity Road, Mayaro, Rio Claro, Cedar Grove Road	Forest edge, littoral woodland, palm forest
<i>Eunectes murinus</i>	SPC, RSM, Aitken <i>et al.</i> 1973	Guayaguayare, Manzanilla, Bush Bush, Ortoire River	Swamp forest
<b>Family Colubridae</b>			
<i>Chironius carinatus</i>	RSM, Aitken <i>et al.</i> 1973	Guayaguayare, Trinity Road, Edward Trace, Bush Bush	Forest edge, littoral woodland, seasonal evergreen
<i>Leptophis coeruleodorsus</i>	MCZ R-79815	12 km south of Mayaro on Guayaguayare Road	
<i>Mastigodryas boddaerti</i>	USNM 166685	Manzanilla-Mayaro Road, near milepost 41.75, Edward Trace	Forest edge
<i>Oxybelis aeneus</i>	DOR/UWI, RSM, SAM	Guayaguayare Road	Forest edge, littoral woodland, seasonal evergreen
<i>Spilotes pullatus</i>	MSUM SH.470	Mayaro, Edward Trace	Forest edge, littoral woodland, seasonal evergreen
<i>Tantilla melanocephala</i>	SPC	Mayaro Bay (near Baywatch Boulevard)	Coastal coconut plantation
<i>Pseudoboia newwedii</i>	GW	Edward Trace	Forest edge
<b>Family Dipsadidae</b>			
<i>Clelia clelia</i>	FMNH 49968	Mayaro	Forest edge, littoral woodland, seasonal evergreen
<i>Dipsas trinitatis</i>	MVZ 84058	Queen's Beach Hotel, Mayaro Beach	Forest edge, littoral woodland, seasonal evergreen
<i>Erythrolamprus melanotus nesos</i>	MCZ R-60809	Guayaguayare Forest	

TAXA/SPECIES	VOUCHER/OBSERVER	LOCATION	HABITAT
<b>SNAKES</b>			
<i>Erythrolamprus cobella</i>	UWIZM.2010.12.99, TRVL 340	Nariva Swamp, Bush Bush	Swamp forest
<i>Erythrolamprus cf. zweifeli</i>	UWIZM.2010.12.108	Mayaro	
<i>Helicops angulatus</i>	USNM 166686, RSM	Manzanilla-Mayaro Road, Lizard River mangrove swamp, Bush Bush	Swamp forest
<i>Imantodes cenchoa</i>	TRVL 340	Bush Bush	Swamp forest
<i>Leptodeira annulata</i>	SPC	Mayaro-Guayaguayare Road (600m south of Baywatch Boulevard)	Roadside edge of anthropogenic savanna
<i>Mastigodryas boddaerti</i>	TRVL 179	Bush Bush	Swamp forest
<i>Oxybelis aeneus</i>	TRVL 376	Bush Bush	Swamp forest
<i>Oxyrhopus petolaris</i>	FMNH 49986	Mayaro	
<i>Siphlophis compressus</i>	TRVL 434	Bush Bush	Swamp forest
<b>Family Elapidae</b>			
<i>Micrurus circinalis</i>	AMNH 101304	Mayaro	
<i>Micrurus lemniscatus diutius</i>	Photo, SAM	Trinity Forest	Seasonal evergreen
<b>Family Viperidae</b>			
<i>Bothrops</i> sp.	Photo, TRVL 424	Rio Claro, Edward Trace, Trinity Road, Bush Bush, Rio Cla- ro-Guayaguayare Road	Seasonal evergreen
<i>Lachesis muta</i>	RSM	Guayaguayare Forest	Seasonal evergreen

sonal communication). The lack of recent observations of *Pipa pipa* is of potential concern. That having been said, this highly aquatic, bottom-dwelling frog can be highly cryptic in the habitats it uses and thus might have been overlooked.

Two of the ponds we sampled were less than 100m from the beach. Salinity levels measured during the 2009 sampling indicated 0.1 ppt (freshwater) and the other 6.8 ppt (brackish). During the dry season sampling period in 2010, the ponds were dry and were covered with thick, short vegetation. During the wet season of 2013 the freshwater pond contained choruses and newly metamorphosed froglets of *Rhinella marina*, *Dendropsophus microcephalus*, *D. minutus*, *Trachycephalus typhonius*, and *Sphaenorhynchus lacteus*. The brackish water pond had choruses of *Rhinella marina*, *Scinax ruber*, and *Scarthyla vigilans*. All three of these species had been previously reported to use brackish water (Barrios-Amoros *et al.* 2006; Rios-Lopez 2008). The presence of the banded water snake, *Helicops angulatus*, in the Lizard River mangroves further documents the use of brackish water habitats by this species.

In the freshwater pond, tadpoles and new metamorphs of *Trachycephalus typhonius* and other species were exceptionally dense in areas with thick submergent and emergent vegetation. In these areas we observed spiders of the genus *Dolomedes* sitting on the water's surface,

hunting for tadpoles (Figure 2). Menin *et al.* (2005) summarised spider predation on Neotropical frogs and their larvae, but no direct predation on tadpoles by spiders was observed during our survey. Both species discussed are included here.



**Fig. 2.** Metamorphosing *Trachycephalus typhonius* and their predator, a fishing spider, *Dolomedes* sp. Photo: JCM.

Unfortunately, the three species of marine turtles (*Derموchelys coriacea*, *Eretmochelys imbricata*, and *Chelonia mydas*) observed were caught in fishermen's nets set in Guayaguayare Bay during the 2009 surveys. A live female *D. coriacea* was seen nesting on the south Mayaro Beach during 2010, and the carcass of another

was seen on the Trinity Road coast in 2009. *Chelonia mydas* was observed, possibly feeding, in the sea grass beds in the shallows of Guayaguayare Bay.



**Fig. 3.** The yellow-footed tortoise, *Chelonoidis denticulata*, feeding on fruits of the *Spondias mombin* tree. Photo: RSM.

The yellow-footed tortoises, *C. denticulata*, observed in the Guayaguayare region were associated with the tree *Spondias mombin* (Anacardiaceae), feeding on fallen fruit (Figure 3). In one case the same individual was observed for five consecutive days feeding at the same tree at the Edward Trace site. Larger specimens were also noted at other fruiting *S. mombin* trees in the Trinity Forest. Two local guides suggested that these tortoises repeatedly visited the trees over the course of the year, possibly implying a restricted range based on food preference. Janzen (1986) found a very high percentage of seed predation (95%) on this tree in Costa Rica. He noted the failure of many seeds to disperse away from the parent tree because of the absence of a herbivorous (frugivorous) megafauna that would have been part of the tree's habitat through most of its evolutionary history. However, Moll and Jansen (1986) and Guzman and Stevenson (2008) reported that this fruit is eaten by *Geochelone denticulata*, *Rhinoclemmys funerea* and *R. annulata*, all of which act as seed dispersal agents for *Spondias mombin*.

Both *Rhinoclemmys punctularia* and *Kinosternon scorpioides* were recorded during river seining at Trinity Forest, Edward Trace Forest, and in smaller tributaries of the Lizard River drainage. During the drought of 2010, *R. punctularia* was observed walking along the forest floor, possibly searching for pools in the Trinity and Edward Trace regions. During heavy rainfall in the 2009 sampling period, both species were observed crossing Edward Trace, moving from flooded swamp forest to higher ground.

*Mesoclemmys gibba* is Trinidad's most aquatic freshwater chelonian. Although rivers and their tributaries were seined extensively at ten sites (both Edward and Trinity during both the 2009 and 2010 surveys), none

was found. Furthermore, none of the accompanying field guide personnel described *Mesoclemmys gibba* when asked about its occurrence in the area. Possibly the species was absent because of the ephemeral nature of the water bodies in the area. Two populations of these turtles are known to occur in the north-central and southwest portions of the island (Mohammed *et al.* 2010) between which there are no connecting drainages. If it is present within the study area, it must be the rarest of the freshwater species of turtles.

The absence of introduced *Anolis* (*A. aeneus*, *A. trinitatis*) species was also somewhat unexpected but may reflect the short time that was spent sampling urban habitats. However, the house gecko, *Hemidactylus mabouia*, and the streak lizard, *Gonatodes vittatus*, both were observed during the survey transects; both thrive in human-modified environments. Most of the other lizards in Trinidad are primarily forest dwellers. During our survey, *Gonatodes ceciliae* was discovered for the first time in the Southern Range (Trinity Hills Wildlife Sanctuary). It was previously reported only from the highlands of Venezuela's Paria Peninsula and from Trinidad, in the Northern Range (including some of the geologically associated satellite islands) and in the Central Range (Murphy 1997). Another discovery was of a single specimen of *Marisora aurulae*, which was caught in a pitfall trap in a coconut plantation at Mayaro Bay. This species has only recently been described and is presumed to be rare, as it seems to have been extirpated from much of its range outside of Trinidad and Tobago; most likely it had not been collected in Trinidad since 1967 (Hedges and Conn 2012). Very little is known about the ecology of *M. aurulae*; our observation demonstrated that it at least sometimes actively forages in the leaf litter of anthropogenically modified coastal habitats. It was not possible for us to determine whether other species of skinks observed in the same plantation were this species or the more expected *Copeoglossum aurulae*.

The snakes found during our survey again were mostly habitat generalists, with a few aquatic and semi-aquatic species (*Eunectes murinus*, *Helicops angulatus*, and *Erythrolamprus cobella*). Anecdotal reports were received of coastal strandings of *Eunectes murinus* along the Trinity Road coast, while documented reports were received of *E. murinus* and *H. angulatus* at Mayaro Beach (Charles 2013). Previously well documented in the Nariva Swamp or Bush Bush area (Boos 2001), a large (~3.0m) *E. murinus* carcass was noted stretched across the Manzanilla Main Road near the Ortoire Estuary in the receding floodwaters of December 2013.

Regarding snakes of the genera *Atractus* and *Ninia*, the lack of published records or museum specimens and our failure to locate specimens of these snakes (which are

fairly common throughout the rest of the island) suggests that much work remains to be done on southeast Trinidad herpetofauna. These species were most likely present in the study area.

The crocodylian *Caiman crocodilus* was observed on several occasions at the Ortoire River, St. Hilaire River, Pilote River, and Lizard River, as well as at Trinity Pond. Charles (2013) noted the stranding of a juvenile near Frontin Road, Mayaro Beach; one of us (RSM) noted a large carcass near the same site in December 2006.

With the influx of large, floating mats of vegetation from the flooding Orinoco River delta, it is plausible to assume that colonizing events such as those documented by Charles (2013) may be adding continually to the herpetofaunal assemblages of southeastern Trinidad and adding new genetic material to established Trinidad populations. For example, several waif specimens of the yellow-spotted river turtle, *Podocnemis unifilis*, were reported to have washed up on the East Coast near Manzanilla in September 2012 (reported in the Trinidad and Tobago *Newsday* newspaper, 10 September, 2012). These specimens have not yet been incorporated into any museum collection.

An important point to note is that at least two species recorded here (*Tantilla melanocephala* and *Mariosora aurulae* – potentially a species of conservation concern) were confirmed only by the brief deployment of drift fence-pitfall trapping, while incidental/opportunistic observations revealed the presence of a number of other species not encountered during standardised visual transect surveys and seining. This underscores the importance of using multiple survey techniques in multiple habitats and locations to assess herpetofaunal biodiversity and the fact that even brief periods of additional and fairly casual observation can increase the yield in species richness counts.

Since publication of Murphy (1997), a considerable number of systematic and nomenclatural changes have been made relating to species of amphibians and reptiles that inhabit Trinidad and Tobago. The most recent changes include descriptions of *Leptophis haileyi* (Murphy *et al.* 2013) and *Plica caribaeana* (Murphy and Jowers 2013), resurrection of the genus *Macrops* for the snakes formerly called *Chironius septentrionalis* and *C. scurrulus* (Pyrton *et al.* 2013), transfer of the snake formerly known as *Pseustes poecilonotus polylepis* to the genus *Phrynonax* and its elevation to species level, transfer of the snake formerly known as *Pseustes sulphureus* to the genus *Spilotes* (Jadin *et al.* 2014), and elevation of the Venezuelan *Erythrolamprus reginae zweifeli* to species level (Rivas *et al.* 2011). These changes all point to the Trinidad and Tobago herpetofauna being much more diverse than previously thought and reinforce the ideas pre-

sented by Murphy and Downie (2012) that the islands' herpetofauna need more careful study and protection from habitat loss.

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# Tadpoles of *Mannophryne trinitatis* and *M. olmonae* (Anura: Aromobatidae): Further Description and Comparison

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## ABSTRACT

*Mannophryne trinitatis* and *M. olmonae* (Anura: Aromobatidae) are endemic to Trinidad and to Tobago, respectively. Previous descriptions have shown that tadpoles of these two species are very similar to one another. We examined a wide range of sizes and stages of tadpoles from one location in Tobago and three locations in Trinidad. Although some variability was found (in dentition, for example), no character alone could be used to distinguish any of the three Trinidad populations, and the Tobago specimens showed overlapping features. The only characters that appeared useful in distinguishing *M. trinitatis* and *M. olmonae* were pigmentation of the tail and origin of the dorsal fin. However, caution is recommended in identifying these species since tail characteristics vary.

**Key words:** Trinidad, Tobago.

## INTRODUCTION

Lehtinen and Hailey (2008) first described the tadpole of the endemic Tobago stream frog, *Mannophryne olmonae*. They compared it with the tadpole of the closely related, endemic Trinidad stream frog, *M. trinitatis*. They were able to examine only two *M. trinitatis* specimens and found it impossible to distinguish them from *M. olmonae*. They reported a possible error in the description of the *M. trinitatis* tadpole provided by Kenny (1969) and suggested that examination of a bigger sample of the *M. trinitatis* tadpoles would be useful.

*Mannophryne trinitatis* inhabits two main localities, both in Trinidad: in the Northern Range, along the margins of small streams from just above sea level on the North Coast to hillside streams on the southern slopes; and in the Central Range, where known localities include Tamana Cave and several sites in the forest and hills to the east and west of Tamana Cave (Jowers and Downie 2004). Manzanilla *et al.* (2007) established that *M. trinitatis* is a separate species from the population found on the Paria Peninsula of Venezuela (called *M. venezuelensis*); these two are sister species and are more distantly related to Tobago's *M. olmonae* than they are to each other. Jowers *et al.* (2011) investigated the genetic and geographic structure of *M. trinitatis* throughout its range but found no evidence for genetic structuring related to geographical distribution.

In constructing his key to the tadpoles of Trinidad, Kenny (1969) relied on a number of morphological char-

acters, principally body dimensions, tail shape and tail patterning, and features of the oral disc. A key feature is the dental formula, which describes the arrangement of the rows of labial teeth borne on the oral disc. Kenny gave the dental formula for *Mannophryne* (then *Phyllobates*) *trinitatis* as 1:2/1:1:1, meaning two anterior rows, the second of which is subdivided (designated 2), and three posterior rows (to the right of /), none of which is subdivided. Altig and McDiarmid (1999) attempted to standardise the presentation of dental formulae; in their system, *M. trinitatis* becomes 2(2)/3, meaning two anterior rows (to the left of the /), the second of which is subdivided (in brackets), and three undivided posterior rows. We follow Altig and McDiarmid's system, as did Lehtinen and Hailey (2008). We report here an analysis of *M. trinitatis* tadpoles from three localities, representing a wide ontogenetic range, and compare them with a new sample of *M. olmonae*.

## MATERIALS AND METHODS

*Mannophryne trinitatis* tadpoles were collected from four sites: 1) a pool on El Tucuche (16/5/1982), 2) the stream through Tamana Cave (7/7/1982; 8/7/1994), 3) a stream by the side of the North Coast Road, a little west of Maracas Bay (8/7/1994), and 4) a stream beside the road a little south of Lopinot Village (26/7/2013). *Mannophryne olmonae* tadpoles were collected from an isolated freshwater pool close to a tributary of the Hermitage River near Charlotteville. Tadpoles were eutha-

nized by immersion in a lethal solution of benzocaine (0.01% aqueous) and then preserved in 10% formalin; two batches of *M. trinitatis* were preserved in Bouin's fluid. Specimens were examined by use of a Wild dissecting microscope and measured with callipers (for whole specimens) and by use of an eyepiece scale for fine features. Drawings were made with the aid of a microscope drawing tube. Tadpoles were staged by use of the method of Gosner (1960). The specimens used in this study have been deposited in the University of Glasgow's Hunterian (Zoology) Museum: *M. trinitatis* (GLAHM: 153253); *M. olmonae* (GLAHM: 153254).

To illustrate the mouthparts, specimens of both species were prepared for scanning electron microscopy by use of the methods described by Nokhbatolfoghahai and Downie (2005) and photographed by use of Image-slave for Windows (Meeco Holdings, Australia). Tadpole measurement comparisons were analysed by one-way ANOVA followed by post hoc Tukey tests, or by non-parametric Kruskal-Wallis tests when the data were not distributed normally.

## RESULTS

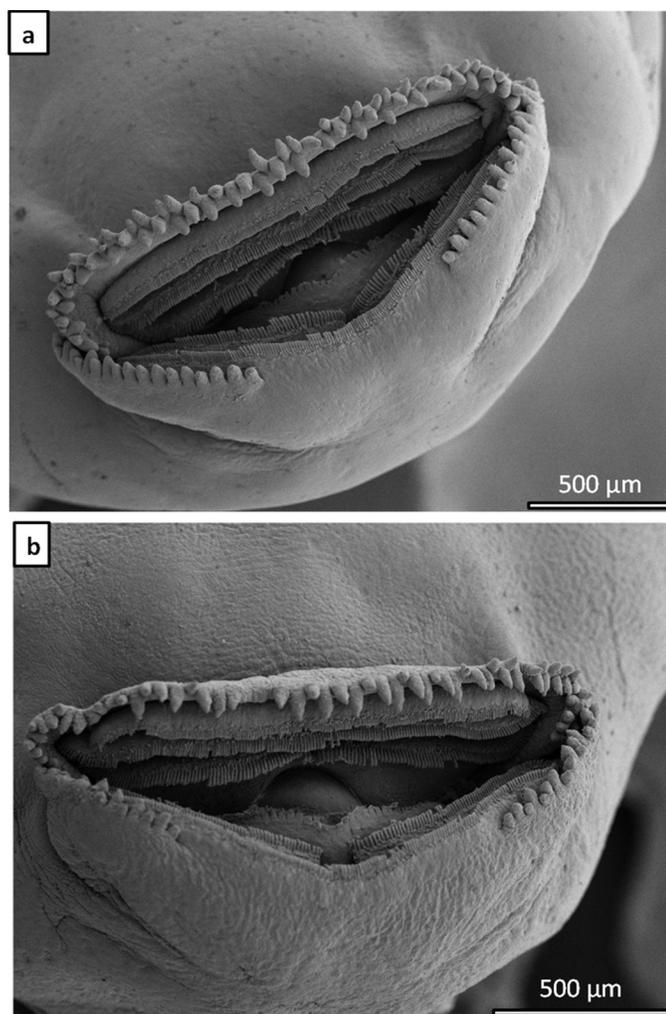
Table 1 presents data on total length, snout to vent length (SVL), tail height, dorsal fin height, and oral disc

width from the three different populations of *M. trinitatis* and from *M. olmonae*. No consistent differences were found that could be used to distinguish the *M. trinitatis* populations from each other or from *M. olmonae*, although a few of the features measured showed statistically significant differences in some cases.

Dental formulae from all populations of *M. trinitatis* and from *M. olmonae* were very similar, with little variability. All tadpoles had two anterior and three posterior tooth rows; no extra tooth rows were found in any specimen. Tooth rows A1, P2, and P3 were always undivided. In *M. trinitatis*, A2 was always divided (36 specimens examined). In some cases (25%), the gap between sub-rows could be detected only by moving the rows. In 11% of the cases, the gap was less than 40  $\mu\text{m}$ ; in 42% around 40  $\mu\text{m}$ , and in 22% it was around 80  $\mu\text{m}$ . P1 was undivided in 39% of specimens, but a division could be detected in the remainder. In nearly all specimens there was no gap, with a tiny gap (< 40 $\mu\text{m}$ ) detectable in two specimens only. In *M. olmonae*, A2 was always divided and always had a detectable gap, around 80  $\mu\text{m}$  in 88% of specimens and as narrow as 40  $\mu\text{m}$  in one specimen only. P1 was undivided in one specimen and divided in the remainder, but with no gap. Representative oral discs are shown in Figs. 1 and 2.

**Table 1.** Comparison of quantitative features among three Trinidad *M. trinitatis* populations and one Tobago *M. olmonae* population. All features are presented as ratios: each feature length divided by total length (mm): mean  $\pm$  SD; analysis conducted on arcsine-transformed ratios. \* = data normally distributed; + = data not all normally distributed.

Species	Location	N	Stage range	SVL +	Maximum tail height +	Maximum dorsal fin height *	Oral disc width *
<i>M. trinitatis</i>	Lopinot (L)	10	26-39	0.65 $\pm$ 0.016	0.41 $\pm$ 0.019	0.22 $\pm$ 0.014	0.34 $\pm$ 0.016
	Tamana (T)	14	26-40	0.63 $\pm$ 0.013	0.42 $\pm$ 0.014	0.23 $\pm$ 0.013	0.31 $\pm$ 0.015
	North Coast (NC)	5	27-31	0.66 $\pm$ 0.006	0.40 $\pm$ 0.018	0.21 $\pm$ 0.02	0.34 $\pm$ 0.015
<i>M. olmonae</i>	Hermitage (H)	8	26-37	0.64 $\pm$ 0.027	0.40 $\pm$ 0.012	0.21 $\pm$ 0.016	0.32 $\pm$ 0.012
Significant differences at P < 0.05				T $\neq$ L	None	NC $\neq$ T	T $\neq$ NC
				T $\neq$ NC		H $\neq$ T	T $\neq$ L

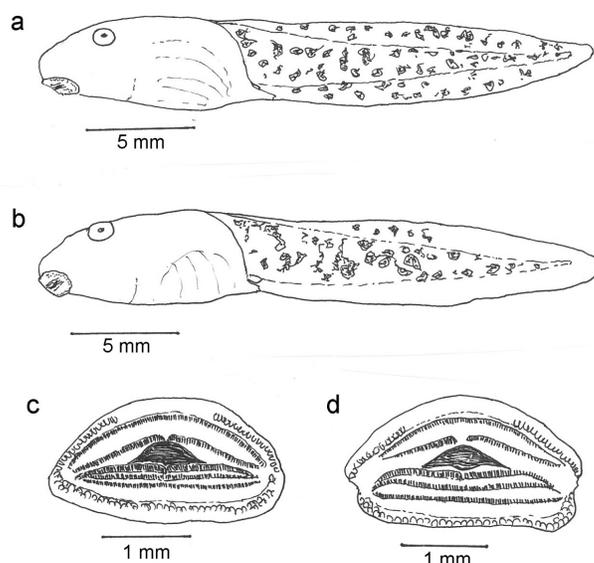


**Fig. 1.** Scanning electron micrographs of oral discs of a) *M. trinitatis* and b) *M. olmonae*.

Tails were tapered in both species and were highly muscular. Tail height is quite uniform over much of its length until it tapers at the end. The ventral fin is uniform over much of its length, but the dorsal fin is short anteriorly. One consistent difference found between the two species was that in *M. trinitatis* the dorsal fin begins level with the base of the hind limbs at the rear end of the body, whereas in *M. olmonae* the dorsal fin begins a little more posteriorly (Fig. 2). Another difference found was in tail pigmentation. In *M. trinitatis*, pigment blotches occur throughout the length of the tail, including the fins, whereas in *M. olmonae*, pigment blotches occur along the central axis of the tail and on the anterior part of the dorsal fin but were absent from the ventral fin and from the posterior part of the dorsal fin (Fig. 2).

## DISCUSSION

Lehtinen and Hailey (2008) were concerned that Kenny's (1969) drawing of the *M. trinitatis* tadpole was in error because it erroneously depicted a large gap in tooth



**Fig. 2.** Drawings of whole tadpoles in lateral view and of oral discs of *M. trinitatis* stage 27 (a, c) and *M. olmonae* stage 28 (b, d). Drawings made with the aid of a drawing tube using formalin-fixed specimens. Dorsal side above in all cases.

row A1. Kenny gave the dental formula as 1:2/1:1:1 [2(2)/3 in Altig and McDiarmid's terminology], indicating A1 as a complete undivided row, so the error was most likely simply in the illustration. Lehtinen and Hailey's (2008) account (page 261) of the *M. olmonae* dental formula noted that row A1 had a small gap (0.1 mm), as illustrated in their Fig. 2, but on page 263 they wrote that A1 is 'typically' undivided. Rick Lehtinen told us (pers. comm.) that there is indeed variation in their sample, with an undivided A1 being the more common condition. In our samples, we also found some variability but not in the same row as Lehtinen and Hailey (2008). We found A1, P2, and P3 always undivided in both species. A2 was always divided in both species, although the size of the gap was very variable. P1 was variable in both species, usually divided in both species but undivided in some individuals. We saw no evidence of an extra row, P4, as seen by Lehtinen and Hailey (2008) in one *M. olmonae* specimen.

It is not our aim here to provide complete descriptions of these two tadpole species, since these already have been written by Kenny (1969) and Lehtinen and Hailey (2008). Rather, we aimed to look for ontogenetic and regional variation in *M. trinitatis*, to clear up ambiguities in the literature, and to find characters that could be used to distinguish these two species of tadpole from each other.

Table 1 shows some evidence for inter-locality differences in *M. trinitatis*, particularly between the Tamana and Northern Range populations, but little consistency was found in differences between *M. trinitatis* and *M.*

*olmonae*. Cummins and Swan (1995) reported some reproductive differences, including tadpole size at deposition, between Northern Range and Tamana populations, and Downie *et al.* (2001) reported differences in tadpole deposition behaviour between North Coast and Northern Range southern slope populations. There may therefore be some fine-scale differences between different *M. trinitatis* populations, but as Jowers *et al.* (2011) and Lehtinen *et al.* (2011) found, these do not show up as consistent differences at the genetic level. Our size-corrected morphometric data showed very little variation over a considerable range of size and stage, indicating that shape characteristics alter little as tadpoles grow.

Regarding distinguishing features, we did detect consistent differences in tail origin between *M. trinitatis* and *M. olmonae* and differences in tail pigmentation. However, tail shape and tail pigmentation are characters known to vary with rearing conditions in some species (Viertel and Richter 1999; Relyea 2004), so such characters may not be reliable as distinguishing features. Overall, the best way to identify *M. trinitatis* and *M. olmonae* tadpoles is to know on which island they were collected.

As Lehtinen and Hailey (2008) noted, rather few tadpoles of the 19 species (Frost 2014) of *Mannophryne* have been described fully. It is surely time that larval descriptions are included alongside those of adult anurans.

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# Nesting in the Gladiator Frog, *Hypsiboas boans* (Anura: Hylidae), in Trinidad and Tobago

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## ABSTRACT

Nests of the gladiator frog, *Hypsiboas boans* (Anura: Hylidae), were monitored in a tributary of the Caura River, north Trinidad, during the wet season (July 2013) and during the following dry season (March 2014). Most nests were found at the stream edge, in easy communication with flowing water. Nests were either small basins excavated in gravel/sand with a mat of eggs floating on the surface of the contained shallow pool of water or were in vegetation-bound inlets out of the current, with eggs present but with no evidence of an excavation. Excavated and non-excavated “nests” occurred in similar frequencies. Mean clutch sizes of wet season nests were  $1078 \pm 170$  SD ( $n = 6$ ), whereas those of dry season nests were  $1070 \pm 271$  ( $n = 6$ ). Even when hatchlings could reach the stream easily, they remained in the nest until seven days after oviposition. One excavated nest was more than 2 m from the stream. During the three-week monitoring period, there were no heavy rains, and the larvae remained in the nest with little sign of growth or progressive development. *Hypsiboas boans* is widely distributed in South America, but these nesting details from Trinidad are different enough from those of South American populations to suggest some local adaptation.

**Key words:** reproduction, development, local adaptations.

## INTRODUCTION

Murphy and Downie (2012) discussed our increasing knowledge of the amphibian and reptile fauna of Trinidad and Tobago, noting that both recent migrations and new methods of analysis add to the islands’ species list. Some of Trinidad and Tobago’s species are endemics, but many are regarded as belonging to wide ranging species often extending far into mainland South America. However, even where there is substantial evidence that a widely occurring taxon should be considered to be a single species, there may be local adaptations in a population that distinguish it from other populations. From a conservation viewpoint, such local adaptations need to be investigated and understood.

The giant treefrog, *Hypsiboas boans* (Anura: Hylidae), is one of these wide ranging species. It belongs to the *semi-lineatus* group of “gladiator” frogs (named from the aggressiveness of the males and their possession of a prepollical spine used in fighting). The species occurs from the lower Amazon Basin north to Panama and the Guianas (Faivovich *et al.* 2005; Frost 2014) and is widely distributed in Trinidad, inhabiting trees bordering streams and rivers; it does not occur in Tobago.

Kenny (1969) reported that *H. boans* spawns during the dry season (December to April), with the female excavating a nest basin up to 45cm in diameter in gravel or sand on the banks of streams. The basin then fills with

water, and the female lays eggs as a floating mat on the surface. Kenny apparently erred in identifying the female as the nest maker; all other accounts refer to the male as nest maker (Murphy 1997; Burger *et al.* 2002; Caldwell 1992; Magnusson *et al.* 1999). Kenny (1969) noted that it was not clear how the hatchlings eventually left the nest. He speculated that this may have happened following showers which, even in the dry season, may have raised the water level high enough to breach the basin walls and allowed the tadpoles to access the stream.

In other parts of *H. boans*’s range, nesting behaviour can be variable. Burger *et al.* (2002) reported nests in Peru very similar to those described by Kenny. However, Caldwell (1992) and Magnusson *et al.* (1999) found that *H. boans* sometimes constructed basins but that they could also lay eggs in secluded, still water sites without making a construction, an example of plasticity in nesting behaviour. In this paper, we report on observations of *H. boans* nests in Trinidad during July, well outside the usual nesting season, and we compare them with observations of dry season nests.

## METHODS

### Genera

The principal location for these observations was an 80m stretch of a tributary of the Caura River (Figure 1: GPS co-ordinates 10° 40, 881’ N, 61° 21, 782’ W, ele-

vation 90.9m) on the southern side of Trinidad's Northern Range. The first set of observations was made each morning from 6-19 July, 2013 and once more on 26 July, 2013. On each visit, the edges of the stream were checked for *H. boans* nests, and the developmental progress of tadpoles in previously located nests was noted. One sample of newly deposited spawn (about 50 eggs) was taken to the laboratory (University of the West Indies, St. Augustine, Trinidad) and incubated in about 1 litre of aerated dechlorinated tap water at ambient temperature to monitor the rate of development. Samples of hatched larvae were taken from two nests in the stream, euthanised by use of a 0.01% aqueous solution of benzocaine and then fixed in formalin to allow accurate measurements to be taken. Larval lengths were later measured by use of a Wild dissecting microscope with a calibrated eyepiece. Clutch sizes were counted in five of the nests on the first or second day after oviposition. We also found and counted one clutch by the side of the Lopinot River (beside the Cemetery Road Bridge). To compare observations made during the wet season (in July 2013) with those made of dry season nests, one of us (MG) revisited the Caura site in March and early April 2014. No nests were found at the original principal location, but careful searching further upstream revealed several recently deposited egg clutches.



**Fig. 1.** The authors searching for *H. boans* nests at the edges of the Caura River tributary.

Lehtinen (2014) reported nest construction by another species of gladiator frog, *H. crepitans*, in Tobago, a behaviour for this species previously reported only from South America. *Hypsiboas crepitans* also occurs in Trinidad; we have found it breeding in blocked drainage ditches in the Caura Valley but not in rivers (JRD, unpublished observations.). The colour pattern of *H. boans* tadpoles is distinctively different from those of *H. crepitans* (Kenny 1969). The tadpoles that we found in the Caura stream were unmistakably those of *H. boans*.

### Description of principal site

The stretch of the Caura River tributary studied is no more than 4m wide and is well shaded by trees and other vegetation. It includes some pools, some shallows with gravel bottoms, and abundant rocks. There are no steep descents on the stretch. During the period studied, despite being in what is normally the wet season, only a few short showers occurred and the water level remained fairly constant, with evidence of a significant rise on only one occasion, during which we observed detritus (plastic waste) deposited at the level of one of the monitored *H. boans* nests (Figure 2). The stream contains abundant guppies (*Poecilia reticulata*) and Hart's rivulus (*Anablepsoides hartii*); burrows in the banks indicated the presence of freshwater crabs.



**Fig. 2.** Small basin nest after water level rise that brought down detritus such as plastic bottles.

## RESULTS

### Rate of development

The developmental progress of the egg clutch monitored in the laboratory is shown in Table 1. The data here allow assessment of the approximate time of deposition of clutches found in the field (there may be small temperature-related differences between field and laboratory-incubated eggs).

**Table 1.** *Hypsiboas boans* early development: egg deposition assumed the middle of the night preceding first observation. Stages according to Gosner (1960).

Time after deposition (d)	Developmental stage
1.5	Neurulae, stage 14
2.8	Around hatching, stage 19
3.5	Small external gills, stage 20
4.5	Maximal external gills, stage 23
5.5	Gills fully resorbed, stage 25, mean total length 10.3mm
6.5	Stage 25, mean total length 11.1mm

### Clutch sizes and nest descriptions

Data on the nests observed in July 2013 are shown in Table 2. The mean clutch size of those that we counted was  $1078 \pm 170$  SD. Only five of the nests were obviously constructed depressions, with diameters 12-15cm; the remaining five clutches were floating on the surface of the water in natural secluded backwaters; most were contiguous with or very close to the stream side – only one was at a significant distance (more than 2m) away.

At the Lopinot River, as well as finding one nest we found abundant *H. boans* larvae at a wide range of sizes/stages in the shallows at the stream margin. On our first visit to the Caura stream (6/7/13), we found no larvae, only four nests. All but one of the nests we found at Caura were in a short stretch (about 10m) of stream with shallow gravel edges and vegetation- or rock-bounded inlets; downstream of this stretch, the stream was narrower, deeper, and faster flowing. We found only one nest there, in a vegetation-bound small inlet.

Over our Caura monitoring period 6-26 July, 2013, there was no rain heavy and prolonged enough to raise

the water level sufficiently to reach Caura nest 1, located more than 2m from the stream side. We sampled hatchlings from this nest regularly over the monitoring period; sizes and stages are shown in Table 3. These larvae would have reached the 11mm stage (Table 1) on 11 July, 2013. Remaining in the nest, they grew slightly over the next few days but then remained at essentially the same length until last sampled on 26 July, 2013, three weeks after oviposition. Development, as assessed by gut coiling, progressed a little over that time.

Observations on the morning of 10 July, 2013 showed that recent rain had raised the stream level enough to reach Caura nests 2-4, all close to the stream. However, many tadpoles remained in all three nests, even the most advanced one (Caura nest 2) with larvae  $12.4 \pm 0.7$ mm ( $n = 7$ ) in length. By the next day, this nest was empty, although nests 3 and 4 still contained many larvae. By the following day (12 July, 2013), nests 3 and 4 still contained some larvae, but many had dispersed around the shallows of the inlet where these nests were located, and some could be found 2-3m downstream. Larvae sampled

**Table 2.** Clutch sizes and nest descriptions; dates given are for the approximate night of laying back-calculated from stage of embryos upon discovery.

Location, date	Clutch size	Nest description
Lopinot, 4/7/13	940	Shallow water-filled depression in gravel, about 15cm diameter, about 10cm from stream edge.
Caura 1, 4/7/13	1300	Shallow water-filled depression in gravel, about 12cm diameter, 2.5m from stream, separated from stream by a slightly elevated gravel bank.
Caura 2, 3/7/13	870	Depression in sand/gravel, 12cm diameter at stream edge, water at margin of depression contiguous with stream.
Caura 3, 4/7/13	1224	Eggs laid at edge of stream in a backwater; no sign of constructed basin.
Caura 4, 2/7/13	not counted	Shallow water-filled basin, about 12cm diameter, leaves and gravel/sand base, 40cm from stream edge.
Caura 5, 13/7/13	not counted	Eggs laid at edge of stream at base of large rock in a backwater; no sign of a constructed basin.
Caura 6, 13/7/13	1140	Eggs laid at surface of water at stream edge in an inlet well shaded by vegetation; not a constructed depression.
Caura 7, 13/7/13	994	Eggs laid at surface of water in a partly isolated puddle well shaded by vegetation, about 12cm diameter, well downstream from nests 1-6.
Caura 8, 14/7/13	not counted	Eggs laid in a constructed basin, about 13cm diameter, with a clear lip at the stream edge, made in a sand bank at the stream edge (Figure 3).
Caura 9, 23/7/13	not counted	Eggs amongst a group of rocks in mid-stream; not a constructed basin.

a little way downstream from nests 2-4 on 13 July, 2013 were  $12.3 \pm 0.8\text{mm}$  ( $n = 9$ ). By 14 July, 2013, very few larvae remained in nests 3 and 4, and tadpoles could be found as far as 30m downstream from these nests.



**Fig. 3.** Basin nest with lip of sand and gravel, constructed at edge of large rock.

**Table 3.** Sizes and stages of larvae remaining in Caura nest 1, 12 to 26 July, 2013. No development past Gosner stage 25. Gut coil development assessed using Nieuwkoop and Faber's (1975) system for *Xenopus laevis*: stages 45-47 would all be classed as Gosner stage 25 (McDiarmid and Altig 1999).

Date	Mean length in MM. $\pm$ SD (sample size in parenthesis)	Stage: gut coil development
12/7/13	$12.1 \pm 0.4$ (9)	Stage 45
13/7/13	$12.4 \pm 0.2$ (9)	Stage 45
15/7/13	$12.9 \pm 0.3$ (10)	Stage 46
17/7/13	$12.5 \pm 0.4$ (10)	Stage 46
19/7/13	$12.8 \pm 0.4$ (10)	Stage 46+
26/7/13	$12.4 \pm 0.3$ (8)	Stage 47

On 15 July, 2013, larvae sampled from the stream were  $14.7 \pm 1.6\text{mm}$  ( $n = 9$ ), excluding one that was close to metamorphosis and which may have come from further upstream. On 19 July, 2013, after some rain, the water level in the stream allowed hatchlings in nests 5 and 8 (now at day 6 and 5, respectively) to access the stream, but each nest still contained large numbers of larvae.

To assess whether our wet season observations were exceptional, we observed dry season (March and April 2014) nests close to the same principal location in the Caura Valley. Of six nests found, three were in vegetation-bound inlets at the stream margin, with no obvious excavation; the other three also were at the stream edge,

but depressions had been excavated in the gravel. Mean clutch size was  $1070 \pm 271$  SD, similar to those of the wet season nests counted in July 2013.

Since we visited the Caura site only during the day, we were unable to observe nest construction and egg deposition. We observed no nest attendance by adults.

## DISCUSSION

The main conclusions to be drawn from these observations are:

1. In Trinidad, *H. boans* is variable in nesting behaviour, depositing its eggs in suitable shallow inlets adjacent to the stream as frequently as it excavates a basin for the eggs. Eggs were deposited in inlets where the vegetation reached to the stream edge and where there was no gravel bank, but there was no lack of gravel banks along the stretch of river that we monitored.
2. If a nest is located at some distance from the stream, the hatchlings have to remain in that nest until the stream level rises sufficiently to reach them; during that time, they grow and develop very little. We found no evidence of any parental action to assist them in accessing the stream.
3. Even when the hatchlings are able to access the stream, they remain in the nest until they reach about 12mm long, approximately seven days after egg deposition.
4. We found no evidence of seasonal variation in clutch size or in nest construction (whether excavated or not).

Plasticity of nesting behaviour in *H. boans*, either basin construction or egg deposition in a secluded spot at the stream margin, has been reported by Caldwell (1992) and Magnusson *et al.* (1999), both from Brazil. Caldwell reported basin construction for 12 of 21 nests found, and Magnusson *et al.* reported basin construction for six of 16 nests/sites found. In contrast, Burger *et al.* (2002) found basin construction as the norm (59 of 60) in Peru. The dimensions of basins in Brazil and Peru were substantially larger than those we found in Trinidad (12-15 cm): mean diameters of 36.2cm (Caldwell 1992) and 34 cm (Burger *et al.* 2002) respectively. In addition, clutch sizes in the South American populations were substantially higher than those in Trinidad (means of 1078 and 1070 in our two samples): means of 2531 ( $n = 4$ ) in Brazil (Magnusson *et al.* 1999) and 1980 ( $n = 47$ ) in Peru (Burger *et al.* 2002).

Magnusson *et al.* (1999) noted that hatchlings remained in basins for at least a week, with some larger ones lingering for two weeks, and that all had dispersed by three weeks; this implies that larvae develop in these basins. Caldwell (1992) found that larger tadpoles in basins predate smaller conspecifics. Our findings were quite different: hatchlings remained in the nest till about seven

days after oviposition but then dispersed if they could. Tadpoles in nests isolated from the stream remained in the nests but stopped growing. Delayed emergence from the nest may provide an advantage in that the late emerging individuals are more advanced in their development and better able to survive than are early emerging individuals, as found for *Physalaemus* (= *Engystomops*) *pustulosus* emergence from foam nests (Downie 1993). However, it seems unlikely that tadpoles in very isolated nests have any advantage, other than in cases of heavy rains just after eggs have been deposited, when eggs closer to the stream may be washed downstream and die.

The nest and clutch sizes we report for Trinidad are very different from those reported for Brazil and Peru, possibly implying some local adaptation. Our findings that dry season nests were not different from rainy season nests accords with a lack of seasonal variation in clutch sizes in the Tobago glass frog (Lehtinen *et al.* 2014).

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# Utilisation of Anvils by the Trinidad Motmot (*Momotus bahamensis*) in Tobago, Trinidad and Tobago

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## ABSTRACT

In June 2012 the remains of terrestrial snail shells were found next to rocks on forest paths in several locations in north-eastern Tobago, W.I. It was surmised that an avian predator had been responsible. In June-July 2013 camera trapping and direct filming revealed that a Trinidad Motmot (*Momotus bahamensis*) was using the rocks as anvils to break open snail shells and other hard-bodied prey items.

**Key words:** predation, feeding behaviour, anvil, *Plekocheilus glaber*.

## INTRODUCTION

Birds have evolved a wide variety of techniques to catch and process different types of prey. One of these techniques is to use a rock or other hard surface as an anvil to either kill or break open hard-bodied prey. The hard remains of the prey are then discarded next to the anvil. Over time a small midden is formed, leaving valuable clues as to the behaviour of the anvil user and to the range of predated species.

Anvil use has been recorded in several bird species around the world (for summaries see Boswall 1977, 1978, 1983; Allen 2004; Lefebvre *et al.* 2002). Perhaps the best known of these is the Song Thrush, *Turdus philomelos*, which has been studied extensively over many decades by a number of researchers (e.g., Goodhart 1958). Other species reported to use anvils include the Chestnut Rail, *Eulabeornis castaneoventris* (Woinarski *et al.* 1998) and the Noisy Pitta, *Pitta versicolor* (Andrade *et al.* 2011). Lefebvre *et al.* (2002) gathered papers showing that a total of 39 species from 11 families have been observed battering prey on a hard surface. Anvil use is an example of borderline tool use, as the rock remains part of the substrate rather than true tool use, in which an object independent from the substrate is manipulated (Boswall 1977).

Like all motmots, the Trinidad Motmot is an adaptable feeder and enjoys a varied diet including berries, large invertebrates such as beetles, centipedes, millipedes, cockroaches and scorpions, and vertebrates such as frogs, small lizards, and small birds (French 1991). Motmots have been observed striking live animal prey items against tree branches or other hard objects to stun

or kill the animal before consumption (Sandoval *et al.* 2008; Skutch 1971), but there are no reports in the literature of the Trinidad Motmot, *Momotus bahamensis*, habitually using a rock as an anvil to extract food.

This paper presents two recorded incidents of Trinidad Motmots using rocks as anvils to break open terrestrial snail shells, information on the content of the remains found around 10 anvils, and information on the characteristics of the anvils used by the motmots.

## METHODS AND RESULTS

In June 2012, one of us (MGR) was undertaking fieldwork in Tobago, W.I., surveying for terrestrial molluscs. During this work, aggregations of broken snail shells were found on trails in forests in the northeast of the island. The shells were always close to a prominent rock, normally a few centimetres high, in the middle of a trail. Several of these rocks or “anvils” were found along a trail heading north from Pirate’s Bay, Charlotteville. A second anvil was found alongside a stream next to a Water and Sewerage Authority (WASA) station on the Coast Road just south of Cambleton. A third was found on the Gilpin Trail in the Tobago Forest Reserve. These sites ranged in altitude from 53m to 313m and were a mixture of primary and secondary forest and recently abandoned agricultural land (Table 1). At the time of the first discovery of an anvil, no sightings were made of any animal utilising them.

It was assumed from the prey remains that an avian predator was involved because the shells showed a similar type of damage to shells found next to anvils used by thrushes in Europe – namely the spire or the body whorl

**Table 1.** Locations of anvils.

Anvil No.	Site Name	Altitude (m)	Latitude, Longitude (Datum: WGS84)	Notes
1	Trail above Pirate's Bay	53	N 11.32832°, W -60.54832°	Site of filming by GB
2	Trail above Pirate's Bay	75	N 11.33086°, W -60.54916°	
3	Trail above Pirate's Bay	72	N 11.33049°, W -60.54947°	Site of camera trap
4	Trail above Pirate's Bay	95	N 11.33014°, W -60.54961°	Remains collected (UWIZM.2012.33.32)
5, 6	Trail above Pirate's Bay	82	N 11.33116°, W -60.54939°	
7	Trail above Pirate's Bay	117	N 11.33163°, W -60.54995°	
8, 9	Trail above Pirate's Bay	118	N 11.33182°, W -60.54998°	
10	Trail above Pirate's Bay	120	N 11.33220°, W -60.55024°	
11	Stream near WASA station	124	N 11.30988°, W -60.55873°	Remains collected (UWIZM.2014.3.1)
12	Gilpin Trail	313	N 11.28562°, W -60.61939°	

of the shell was damaged but the lip remained intact. There was no sign of tooth marks on the shells, which would indicate predation by a mammal. A search of the literature was conducted, but no references to anvil use by birds in the Caribbean was found.

#### Anvils in use

To ascertain which species was responsible, further research was conducted in June 2013. A time-lapse camera trap (Wingscapes Timelapse Camera 8.0) was set up by MGR on a tree trunk overlooking Anvil 3. It was programmed to take a photograph every minute during daylight hours. The camera was set out for three days from the 9 -12 June. Three photographs taken at 1625 h, 1626 h, and 1627 h on 10 June, 2013 showed a Trinidad Motmot, *Momotus bahamensis*, standing on the anvil and engaging in a vigorous head-banging movement against

the rock (Fig. 1). Freshly broken snail shells were found near the rock after the incident, adding to the evidence that the motmot was the predator.

To gain video footage of the behaviour, GB observed an anvil for several hours on most days from late June through to the end of July 2013. Chosen as the study site was Anvil 1 (Fig. 2), situated in the middle of a trail above Pirate's Bay, Charlotteville, in a fairly open area of secondary forest that provided suitable cover for GB to hide. A Sony Handycam® was used to record events. On 16 July, 2013 at 1345 h, approximately three minutes of footage was recorded showing a motmot breaking open a land snail. The film clip started after the bird had arrived at the rock with a snail in its beak. For the first 2 minutes and 17 seconds, the bird held the snail by the spire of the shell. Each time the motmot struck the shell against the anvil, the snail flew out of the bird's grasp. The bird

**Fig. 1.** Motmot at Anvil

repeated this action 13 times; each time the motmot had to retrieve the snail from the surrounding leaf litter. At 2 minutes and 18 seconds, the bird changed its grip, now holding onto the aperture; it then smashed the spire of the snail shell nine times against the rock until it broke at 2 minutes and 25 seconds. The bird then took a few seconds to extract and eat the snail before flying to a nearby tree, where it wiped its beak several times on a branch and then flew away. The recording of the incident can be seen at: <http://youtu.be/HUC35Rtbqo0>



Fig. 2. Anvil 1 surrounded by broken shells.

During one earlier observation made by GB on the 26 June, 2013, a motmot cracked open a snail shell on an anvil after only four or five attempts. After eating the snail, the bird wiped its beak against a tree branch. The entire incident took around one minute but was not recorded.

### Prey species found at anvils

The majority of remains found at all anvils were shells of a single species of land snail, *Plekocheilus glaber* (Gmelin 1791) ([Stylommatophora]: Orthalicidae). This is a fairly large species with an average shell length of approximately 44 mm (Robinson *et al.* 2004). It is common in the forests of Tobago and has been observed on the ground, in low vegetation, and higher up in the canopy and has been found to be active during both day and night (MGR, pers. obs.). The pattern on the shell varies from nearly entirely cream coloured to having dark brown stripes; examples of both types were found at the anvils. All specimens collected from the anvils were adults, indicated by the presence of a thick lip around the aperture as opposed to juveniles which have a thin lip.

The middens around the anvils varied from containing less than ten snail shells and other remains to containing more than 60 different items. All specimens from the middens surrounding Anvils 4 and 11 were collected for analysis. Middens at Anvil 4 contained 41 snail shells; of those, 40 had an intact lip around the aperture. Those at Anvil 11 contained 58 snail shells, 42 with in-

tact lips and 16 with broken lips. The shells from Anvils 4 and 11 were deposited in the University of the West Indies Zoology Museum (UWIZM), Saint Augustine, Trinidad, accession numbers UWIZM.2012.33.32 and UWIZM.2014.3.1, respectively.

The broken remains of several non-snail taxa were also found in the middens. The elytra of at least two different species of beetles (*Passalus* sp. [Coleoptera: Passalidae] and *Neoptychodes* sp. [Coleoptera: Cerambycidae]) were found at Anvils 8 and 9. These are fairly large beetles with body lengths ranging from 30mm to 50mm. The chelae and broken pieces of the carapace of the manioc crab, *Eudaniela garmani* (Decapoda: Pseudothelphusidae) were found at two anvils. The size of the chelae indicated that the carapace width of the crab had been around 35mm. Body segments from large snake millipedes (Diplopoda: Spirostreptidae) were found at Anvils 5 and 6; these millipedes can reach around 150mm in length. A single unbroken specimen of the predatory marine snail *Plicopurpura patula* (Neogastropoda: Muricidae) was found next to Anvil 9; however, it is not known if its presence was a result of being collected by a motmot.

### Anvil characteristics

Ten anvils along the Pirate's Bay trail were measured. Most anvils were more than 50m apart, but some (Anvils 5 & 6 and 8 & 9) were within one metre of each other. Anvils varied in size from 66cm to 17cm long by 28cm to 11cm wide and from 6cm to 12cm high (see Table 2). Most were near the middle of the trails in which they were found, with the surrounding area containing leaf litter and smaller rocks but no vegetation.

Table 2. Anvil characteristics.

Anvil Number	Length (cm)	Width (cm)	Height (cm)
1	31	25	11.5
2	29	15.5	8.5
3	17.5	16.5	6.5
4	41	24	11
5	19	15	6
6	17	13	9
7	21	15	12
8	21	11	5
9	23	21	8
10	66	28	11
<b>Average</b>	<b>28.55</b>	<b>18.4</b>	<b>8.85</b>

## DISCUSSION

Utilisation of anvils to feed on snails by *M. bahamensis* in Tobago is an interesting behaviour as it provides evidence of borderline tool use in a species and a family in which it has not been recorded before, and it highlights a potentially important method of exploiting food sources that might otherwise not be available to the predator.

The wide area over which anvils were found during this study indicates that the behaviour is fairly common among individuals of *M. bahamensis*. It is still to be determined if all motmots in Tobago utilise anvils or if only certain individuals in certain areas utilise them. Differences in rates of anvil utilisation between sexes and between adult and juvenile motmots could also provide valuable data. It would also be interesting to see if different species of motmots in other countries exhibit this behaviour. Haverschmidt (1968) mentioned that the stomach contents of a *Momotus momota* from Suriname included molluscs but provided no information on how the molluscs were obtained.

The method by which the motmot held the snail shell seemed to make a significant difference in the effectiveness of the hammering. In the filmed incident, when the bird gripped the shell by the spire, the shell was likely to be dislodged from the beak when hammered, whereas when the bird gripped the shell by the lip, the shell was held securely and could be broken after a few hammers. A motmot consistently grasping the shell by the lip would decrease shell handling time and thereby develop a more efficient feeding strategy. The majority of shells found in the middens had intact lips but broken spires, suggesting that in the majority of cases the snail had been held by the lip while the spire end of the shell was being struck against the rock.

The use of a surface against which to batter prey has been noted before in motmots, which are well-known to feed on beetles and other large insects. Skutch (1971) observed Broad-billed Motmots, *Electron platyrhynchum*, and Rufous-capped Motmots, *Baryphthengus ruficapillus*, battering insects against tree branches for consumption both by themselves and by their chicks. Regarding a *B. ruficapillus* that he observed feeding on a large millipede, he wrote that, "standing on the ground, the bird beat its prey until it broke, and swallowed it piecemeal." However, Skutch never mentioned utilisation of an anvil or of middens being formed.

One of the common features of the anvil sites was that they tended to have little vegetation around them and generally only a thin layer of leaf litter in the immediate vicinity; a condition that could possibly make it easier for a motmot to retrieve a prey item lost during the beating process and thus to decrease the time needed for it to extract the food.

It is currently unknown what percentage of the diet of

*M. bahamensis* consists of snails and other species whose edible parts they can access by means of anvil utilisation. Also unknown is how the use of anvils and rates of predation upon snails varies throughout the year, from wet season to dry season. Predation upon terrestrial gastropods by birds is not all that common, except for species in the family Turdidae, many species of which prey heavily upon snails. This is possibly a result of the long handling time for minimal return (Allen 2004) but incidents have been recorded of birds consuming snails during migration events (Shachak *et al.* 1981) when choices of food may be limited. Several species of birds such as Limpkins, various species of oystercatchers, and Snail Kites feed almost exclusively on molluscs, but these are mainly freshwater and marine molluscs, and the birds do not utilise anvils to extract their prey.

Although several different species of snails were present as remains at the anvils, the vast majority were those of the land snail *P. glaber*. Despite the presence of at least three other similar-sized species of snails (*Drymaeus vincentinus*, *Orthalicus undatus*, and *Megalobulimus oblongus*) in the surrounding forest habitat, it is unknown why no remains of these species were discovered in anvil middens.

Many questions await answers regarding this behaviour, including: Do motmots consume snails all year round or is there seasonal variation? Do young motmots learn the behaviour from watching adults or is it to some degree innate, as in Song Thrushes (Henty 1986)? Does prey handling time vary among individuals and is this a factor of the age of the individual? What percentage of a motmot's diet is made up of snails predated in this way? Does a motmot use the same anvil each time or does it vary depending upon where the prey is collected? Are motmots territorial around the anvils? If all remains around an anvil are removed, does this affect the motmot's ability to find or relocate the anvil? We hope that this paper stimulates more research into this fascinating behaviour.

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# An Updated List of the Mantodea of Trinidad and Tobago, with Three New Records for Trinidad

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## ABSTRACT

The collections of the University of the West Indies Zoology Museum (UWIZM) were examined and the literature was searched in order to provide an updated list of the Mantodea of Trinidad and Tobago. 216 specimens were found, three species not previously recorded from Trinidad were identified and a key of the known species was produced.

## INTRODUCTION

The order Mantodea is found in both temperate and tropical habitats and contains over 2400 species from around 446 genera (Ehrmann 2002; Otte *et al.* 2005). As they are fairly charismatic insects they have been well documented but there are still many questions to be answered concerning their taxonomy, life history and distribution. Over the last 100 years there have been several publications on the Mantodea of Trinidad, however the most recent paper was only published in 1953 and since then there have been numerous changes to the nomenclature at several taxonomic levels. This paper represents the results of cataloguing the collections currently housed in the University of the West Indies Zoology Museum (UWIZM) and updating the nomenclature of the species list for Trinidad and Tobago.

In most cases mantids are consummate opportunistic ambush predators, standing motionless until suitable prey passes at which point they use their raptorial front legs to ensnare their victim. However, some species, such as *Liturgusa trinidadensis*, will actively stalk cryptic conspecifics (Prete and Mahaffey 1993). Although they usually prey on other insects, they are known to occasionally take small vertebrates such as lizards, frogs and hummingbirds (Prete and Wolfe 1992). Their efficient hunting techniques mean that they play a potentially important role in the control of insect pests (Sampaio *et al.* 2008).

Mantids show considerable variation in their morphology to facilitate their ambush hunting behaviour and camouflaging abilities and in Trinidad and Tobago a wide variety of species can be found. They vary from the stick mantids of the Thespidae to the bark mantids of the Liturgusidae, and from the dead leaf mantids of Acanthopidae to the charismatic large green mantids of Stagmatopterinae.

## History of the collection

The Mantodea collection in the UWIZM contains specimens dating back almost a century and came together from three main sources. The oldest part is from the University of the West Indies (UWI) collection that was inherited from the Imperial College of Tropical Agriculture (ICTA). The second part of the collection came to the UWIZM from CAB International (CABI) in 2012. The final part of the mantid collections came from the Caribbean Epidemiology Centre (CAREC), previously known as the Trinidad Regional Virus Laboratory, in 2013. In general the mantids in the museum were often collected when circumstances presented themselves rather than as part of specific studies.

## METHODS

The UWIZM insect collections were examined and all Mantodea gathered together. The specimens were identified through the use of keys, literature and previously identified individuals. Each specimen was then photographed, accessioned and added to the museum database.

On-line databases from various natural history collections were searched for specimens from Trinidad and Tobago and enquiries were made to the relevant staff member for further information.

The literature was reviewed for any mention of Mantodea from Trinidad and/or Tobago and information regarding which museums contained specimens was sought.

The previous species lists were tabulated allowing the change of names over time to be shown. The literature was reviewed for reference to Trinidad or Tobago within lists of Neotropical Mantodea (Agudelo *et al.* 2013; Ehrmann 2002; Jantsch 1999). Species were then reviewed

as to their probability of being in Trinidad and Tobago, with some species being removed from the final list with notes on the reason for each removal.

## RESULTS AND DISCUSSION

An updated list of the mantids of Trinidad and Tobago was prepared (Table 1). The accessioned specimens can be viewed online at <http://sta.uwi.edu/fst/lifesciences/collections.asp> by searching for Order Mantodea.

In the original UWI collection, the bulk of the mantid specimens were collected from the early 1920s to the mid-1940s by ICTA staff and were from in and around St. Augustine, Trinidad. Another significant contribution to the UWI collection was made by A.W. Hook who collected in the Northern Range, Trinidad in the 1990s. In total there are 126 specimens.

The CABI collection was assembled mainly from the 1950s to the 1980s and consists largely of mantids collected in and around Curepe, Trinidad. In total there were 84 specimens. From the CAREC collection there were only 6 specimens collected between 1957 and 1965, mainly from around Port of Spain.

A list of the species, locations and break down for each collection can be seen in Table 2.

The only foreign collection with specimens available on-line was the Staatliches Museum für Naturkunde Karlsruhe (SMNK) in Germany.

From the literature it was found that specimens from Trinidad and Tobago were stored at the Museu de Zoologia da Universidade de São Paulo, Brazil (Rodrigues and Cancellato 2013), the Academy of Natural Sciences of Philadelphia, U.S.A., the American Museum of Natural History, New York, U.S.A., the University of Minnesota Insect Collection, U.S.A., the Natural History Museum, London, U.K. and the Muséum National d'Histoire Naturelle, Paris, France.

### Species and name changes

Since the last species list for Trinidad was produced, the order Mantodea has had many taxonomic changes. Mantodea has relatively recently undergone modifications in the suprageneric organisation. This has resulted in several theories to the relationship of the Dictyopteran subgroups. Of the proposed hypotheses, the placement of Mantodea as being the sister group of Blattodea (including termites) has gained the strongest support from many morphological and molecular studies (e.g., Deitz *et al.* 2003; Svenson and Whiting 2004; Ware *et al.* 2008). Within Mantodea, Ehrmann (2002) categorised the group into 15 families with 48 subfamilies from the original 8 families with 28 subfamilies. Within Trinidad this re-categorised the previous 4 families and 9 subfamilies used

in Kevan (1953) (as the most recent literature within Trinidad and Tobago) to 5 families and 10 subfamilies (Table 1). With the addition of the three new species, currently for Trinidad there are 5 families, 11 subfamilies, 19 genus and 19 species.

The group was first studied locally in 1906 as part of Lawrence Bruner's "Report on the Orthoptera of Trinidad, West Indies." It took almost 50 years before more research was conducted with two papers coming out in the early 1950s, Beebe *et al.* (1952) and Kevan (1953). Both papers add to the list of species found in Trinidad. Since 1953 there have been seven name changes to species mentioned, with three changes directly relating to Trinidad. *Acanthops falcata* within Trinidad has been reclassified as *A. parafalcata* and has created a new endemic species for Trinidad (Lombardo and Ippolito 2004). The *Liturgusa* genus within the Neotropics has very recently been revised and *L. maya* within Trinidad has been classified as a new species, *L. trinidadensis* (Svenson 2014). In addition, the species first described in Bruner (1906) *Parastagmatoptera vitrepennis* has been synonymised with *P. unipunctata* (Umbriaco 2011).

One missing specimen of *Pseudomiopteryx* sp. is recorded in the UWIZM collection from labels; this is a misidentification of *Bantiella trinitatis* and was included in Kevan (1953) under *B. fusca* and therefore is *B. trinitatis*.

During examination of the collections, three new species to Trinidad were identified: *Phyllovates tripunctata*, *Paraphotina reticulata* and *Brunneria subaptera* (see Table 1). *P. tripunctata* is also found in Brazil, Colombia, Ecuador, French Guiana, Mexico, Peru, Suriname, Jamaica and Venezuela (Agudelo *et al.* 2013). *P. reticulata* is also found in Brazil, Colombia and Venezuela (Agudelo *et al.* 2013). *B. subaptera* is also found in Argentina, Bolivia, Brazil, Paraguay and Venezuela (Agudelo *et al.* 2013). With each species also present in Venezuela, it is not surprising that they are also found in Trinidad.

Specimens of note include a *Stagmatoptera septentrionalis* collected by C.B. Williams in 1918 in San Fernando (UWIZM.2013.28.100) as it is the oldest specimen in the collection (Fig.1). There are also several figured specimens from Kevan's 1953 paper.



**Fig. 1.** *Stagmatoptera septentrionalis* collected in San Fernando in 1918.

As well as the taxonomic works mentioned previously, there have been several papers published documenting other aspects of mantids in Trinidad. Crane (1952) and Quesnel (1967) both conducted studies on the defensive behaviour of certain species and the mating and display behaviour of *Tithrone roseipennis* was studied by Barabás and Hancock (1999) and Thornham (2007).

## CONCLUSION

Whilst a good body of work has been carried out on the mantids of Trinidad, similar studies in Tobago are very limited, with no comprehensive species list for the island and only three specimens representing two species within the UWIZM collection. Priorities for research include species lists for Tobago and the small offshore islands, further investigations on life history of the lo-

cal mantids and study of their role in the ecosystem with regards to pest control. We hope that this paper helps to stimulate a resurgence in Mantodea studies in Trinidad and Tobago.

## ACKNOWLEDGEMENTS

We are grateful to the following curators for searching their collections for relevant specimens: George Becaloni, Natural History Museum, London, UK; Reinhard Ehrmann and Alexander Riedel, Staatliches Museum für Naturkunde Karlsruhe, Germany; Geoff Hancock, Hunterian Museum, Glasgow, UK; Julio Rivera, Department of Ecology and Evolutionary Biology, University of Toronto, Canada.

**Table 1.** Species names as found in Bruner (1906), Beebe *et al.* (1952) and Kevan (1953), all species found in more recent literature listing Neotropical mantids, species realistically present in T&T with updated names and confirmed presence in Trinidad or Tobago.

<u>Bruner, L. (1906)</u>	<u>Beebe, W., Crane, J. &amp; Hughes-Schrader, S. (1952)</u>	<u>McE. Kevan, D.K. (1953)</u>	<u>Additions recorded from other literature</u>	<u>Current name and species</u>	<u>T'dad</u>	<u>T'bgo</u>
	<u>Mantoididae</u>	<u>Mantoididae</u>	<u>Mantoididae</u>	<u>Mantoididae</u>		
	<i>Mantoida</i> sp. Newman 1838	<i>Mantoida</i> sp. aff. <i>M. fulgidipennis</i> Westwood 1889	<i>Mantoida fulgidipennis</i> Westwood 1889	<i>Mantoida fulgidipennis</i> Westwood 1889	Yes	
<u>Mantidae</u>	<u>Mantidae</u>	<u>Thespidae</u>	<u>Thespidae</u>	<u>Thespidae</u>		
		<u>Thespinae</u>	<u>Thespinae</u>	<u>Thespinae</u>		
<i>Mionyx surinamus</i> (Saussure 1869)	<i>Musonia surinama</i> (Saussure 1869)	<i>Musonia surinama</i> (Saussure 1869)	<i>Musonia surinama</i> (Saussure 1869)	<i>Musonia surinama</i> (Saussure 1869)	Yes	
	<i>Catamusonia</i> sp. Giglio-Tos 1927	<i>Catamusonia</i> sp. Giglio-Tos 1927	<i>Macromusonia</i> sp. Hebard 1923	<i>Macromusonia</i> sp. Hebard 1923	Yes	
		<i>Thespis media</i> (Giglio-Tos 1916)	<i>Thespis media</i> (Giglio-Tos 1916)	<i>Thespis media</i> (Giglio-Tos 1916)	Yes	
		<u>Oligonicinae</u>	<u>Oligonicinae</u>	<u>Oligonicinae</u>		
		<i>Thesprotia macilenta</i> Saussure & Zehntner 1894	<i>Thesprotia macilenta</i> Saussure & Zehntner 1894 <sup>1</sup>			
		<i>Thesprotia subhyalina</i> (Saussure 1870)	<i>Thesprotia subhyalina</i> (Saussure 1870) <sup>2</sup>			
	<i>Thesprotia filum</i> (Lichtenstein 1796)	<i>Thesprotia filum</i> (Lichtenstein 1796)	<i>Thesprotia filum</i> (Lichtenstein 1796)	<i>Thesprotia filum</i> (Lichtenstein 1796)	Yes	
		<i>Thesprotia</i> sp. Stål 1877	<i>Thesprotia</i> sp. Stål 1877 <sup>3</sup>			
		<u>Pseudomyopteryginae</u>	<u>Pseudomyopteryginae</u>	<u>Pseudomyopteryginae</u>		

<u>Bruner, L. (1906)</u>	<u>Beebe, W., Crane, J. &amp; Hughes-Schrader, S. (1952)</u>	<u>McE. Kevan, D.K. (1953)</u>	<u>Additions recorded from other literature</u>	<u>Current name and species</u>	<u>T'dad</u>	<u>T'bgo</u>
		<i>Bantiella trinitatis</i> Giglio-Tos 1915	<i>Bantiella trinitatis</i> Giglio-Tos 1915	<i>Bantiella trinitatis</i> Giglio-Tos 1915	Yes	Yes
		<i>Bantiella fusca</i> Giglio-Tos 1915	<i>Bantiella fusca</i> Giglio-Tos 1915 <sup>4</sup>			
			<u>Miopteryginae</u>			
	<i>Promiopteryx granadensis</i> (Saussure 1870)		<i>Promiopteryx granadensis</i> (Saussure 1870) <sup>5</sup>			
			<i>Promiopteryx simplex</i> Giglio-Tos 1915 <sup>6</sup>			
		<i>Oligonyx</i> sp. Saussure 1869	<i>Oligonyx</i> sp. Saussure 1869 <sup>7</sup>			
<u>Hymenopodidae</u>	<u>Hymenopodidae</u>	<u>Hymenopodidae</u>	<u>Acanthopidae</u>	<u>Acanthopidae</u>		
		<u>Acontiothespinae</u>	<u>Acontiothespinae</u>	<u>Acontiothespinae</u>		
<i>Acontista multicolor</i> Saussure 1870	<i>Acontiothespis multicolor</i> (Saussure 1870)	<i>Acontiothespis multicolor</i> (Saussure 1870)	<i>Acontista multicolor</i> Saussure 1870	<i>Acontista multicolor</i> Saussure 1870	Yes	
		<i>Acontista minima</i> Giglio-Tos 1915	<i>Acontista minima</i> Giglio-Tos 1915 <sup>8</sup>			
<i>Tithrone roseipennis</i> (Saussure 1870)	<i>Tithrone roseipennis</i> (Saussure 1870)	<i>Tithrone roseipennis</i> (Saussure 1870)	<i>Tithrone roseipennis</i> (Saussure 1870)	<i>Tithrone roseipennis</i> (Saussure 1870)	Yes	
		<u>Mantidae</u>	<u>Acanthopidae</u>	<u>Acanthopidae</u>		
		<u>Epaphroditinae</u>	<u>Acanthopinae</u>	<u>Acanthopinae</u>		
<i>Acanthops</i> sp. Serville 1831	<i>Acanthops falcata</i> (Stål 1877)	<i>Acanthops falcata</i> (Stål 1877)	<i>Acanthops parafalcata</i> Lombardo & Ippolito 2004	<i>Acanthops parafalcata</i> Lombardo & Ippolito 2004	Yes	
<u>Mantidae</u>	<u>Mantidae</u>	<u>Mantidae</u>	<u>Mantidae</u>	<u>Mantidae</u>		
		<u>Angelinae</u>	<u>Angelinae</u>	<u>Angelinae</u>		
	<i>Angela quinque-maculata</i> (Olivier 1792)		<i>Angela quinque-maculata</i> (Olivier 1792)	<i>Angela quinque-maculata</i> (Olivier 1792)	Yes	
	<i>Angela</i> sp. Serville 1839	<i>Angela</i> sp. Serville 1839	<i>Angela</i> sp. Serville 1839 <sup>9</sup>			
		<u>Mantinae</u>	<u>Stagmomantinae</u>	<u>Stagmomantinae</u>		
	<i>Stagmomantis carolina</i> (Johannson 1763)	<i>Stagmomantis polita</i> Giglio-Tos 1917	<i>Stagmomantis carolina</i> (Johannson 1763)	<i>Stagmomantis carolina</i> (Johannson 1763)	Yes	
			<i>Stagmomantis theophila</i> Rehn 1904 <sup>10</sup>			
			<i>Stagmomantis centralis</i> Giglio-Tos 1917 <sup>11</sup>			
		<i>Stagmomantis</i> sp. Saussure 1869	<i>Stagmomantis</i> sp. Saussure 1869 <sup>12</sup>			

<u>Bruner, L. (1906)</u>	<u>Beebe, W., Crane, J. &amp; Hughes-Schrader, S. (1952)</u>	<u>McE. Kevan, D.K. (1953)</u>	<u>Additions recorded from other literature</u>	<u>Current name and species</u>	<u>T'dad</u>	<u>T'bgo</u>
		<u>Mantinae</u>	<u>Stagmatopterinae</u>	<u>Stagmatopterinae</u>		
	<i>Stagmatoptera septentrionalis</i> Saussure & Zehntner 1900	<i>Stagmatoptera septentrionalis</i> Saussure & Zehntner 1894	<i>Stagmatoptera septentrionalis</i> Saussure & Zehntner 1894	<i>Stagmatoptera septentrionalis</i> Saussure & Zehntner 1894	Yes	Yes
			<i>Stagmatoptera abdominalis</i> (Olivier 1792) <sup>13</sup>			
<i>Stagmatoptera praecaria</i> (Linnaeus 1758)			<i>Stagmatoptera praecaria</i> (Linnaeus 1758) <sup>14</sup>			
			<i>Stagmatoptera supplicaria</i> (Stoll 1813) <sup>15</sup>			
<i>Parastagmatoptera vitrepennis</i> Bruner 1906	<i>Parastagmatoptera vitrepennis</i> Bruner 1906	<i>Parastagmatoptera vitrepennis</i> Bruner 1906	<i>Parastagmatoptera unipunctata</i> (Burmeister 1838)	<i>Parastagmatoptera unipunctata</i> (Burmeister 1838)	Yes	
<i>Oxyopsis rubicunda</i> (Stoll 1813)	<i>Oxyopsis rubicunda</i> (Stoll 1813)	<i>Oxyopsis rubicunda</i> (Stoll 1813)	<i>Oxyopsis rubicunda</i> (Stoll 1813)	<i>Oxyopsis rubicunda</i> (Stoll 1813)	Yes	
		<i>Oxyopsis</i> sp. aff. <i>O. festai</i> Giglio-Tos 1914	<i>Oxyopsis festae</i> Giglio-Tos 1914 <sup>16</sup>			
			<i>Oxyopsis saussurei</i> Giglio-Tos 1914 <sup>17</sup>			
		<u>Vatinae</u>	<u>Vatinae</u>	<u>Vatinae</u>		
	<i>Vates lobata</i> (Fabricius 1798)	<i>Vates</i> sp. aff. <i>V. lobata</i> (Fabricius 1798)	<i>Vates lobata</i> (Fabricius 1798)	<i>Vates lobata</i> (Fabricius 1798)	Yes	
			<i>Vates pectinicornis</i> (Stål 1877) <sup>18</sup>			
			<i>Vates serraticornis</i> (Stål 1877) <sup>19</sup>			
				<i>Phyllovates tripunctata</i> (Burmeister 1838)	Yes	
				<u>Photininae</u>		
				<i>Paraphotina reticulata</i> (Saussure 1871)	Yes	
				<i>Brunneria subaptera</i> Saussure 1869	Yes	
<u>Mantidae</u>	<u>Mantidae</u>	<u>Mantidae</u>	<u>Liturgusidae</u>	<u>Liturgusidae</u>		
			<u>Liturgusinae</u>	<u>Liturgusinae</u>		

<u>Bruner, L. (1906)</u>	<u>Beebe, W., Crane, J. &amp; Hughes-Schrader, S. (1952)</u>	<u>McE. Kevan, D.K. (1953)</u>	<u>Additions recorded from other literature</u>	<u>Current name and species</u>	<u>T'dad</u>	<u>T'bgo</u>
	<i>Liturgousa</i> sp. Saussure 1869	<i>Liturgousa</i> sp. aff. <i>L. maya</i> Saussure & Zehntner 1894	<i>Liturgousa maya</i> (Saussure & Zehntner 1894)	<i>Liturgousa trinidadensis</i> Svenson 2014	Yes	
<i>Liturgousa cayennensis</i> Saussure 1869			<i>Liturgousa cayennensis</i> (Saussure 1869) <sup>20</sup>			

**Notes:**

1. Unlikely to be present in T&T as found in Bolivia, Paraguay and Brazil.
2. Found in Brazil and Kevan (1953) believes it was a misidentification of *T. filum*.
3. This refers to a nymph that was not identifiable to species.
4. This is a synonym of *B. trinitatis*.
5. *Promiopteryx granadensis* is not present in Trinidad.
6. *Promiopteryx simplex* is not present in Trinidad.
7. Only found in Central America and therefore unlikely to be present here. Expected to be a misidentification of *Thesprotia filum*.
8. Specimens in T&T are actually *A. multicolor* as *A. minima* has only been confirmed in Colombia (Agudelo 2013).
9. Was unsure if it was a female *A. quinquemaculata* or new species in Beebe *et al.* (1952) and Kevan (1953). Without sufficient specimens, we are unable to make the decision that this is a new species.
10. Unlikely to be in T&T as found in Central Southwestern America (Lombardo and Agabiti 2001).
11. Through examination of *Stagmomantis* within the collection and use of keys, along with doubt of presence within Venezuela, we do not expect them to be present.
12. This refers to a nymph that was not identifiable to species.
13. Only recorded from Suriname – Terra (1995) and Jantsch (1999) show in T&T. 2 specimens are recorded from Arima in the Dept. Ento. Uni. of Minnesota, however through examination of the *Stagmatoptera* within the collection and use of keys, we expect them to be misidentifications of *S. septentrionalis* and therefore not present.
14. Due to Bruner's (1906) paper, Kevan (1953) is certain that this is a misidentification of *S. septentrionalis*.
15. 2 specimens are recorded from Arima in the SMNK, however through examination of the *Stagmatoptera* within the collection and use of keys, we expect them to be misidentifications of *S. septentrionalis* and therefore not present.
16. Unlikely to be in T&T as only 1 specimen was previously found from Ecuador (Lombardo and Agabiti 2001).
17. Only recorded from Suriname.
18. Only recorded from Panama.
19. Only recorded from Colombia.
20. This is due to misidentification in Bruner (1906) and Rehn (1935) states that the specimens from Trinidad are *L. maya* and therefore *L. trinidadensis*.

**Table 2.** Composition of the UWIZM Mantodea collections split into UWIZM, CABI and CAREC collections showing number of specimens, range of date collected and collection site for each species.

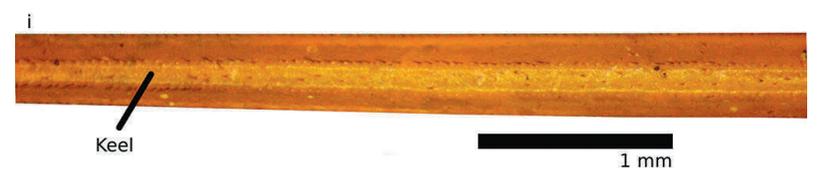
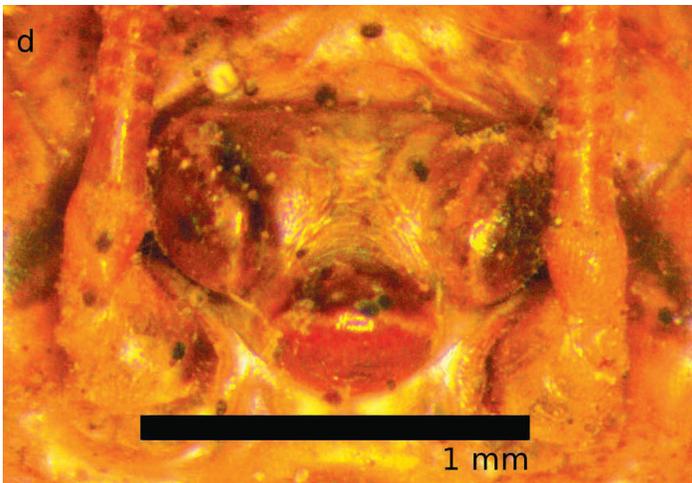
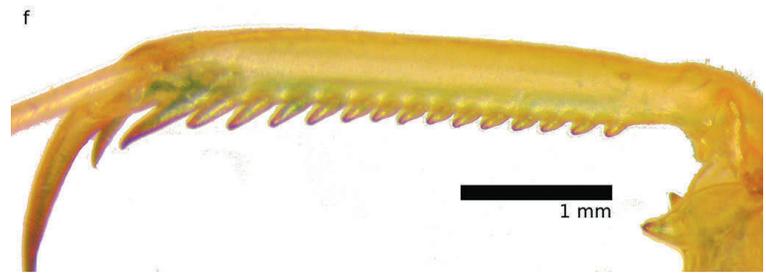
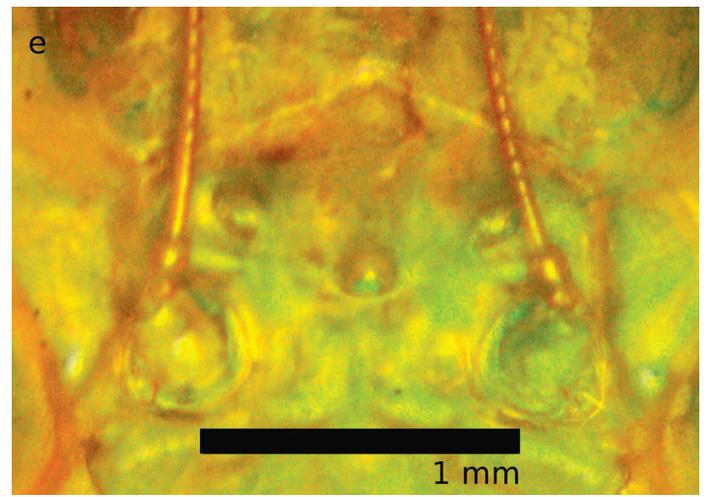
Species	Collection								
	UWI			CABI			CAREC		
	Number in Collection	Date Range	Collection Site	Number in Collection	Date Range	Collection Site	Number in Collection	Date Range	Collection Site
<i>Mantoida fulgidipennis</i> Westwood 1889	4	1938 - 2014	St. Augustine	4	1967 - 1972	Curepe	1	1965	P.O.S.
<i>Musonia surinama</i> (Saussure 1869)	9	1941 - 2008	St. Augustine, Tunapuna	8	1954 - 1978	Curepe, P.O.S., Diego Martin			
<i>Thespis media</i> (Giglio-Tos 1916)	9	1923 - 2014	St. Augustine, Warren, Aripo Savanna	3	1971 - 1989	Curepe, Simla			
<i>Thesprotia filum</i> (Lichtenstein 1796)	4	1942	St. Augustine, Claxton Bay	2	1967	Curepe			
<i>Bantiella trinitatis</i> Giglio-Tos 1915	12	1941 - 2014	Maracas Valley, Mt. St. Benedict, Cumaca, Goldsborough, Mayaro, Arima Valley	2	1954 - 1967	Curepe, Diego Martin			
<i>Acontista multicolor</i> Saussure 1870	13	1923 - 1999	St. Augustine, Mt. St. Benedict, Wallerfield, Las Lomas, San Rafael	8	1946 - 1977	Curepe, Mayaro, St. Augustine, Tunapuna			
<i>Tithrone roseipennis</i> (Saussure 1870)	16	1929-1999	Maracas Valley, Mt. St. Benedict, Morne Bleu, Blanchisseuse	5	1954 - 1989	Arima Valley, Aripo Savanna, Maracas Valley			
<i>Acanthops parafalcata</i> Lombardo & Ippolito 2004	18	1923 - 2010	St. Augustine, Simla, Trinity Hills, P.O.S., Maracas Valley	12	1953 - 1954	Curepe, Balandra, St. Augustine	5	1957 - 1964	P.O.S., Nariva Swamp
<i>Angela quinquemaculata</i> (Olivier 1792)	3	1959 - 1996	Mt. St. Benedict	3	1971	Curepe			
<i>Stagmomantis carolina</i> (Johannson 1763)	5	1942 - 1959	St. Augustine, Mt. St. Benedict	4	1968 - 1971	Curepe, Centeno			
<i>Stagmatoptera septentrionalis</i> Saussure & Zehntner 1894	21	1918 - 1990	St. Augustine, Maraval, Arima, San Fernando, Aripo Savanna, Crown Point	8	1967 - 1989	Curepe, Morne Bleu, Nariva Swamp			
<i>Parastagmatoptera unipunctata</i> (Burmeister 1838)	1	2013		13	1967 - 1979	Curepe			
<i>Oxyopsis rubicunda</i> (Stoll 1813)	2	1989	Maracas Valley						

Species	Collection								
	UWI			CABI			CAREC		
	Number in Collection	Date Range	Collection Site	Number in Collection	Date Range	Collection Site	Number in Collection	Date Range	Collection Site
<i>Vates lobata</i> (Fabricius 1798)	1	1959	St. Augustine	4	1981 - 1989	Curepe, Simla, Valencia			
<i>Liturgusa trinidadensis</i> Svenson 2014	11	1922 - 2004	St. Augustine, Lopinot Valley, Caura Valley, La Lune	4	1972 - 1979	Curepe			
<i>Phyllovates tripunctata</i> (Burmeister 1838)	1	1998	Trinity Hills	1	1967	Curepe			
<i>Paraphotina reticulata</i> (Saussure 1871)	1	1988	Mt. St. Benedict						
<i>Brunneria subaptera</i> Saussure 1869				1	1987	Aripo Savanna			

### Taxonomic Key to the Mantodea of Trinidad Mark S. Greener

The following is a dichotomous key that can be used to identify the mantids to species and is based upon work published by (Beier 1934, 1935, 1937; Giglio-Tos 1927; Terra 1995) as well as personal observations. See Figures 2, 3 and 4 for guide to terms used.

1. Pronotum as wide as long (Fig. 2a).....*Mantoida fulgidipennis*  
Pronotum not as wide as long.....2
2. Homochromy with dead leaves.....*Acanthops parafalcata*  
No homochromy with dead leaves.....3
3. Homochromy with lichen.....*Liturgusa trinidadensis*  
No homochromy with lichen.....4
4. Anterior femur with 3 discoidal spines.....5  
Anterior femur with 4 discoidal spines.....8
5. Pronotum with granules at lateral margins (Fig. 2c).....*Brunneria subaptera*  
Pronotum without granules at lateral margins (Fig. 2b).....6
6. Ocelli prominent (Fig. 2d).....*Paraphotina reticulata*  
Ocelli not very prominent (Fig. 2e).....7
7. External spines of anterior tibia straight and spaced. Has a green elytra covering wings which are red (Fig. 2f).....*Tithrone roseipennis*



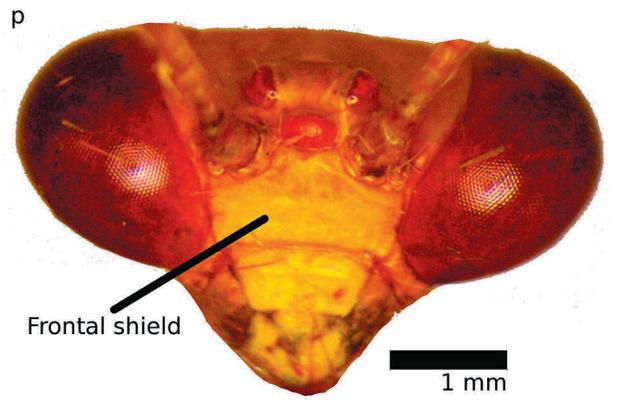
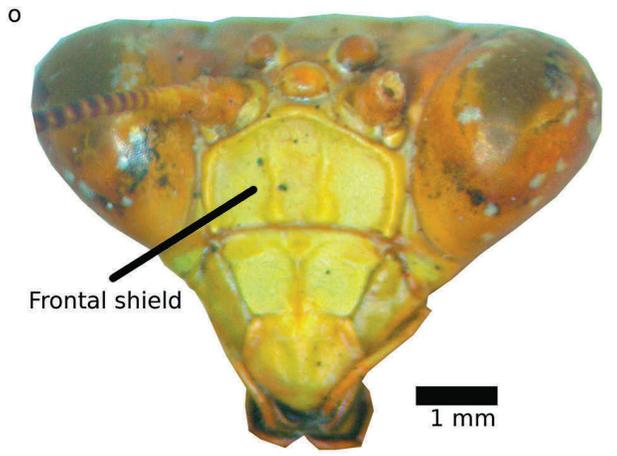
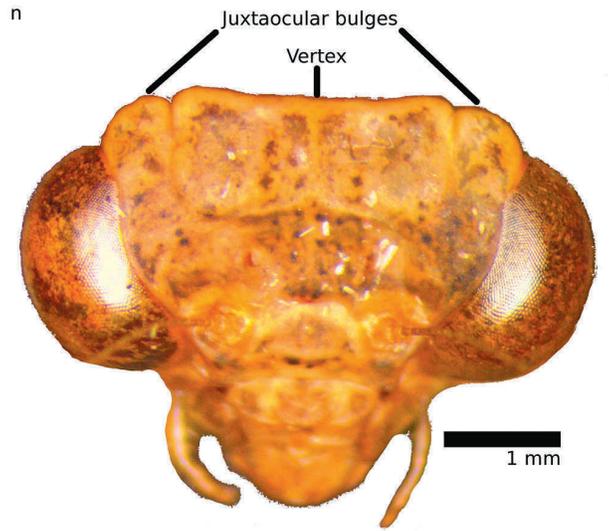
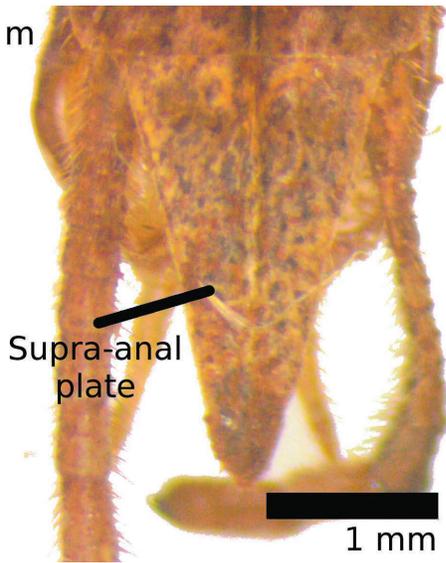
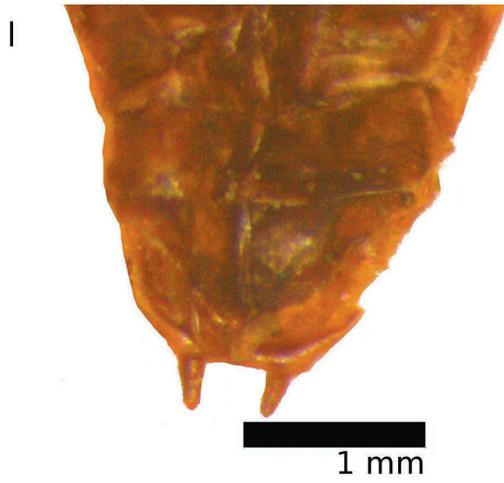


Fig. 2. Features mentioned in key.

External spines of anterior tibia closely packed and layered (Fig. 2g).....*Acontista multicolor*

8. Posterior tibia fully round (Fig. 2h).....9  
 Posterior tibia with dorsal keel (Fig. 2i).....12

9. Cerci expanded, flattened, foliaceous (Fig. 2k).....*Angela quinquemaculata*  
 Cerci rounded and not expanded (Fig. 2j) .....10

10. Supra-anal plate not as long as wide (Fig. 2l).....*Bantiella trinitatis*  
 Supra-anal plate longer than wide (Fig. 2m).....11

11. Anterior tibia much less than half the length of femur.....*Thesprotia filum*  
 Anterior tibia half or more the length of femur.....12

12. Anterior coxa as long as metazone of pronotum.....*Musonia surinama*  
 Anterior coxa shorter than metazone of pronotum.....13

13. Juxtaocular bulges and top of vertex at same level (Fig. 2n).....*Thespis media*  
 Juxtaocular bulges significantly higher than top of vertex which appears concave.....*Macromusonia sp.*

14. Ocellar tubercle with projection.....15  
 Ocellar tubercle without projection.....16

15. Lobes present on posterior legs.....*Vates lobata*  
 Lobes absent on posterior legs.....*Phyllovates tripunctata*

16. Eyes tapered.....*Oxyopsis rubicunda*  
 Eyes rounded.....17

17. Tegmina of females shorter than abdomen.....*Stagmomantis carolina*  
 Tegmina of females longer than abdomen.....18

18. Frontal shield a little broader than tall and has 2 vertical ridges (Fig. 2o).....*Stagmatoptera septentrionalis*  
 Frontal shield narrowed transversely and has no ridges (Fig. 2p).....*Parastagmatoptera unipunctata*

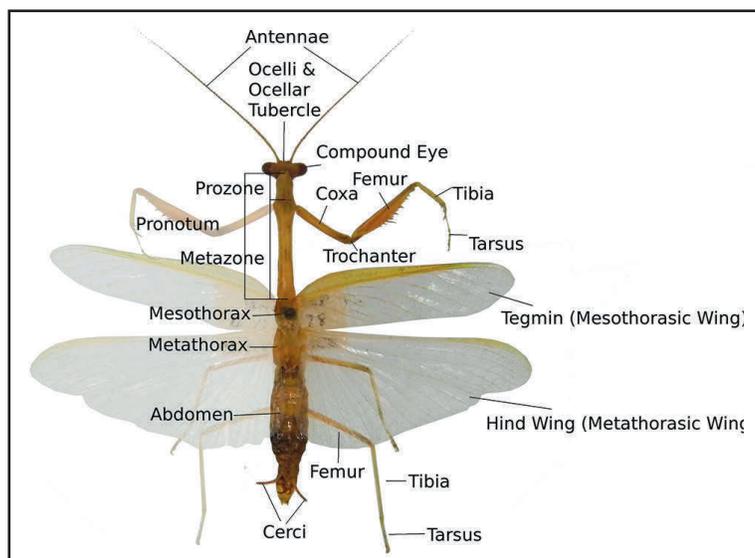


Fig. 3. Main anatomical features of mantid.

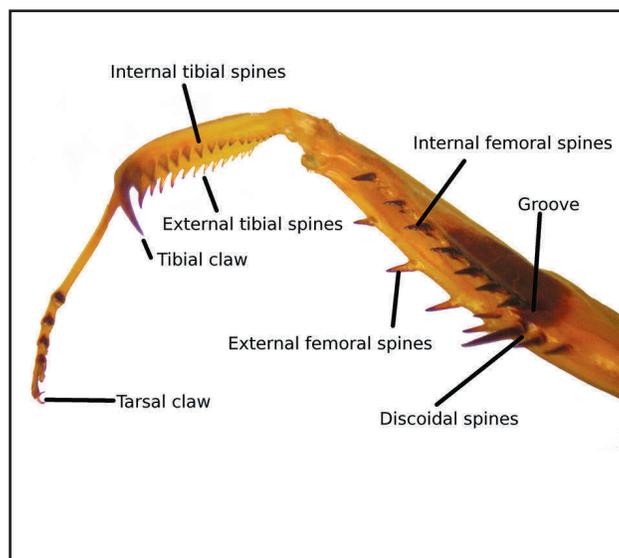


Fig. 4. Anatomical features of forehand.

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## NATURE NOTES

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### New Bat Record (Mammalia: Chiroptera) for Huevos Island, Trinidad and Tobago

During a TTFNC overnight trip to Huevos Island, an evening bat survey was conducted on 22 February, 2014. Three 12m nets and a harp trap were set up in the dry forest north of the only house on the island and were open from 1845 until 2110 h. The first net was set up diagonally (southwest - northeast) along the side of a gully and across a dry stream bed, ending on the other side. The second net was set up (north - south) on the east side of the gully on a flat patch of ground about 4m above the dry stream bed. The third net was set up (west - east) south of the second net on the same flat ground running alongside a fallen wall that was set just before the edge of the cliff at the back of the house. The harp trap was set up farther up the gully from the first net.

During the survey, 12 bats were caught, of which three were observed but escaped the nets either during handling or before they could be extracted from the nets. Nine others were identified by use of Carter (2004), weighed, sexed, and measured by MSG. Of these nine individuals, eight were male Jamaican fruit-eating bats, *Artibeus jamaicensis*, and one was a male common big-eared bat, *Micronycteris megalotis* (Fig.1). The latter was a new species record for the island. *Micronycteris megalotis* was an adult and was identified by its greyish brown breast as opposed to the light-coloured breast of *M. minuta*, with the calcar being longer than the foot and with pronounced hair on the ears. The ears of both species are joined over the forehead, but *M. minuta* has a notched band that divides into two relatively deep triangular furrows, whereas *M. megalotis* has a shallower and less intricately designed notched band of skin that lacks triangular furrows.

*Artibeus jamaicensis* had been caught in the only previous bat survey conducted on the island in 1965 (Manuel 1967). That survey also recorded the common long-tongued bat, *Glossophaga soricina*, and greater long-tongued bat, *G. longirostris*, as well as the greater fishing bat, *Noctilio leporinus*. No sightings of *N. leporinus* were made during the 2014 trip; the water within the bay was fairly rough on the night of 22 February, 2014, which may have prevented bats from fishing.

Further studies are required on the bats of the Bocas Islands and their relationship to the species on the mainland of Trinidad.



Fig. 1. The common big-eared bat, *Micronycteris megalotis*.

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## Guarding by Males in the Opilionid Family Cranaiidae

One of the most abundant and common arthropod groups found in tropical forests is the harvestmen, which are potentially useful indicator species (Wade *et al.* 2011). Of the four suborders of Opiliones, Laniatores is the most diverse, with 26 families and 3,700 species, most of which are found in the Southern Hemisphere. One of these families is the large-bodied Cranaiidae (Machado and Warfel 2006), which has a range extending from “the northern region of South America along the Andes and Amazon Basin up to Panama and Venezuela” (Pinto-da-Rocha and Kury 2003). *Phareicranaus calcariferus*, formerly known as *Santinezia serratobialis*, was synonymised by Pinto-da-Rocha and Bonaldo (2011). It is the only species of cranaid found in Trinidad and Tobago, and is one of the most common species of harvestman on Trinidad (Machado and Warfel 2006). Parental care of offspring has been documented in all orders of arachnids (Mora 1990), with most species of harvestmen exhibiting maternal care (Machado and Macías-Ordóñez 2007). The superfamily Gonyleptoidea, which includes the Cranaiidae, has been documented as containing nearly 80% of the total cases of maternal care reported in the order (Machado and Warfel 2006). The first reported observations of maternal care in the family Cranaiidae were made in Trinidad (Machado and Warfel 2006; Hunter *et al.* 2007) and noted guarding of eggs and early nymphs. Little information on paternal care in these animals is known; it has been observed in relatively few species, including *Zygopachylus albomarginis*, which formerly was assigned to the family Gonyleptidae (Mora 1990) but which has been reassigned to the Manaosbiidae (Kury 2003), and *P. calcariferus* (Machado and Warfel 2006). The objective of this paper is to provide further insights into the association of nymphs and adult males of the harvestman *P. calcariferus* over an extended period of time.

Observations were made during July 2010 and July 2011 in two localities in Trinidad: Acono Road, Maracas Valley (10° 43.147' N; 61° 23.639' W) at an elevation of approximately 190 metres, and Caura Valley (10° 41.309' N; 61° 22.248' W) at an approximate elevation of 127 metres. Both localities are situated in the Northern Range. Observations on egg clusters in Maracas Valley were made in July 2010, while those in Caura Valley were recorded in 2010 and 2011.

Each batch of eggs along with the guarding adult were photographed to count the eggs and identify the species. A positive identification was made from a collected adult specimen by use of the key developed by Townsend *et al.* (2008). Voucher specimens (Catalogue nos. UWIZM.2014.2.1 and UWIZM.2014.2.2) were

deposited in the Land Arthropod Collection of the University of the West Indies, St. Augustine, Trinidad and Tobago.

Three batches of eggs in Maracas Valley were observed from the 14 July to 2 August, 2010 between 0745 and 1400 h. All clusters of eggs were situated under a rock sticking out horizontally from a vertical bank at the side of the trail. The surrounding area was heavily shaded and moist. The first batch (Fig. 1) contained 52 eggs and was located approximately 10 cm from the edge of the protruding rock, while the second batch contained 117 eggs and was situated approximately 36 cm from the edge of the first cluster and 13 cm from the edge of the rock. The batches were comprised of eggs in different stages of development. Younger eggs were cream coloured with little speckling, while older ones were brown and speckled with black, with much of the embryos visible through the eggshells. The male on batch one abandoned the cluster on day 18, while the guarding male on batch two persisted until all but one of the embryos had developed and hatched; that batch was abandoned by the adult three days later (day 19), after which 17 nymphs remained around the cluster, comprising a little more than half the egg mass area. Eggs in batch one were also covered with mould. A similar substance covered one undeveloped egg in batch two after all of the other eggs had hatched.



**Fig. 1.** Eggs of *Phareicranaus calcariferus*, Maracas Valley, July 2010.

Batch three contained 91 eggs and was situated under an overhanging rock at a lower elevation (10° 43.067' N; 61° 23.669' W) along the side of the trail. The cluster was located approximately 20cm from the edge of the rock. This batch was first observed on 23 July, 2010 with only six eggs still remaining unhatched when observed a week later. This batch appeared to consist of eggs all in the same stage of development, with all being white in

colour. Three days later, the egg mass and guarding adult were absent, with two individuals of a different, unidentified species of harvestmen occupying the space.

In Caura Valley, observations were recorded from a single batch of eggs from 25 July to 5 August, 2010 and from 9-19 July, 2011. The batch was located under a small, exposed rock 5-8cm wide under an overhanging dirt bank, approximately 125cm above ground level and 13cm from the edge of the rock. The eggs in both batches were all white in colour and appeared to be in the same developmental stage. First observed on 25 July, 2010, the egg batch was next observed seven days later; during the intervening time, the embryos had developed. Two days later, no eggs, larvae, or nymphs were present; however, the adult male was still present, and it remained until two days later. It was noted that when no eggs were present, the flash of the camera caused the male to move off his batch; however, when eggs were present, the male did not move in response to the flash.

The typical position of the male was at the side of the cluster of eggs, covering 5-15 eggs with the body and two legs on the same side of the body. It maintained this body position throughout the development of the eggs, even when the eggs became covered in mould. When the spiderlings hatched, the male kept its legs behind its body.

The evolution of parental care and the matter of which parent cares for the offspring is determined by factors such as the mode of fertilisation, the order of gamete release, and the certainty of paternity. Maternal care is expected when females are able to fulfil the following three requirements: 1) they are long-lived so that they can provide some benefit to the offspring after oviposition, 2) they can defend the offspring, and 3) they are constrained to semelparity. However, parental care by males is considered costly not only because it exposes them to predators and reduces their foraging time, as is the case with females, but males are also using energy not directly related to their maintenance and growth (Requena *et al.* 2009). There have been no reports of males and females caring for offspring at the same time in opilionids (Mora 1990); however, Requena *et al.* (2009) showed that paternal care is just as effective as that given by females in opilionids. Furthermore, it has been suggested that caring for an egg batch makes a male a more attractive mate and that as a result the pair will copulate more frequently (Requena *et al.* 2009). This may be the same benefit to *P. calcariferus* males that cared for clutches that contained eggs in different stages of development as that which has been reported for other species of opilionid males that exhibited parental care; it also may be the result of multiple ovipositions from different females, as referred to by

Requena *et al.* (2009).

One of the most important functions of parental care is guarding against egg mortality. An important source of egg mortality is fungal attack (Requena *et al.* 2009), which is not surprising due to the moist conditions in which the batches were found, conditions ideal for fungal growth. The guarding males of species like *Z. albomarginis* have been noted to chase away potential predators like ants and conspecifics and to remove fungus from eggs (Mora 1990). *Iporangaia pustulosa* males apply a mucus coating to eggs, which most likely physically deters egg predators (Requena *et al.* 2009). However, males of *P. calcariferus* did not appear to utilise measures to deter egg predators, nor were they observed to remove any fungus that had accumulated on the batches. Opilionid males have been observed to leave the clutches unattended frequently and to move as far as five metres away from the egg batch (Requena *et al.* 2009); however, this was not observed in males of *P. calcariferus*.

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## New Scorpion Records for Chacachacare and Huevos Islands, Trinidad and Tobago

The scorpion fauna of Trinidad and Tobago is well-known, with nine species in two families having been recorded throughout the islands (Kjellesvig-Waering 1966; Lourenço and Huber 1999; Prendini 2001). However, there are still gaps in the exact distribution of the species especially in the smaller islands off the northwestern point of Trinidad. Here we provide details of three new records for Chacachacare and Huevos islands.

On 29 September, 2012, during a University of the West Indies field trip, a single specimen of *Ananteris cussinii* Borelli 1910 was collected by RB. It was found by use of UV light in leaf litter near the abandoned nurses' quarters in the southern half of Chacachacare Island. It was identified by MGR and was deposited at The University of the West Indies Zoology Museum (UWIZM) under accession number UWIZM.2014.7.1.

This brings the total number of scorpion species recorded for Chacachacare Island to four alongside *Microtityus rickyi* Kjellesvig-Waering 1966, *Tityus trinitatis* Pocock 1897, and *Tityus melanostictus* Pocock 1893 (Lourenço and Huber 1999).

On 22 February, 2014, during a TTFNC overnight trip to Huevos Island, Trinidad and Tobago, several scorpions were collected in the gully leading up from the house on the south side of the island. MGR collected a large *Tityus trinitatis* Pocock 1897 as it walked across leaf litter, SS collected one juvenile *T. trinitatis* and several juvenile *Tityus melanostictus* Pocock 1893 from tree trunks and leaf litter by use of UV light, and MSG collected a

single large female *T. melanostictus* as it walked across leaf litter. All specimens were identified by MGR. The *T. trinitatis* specimen was deposited in the UWIZM under accession number UWIZM.2014.5.15 and the *T. melanostictus* under number UWIZM.2014.5.16.

Huevos Island had not been surveyed before for scorpions, making these the first records for the island and putting the current total for the island at two species.

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## An Encounter with a Large School of Dolphins off the Coast of Charlotteville, Trinidad and Tobago

The waters surrounding Trinidad and Tobago are known to be used by at least 19 species of cetacean, including 14 species of dolphin (Cetacean Conservation and Research Organization [CCARO], online). Very little information is known about the distribution, abundance or habitat use of cetaceans around either island, especially Tobago. Here, we describe the first recorded sighting of Atlantic spotted dolphins (*Stenella frontalis*) off the coast of Tobago, and the largest group containing this species recorded for either island.

On 6 August, 2012 at around 1400 h, AED and two companions were being transported by a small fishing pirogue to St. Giles Island to do some recreational snorkelling.

About halfway between the jetty and the destination (approximately 11° 20' 52" N; 60° 33' 52" W; Fig. 1), the boatman alerted the passengers to the presence of dolphins ahead of the boat. Within minutes the boat was surrounded by between 50 and 100 individuals (lower and upper estimates).



Fig. 1. Map showing approximate location of encounter.

Several were swimming alongside the boat and displaying wake-riding and bow-riding behaviours. Others were milling in the wider area, surfacing often. Aerial behaviours were observed in at least one individual (Fig. 2). The encounter lasted around 15 minutes, after which the group moved away from the boat.

Some of the dolphins were easier to identify than others. Many of the individuals that approached the boat close enough to be clearly seen were grey with spots, had a dark cape on the back, a lighter underside and a pale spinal blaze extending into the dark cape ending just under the dorsal fin (Fig. 3). The tri-colour patterning in conjunction with the observed pale blaze identifies these



Fig. 2. Aerial behaviours of *Stenella frontalis*.



Fig. 3. This individual displays the 'pale spinal blaze' and spotting that are characteristic of *S. frontalis*.



Fig. 4. Extent of spotting increases with age in *S. frontalis*; the individual in the foreground is heavily spotted, to the point that it obscures the cape and blaze.

spotted individuals as *Stenella frontalis*, Atlantic spotted dolphins. Atlantic spotted dolphins typically display a distinct variation in patterning with age. At birth, calves have a two-toned pattern and are unspotted. As the animal matures, spotting increases until some adults become heavily spotted, obscuring the cape and blaze (Herzing 2006). The group observed here included several heavily spotted individuals (Fig. 4), as well as those on which the cape and blaze were visible.

Other individuals, seen and photographed further away from the boat, appeared unspotted and uniformly grey with a narrow rostrum (Fig. 5). It was not possible to see the lower sides and underside of the unspotted individuals, thus the species could not be confirmed.



**Fig. 5.** Unspotted individuals. These individuals had a relatively long, narrow rostrum and seemed a uniform colour, but as the underside was not visible, confirmation of species was not possible.

There are two possibilities here. The first is that we were in fact observing a mixed species group and these unspotted individuals were *Tursiops truncatus* (bottlenose dolphins). This species is commonly observed in the coastal waters of Trinidad and Tobago (Naranjit, unpublished) and is known to associate with *S. frontalis* (Herzing and Johnston 1997). However, it must be noted that the rostrums of the unspotted individuals were relatively long and narrow in comparison to locally observed bottlenose dolphins, and more similar to those of *S. frontalis*.

The second possibility is that all the individuals were *S. frontalis*, and the variation observed was intra-species variation. The extent of spotting on *S. frontalis* is known to vary geographically; a heavily spotted form is commonly observed over the continental shelf, while oceanic populations tend to include more lightly spotted individuals (Jefferson *et al.* 2011). In Trinidad, many of the Atlantic spotted dolphins seen are lightly spotted (Naranjit, unpublished), and there have been observations of virtually unspotted individuals off the coast of Brazil (Jefferson *et al.* 2011). Therefore, the possibility remains that we were observing natural variation in extent of spotting within this species rather than a mixed species group.

This is the first recorded sighting of Atlantic spotted

dolphins around Tobago. Coastal groups of this species tend to number between 5 and 15 (Jefferson *et al.* 2011) although offshore groups may contain more than 200 individuals (Shirihai 2006). In Trinidad and Tobago the majority of reported dolphin groups of any species contain fewer than 20 individuals, and the largest group of *S. frontalis* previously recorded for Trinidad contained at least 17 individuals (Naranjit, unpublished). This makes the encounter described in this note the largest group containing *S. frontalis* individuals currently recorded for either island.

It is important to consider that in Trinidad and Tobago:

- the number of cetacean sightings reported is very low
- most sightings of dolphin groups are probably not reported
- most reported sightings are around the island of Trinidad
- there have been no previous sightings of *S. frontalis* reported around Tobago.

These factors make it difficult to draw accurate conclusions about what is typical for *S. frontalis* groups around Trinidad and Tobago.

More data are needed on cetaceans in Trinidad and Tobago if we are to understand the habitat use and behaviour of these animals, their population dynamics and the potential threats they face, such as disease, predators, marine pollution (noise, chemical, debris), vessel strikes, entanglement in fishing gear, prey depletion and hunting. Such information will aid in the development of effective conservation strategies to protect cetaceans in Trinidad and Tobago.

One successful means of obtaining some of this information is through collecting reports of whales and dolphins from the general public. Information on the date, time, location, number, description and behaviour of the animals is most helpful, as are photographs and videos of an encounter. In Trinidad and Tobago, the CCARO collects such reports through forms on their website ([www.ccaro.org](http://www.ccaro.org)) and encourages members of the public to contribute to the scientific understanding of these animals by reporting sightings.

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## A Safe Haven for Three Freshwater Invasive Alien Species in Tobago, Trinidad and Tobago

Invasive alien species are non-native species that have been introduced either through self-introduction or by man and which have subsequently become a threat to a country's economy (e.g., agriculture and trade, infrastructure [e.g., water supplies], human health, etc.). They may also impact biodiversity, habitat quality, and ecosystem functions. Aquatic invasive alien species (IAS) have been documented in both Trinidad and Tobago but generally are regarded as established or naturalised exotics, as their potential negative impacts are not appreciated fully. These exotics include a wide range of taxa such as the Malaysian prawn, *Macrobrachium rosenbergii*, in Trinidad (Rostant 2005; Mohammed *et al.* 2011); the red-rimmed melania (snail), *Melanooides tuberculata*, in Trinidad (Snider 2001) and in Tobago (Bass 2003); the quilted melania (snail), *Tarebia granifera*, in Trinidad (Snider 2001) and in Tobago (van Oosterhout *et al.* 2013); the apple snail, *Pomacea diffusa*, in Trinidad (Mohammed and Rutherford 2012) and in Tobago (Rutherford and Mohammed 2013); the red-eared pond slider (turtle), *Trachemys scripta elegans*, in Trinidad (Mohammed *et al.* 2010); and the three-spotted gourami, *Trichogaster trichopterus* (Mohammed *et al.* 2010), among others. The invasive snails arrived via the aquatic ornamental pet trade, presumably with aquatic plants and, as in the case of *Pomacea diffusa*, as intentional purchases as pets (pers. obs.).

Several monitoring events over the last five years throughout Tobago's drainages revealed three aquatic invasive species to be established at one site in southwestern Tobago: *Melanooides tuberculata*, *Pomacea diffusa*, and *Oreochromis mossambicus*. The site was visited

three times in 2013 (March, June, and November). The main water source was found to be a limestone spring (GPS UTM 20P 737032, 1234456) just north of Milford Road, south of the Pigeon Point mangroves. The vegetation at the site includes a variety of swamp sedges: *Typha latifolia* (cattail), *Pistia stratiotes* (water lettuce), *Eichhornia crassipes* (water hyacinth), and *Salvinia* species (floating ferns); the latter are the predominant aquatic plants at the lower stream and lagoon area. Clear water flowed continuously (approximately 5m per min.) from the main limestone outcrop during all three visits and appeared to be independent of rainfall intensity. Coralline rocks and pebbles were visible within the thick detritus substrate. The riparian vegetation was comprised of an invasive terrestrial plant, the Noni fruit, *Morinda citrifolia*. The site seems to have had very little anthropogenic impacts except the exotic biota.

The Noni fruit is native to Southeast Asia and Australia. It has a wide habitat preference which includes shady forests, open rocky to sandy shores such as volcanic terrains, lava-strewn coasts, clearings or limestone outcrops, as well as in coralline atolls. It is tolerant of saline soils and drought conditions (Nelson 2003). Important amino acids such as aspartic acid and several minerals are found in the fruit (Chan *et al.* 2006). This plant was originally cultivated in Tobago as both an ornamental and oddity fruit; however, it is now widely distributed on the island.

Two of the three aquatic IAS at the spring are mentioned above: *M. tuberculata* and *P. diffusa*. The third IAS is a tilapine cichlid, *Oreochromis mossambicus*. Small depressions in the substrate characteristic of Tilapia were observed by G. White in the late 1980s at

Hillsborough Dam. The species was observed by the author in 2004 in shallow, brackish streams leading into the Bon Accord mangroves and also in small storm drains leading into Scarborough Bay. *Oreochromis mossambicus* was first documented in Scarborough (Phillip 1998). It was introduced to Tobago for aquaculture but was poorly managed with regards to housing and to distribution of fingerlings. Its impact can be rated as minimal overall because populations are restricted to southern Tobago. This species is herbivorous but will occasionally prey upon smaller fish. At the spring site, the population density of *O. mossambicus* ranged from 5 to 10 per m<sup>2</sup> during all three visits, whereas at the runoff drainage near Scarborough the density was greater, ranging from 10 to 20 per m<sup>2</sup>. Some individuals were quite large (> 25.0cm in total length).

At the spring, the food web seemed to be fuelled by the dropped Noni fruits, as both *O. mossambicus* and the two species of snails mentioned above were observed feeding on Noni fruits. A native snail, *Marisa cornuarietis*, also was observed at the spring; individuals of all three species exhibited some degree of gigantism. Juveniles were observed, but the density of large individuals was high, with giants predominating the size classes for all three species. Density was highest ( $\approx 60$  per m<sup>2</sup>) in the native species, followed by that of *M. tuberculata* and *P. diffusa*, respectively ( $\approx 30$  per m<sup>2</sup> and 5 per m<sup>2</sup>). Our observations were consistent with those of Berry (1962) and McKillop and Harrison (1972), who documented increases in densities of terrestrial snails at the base of limestone hills; they attributed this increase to the snails' use of calcium and its availability in water flowing through limestone. The habitat at the spring was determined to be conducive for population expansion for all three species, as all snail and fish species have adequate food sources with reduced competition for food. The enemy release hypothesis (Blossey and Notzold 1995) indicates that when an exotic is introduced to a new range, population expansion can be rapid because of lack of predator or parasite pressure; in other words, a species is released from its natural enemies. At the spring, all species (the exotic fish, both species of exotic snails, and the single native snail species) have no predators, and they also have an unlimited food resource, conditions allowing for gigantism and also for increased fecundity.

This site, which provides a safe haven for aquatic IAS, should be monitored continuously as it could serve as a pool for proliferation of invasive species. In addition, introduction of other species, such as *Tarebia granifera*, could result in negative effects on the other species. Both *M. tuberculata* and *T. granifera* have been documented in high densities, outcompeting native gastropods, at other

sites in both Trinidad and Tobago (van Oosterhout 2013). The dynamics of the Noni-powered food web, the occurrence of the giant snails, and the ecological impacts of these organisms on native wildlife need further investigation.

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## A Leucistic Copper-rumped Hummingbird (*Amazilia tobaci*) on Tobago, Trinidad and Tobago

A leucistic hummingbird was seen on Tobago (Fig. 1). This may be the first all-white hummingbird recorded in Trinidad and Tobago. The bird was first seen on 24 November, 2013 at 1055 h at Adventure Farm and Nature Reserve Bird Observation Centre near Arnos Vale in Tobago. Adventure Farm maintains flowers, gardens and bird feeding stations to encourage the viewing of the local birds.

Leucism is a rare condition which affects the pigment in skin, hair and feathers of animals “characterised by reduced pigmentation,” as opposed to albinism, which is “a congenital disorder characterised by the complete or partial absence of pigment in the skin, hair and eyes due to absence or defect of tyrosinase, a copper-containing enzyme involved in the production of melanin” (Wikipedia).

The white hummingbird, which was determined to be a Copper-rumped Hummingbird (*Amazilia tobaci*), became an instant hit. I saw the bird on 8 December, 2013. The bird returned to the hummingbird feeders about every 20 minutes.

The body and head were all pure white, except for the bill which was dark, mostly straight and had a pink lower mandible. The legs and feet were dark, as were the eyes. The primaries were a light-brown colour. The outer, or primary feathers appeared to be frayed and somewhat ragged with the leading edge completely worn, and the dark skin showing through. The flight also appeared not to be as strong as the other hummingbirds, with more pe-

riods of gliding and less acrobatic flight than of the other hummers. Despite the territoriality of the other hummingbirds present, this bird held his own at the feeders.

The bird visited the feeders daily for about six weeks, but was not seen subsequently.

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**Fig. 1.** Leucistic Copper-rumped Hummingbird in Tobago. Photographed: 8 December, 2013.

## First Records of Mantids (Insecta: Mantodea) on Huevos Island, Trinidad and Tobago

Huevos Island is one of several islands off the north-west tip of Trinidad. It is privately leased and therefore rarely visited. However on 22 February, 2014, as part of a TTFNC overnight trip to the island, a wide-ranging survey of the wildlife was undertaken. Dry forest in the gully just north of the only house on the island was surveyed from approximately 0830 to 1100 h during which time several mantid specimens were hand collected. A light trap was set up by KS in the gully and ran from dusk until around 0230 h. Of the 19 species that have so far been recorded on the two main islands of Trinidad and Tobago, 4 were found on Huevos during our survey. All specimens collected were identified by MSG and have been deposited in The University of the West Indies Zoology Museum.

One mature male *Mantoida fulgidipennis* Westwood 1889 was caught by KS after appearing at the light trap. Accession number UWIZM.2014.5.13.

One immature female *Angela quinque maculata* (Olivier 1792) was found by AED around 1m off the ground on the side of a small tree. The insect was stretched out as to appear like a stick. Whilst in the collection vessel, the insect shed its exoskeleton which was also retained. Accession number UWIZM.2014.5.14.

The presence of *Parastagmatoptera unipunctata* (Burmeister 1838) was determined from a photograph taken by KS at the top of a ridge in the centre of the island on a patch of herbaceous plants around 1.5m tall (Fig.1). A shed exoskeleton was later found in the same location. Accession number UWIZM.2014.5.12.

Two immature male *Liturgusa trinidadensis* Svenson 2014 were found by MGR and AED on the sides of small trees around 1m off the ground in the same location as the *Angela quinque maculata* above. Accession numbers UWIZM.2014.5.10 and.11

Mantis surveying has never been conducted on Huevos or any of the islands to the west of Chaguaramas. Bruner (1906), Beebe, Crane and Hughes-Schrader (1952) and Kevan (1953) made no mention of surveys or specimens from any of the islands. Finding representatives on Huevos of three of the five Mantodea families present in Trinidad shows that the islands have suitable habitat for a variety of species, and suggests that further surveys would be likely to reveal the presence of even more. This survey has highlighted the potential for further work on the Bocas Islands to catalogue the mantids present and compare the mantid communities between the Bocas Islands with mainland Trinidad.

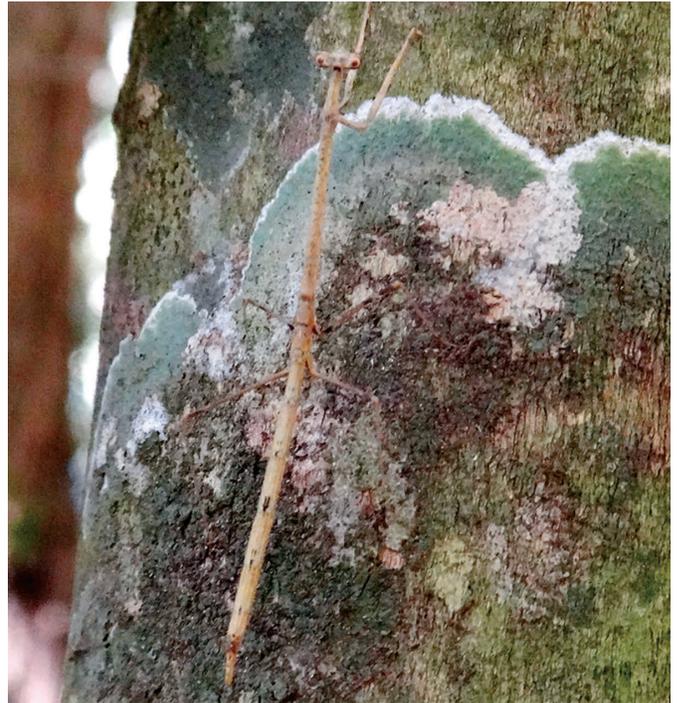


Fig. 1. *Angela quinque maculata*, Huevos Island, February 2014.

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## Observations of Colonies and Responses to Disturbance by the Uloborid Spider *Philoponella republicana* (Araneae: Uloboridae) at Simla Research Station, Trinidad and Tobago

Social behaviour is uncommon in spiders. Out of the documented 44,540 spider species (Platnick 2014), only a few dozen exhibit sociality (Avilés 1997). Such sociality varies from forming aggregations of individual webs to cooperative brood care. According to Avilés (1997), social behaviour in spiders can be placed in four categories: 1) non-territorial permanent-social (quasi social), 2) territorial permanent-social, 3) non-territorial periodic-social (sub-social), and 4) territorial periodic-social.

Increased foraging efficiency is one of the reasons cited most frequently as an advantage of social behaviour in spiders (Binford and Rypstra 1992); therefore, for web-building spiders this is dependent upon the location and condition of their webs. Thus, by continual disturbance of the colony (webbing), one can observe how the colony adapts to either increasing or maintaining their foraging efficiency. This short communication describes the physical structure and colony composition of nine colonies of *Philoponella republicana* (Araneae: Uloboridae), a territorial permanent-social species, in the secondary forest bordering the property of the Simla Research Station in the Arima Valley, Trinidad, W.I. Observations were made between 0930 and 1230 h from 10-24 July, 2011. The largest colony was selected and disturbed on each of the final five days of observation and the web structure of the colony recorded.

The presence of this species in secondary vegetation is not surprising because of the abundance of attachment sites for web construction (Smith 1985). Colonies were on average 15.7cm above the ground, 59.2cm in width, and 63.3cm in length. Two colonies consisted of an elongated tangle retreat flanked by a series of small orb webs. These webs were arranged in a straight line in one colony. In the second colony they were arranged in a semi-circle on the right side of the tangle retreat, with one orb web near the bottom of the semi-circle arrangement being horizontally oriented. Both colonies contained spiderlings of two age groups, approximately one instar apart. In both colonies, the younger nymphs occupied the tangle retreat while the older individuals occupied the orb webs. However, older individuals were also observed in the tangle retreat, but no younger individuals were found in the orbs.

Five colonies consisted only of a tangle retreat placed

on the left, with sparse supporting threads forming a rough triangle on the right. However, all five colonies were occupied by individuals of the same age class, either all late instar nymphs or penultimate nymphs. In two colonies, the retreat was located in the base of the web complex in one colony and in the centre of the complex in the other colony.

In colonies in which the tangle retreat was on the left, in one colony the individuals were roughly evenly distributed between the tangle retreat and the support threads on the right side of the web, whereas in the remaining colonies, approximately 95% of individuals occupied the tangle retreat.

**Table 1.** Composition of colonies of *Philoponella republicana* collected at the Simla Research Station, Trinidad, W.I., 10-24 July, 2011. *Note:* Colonies 7, 8, and 9 were collected.

Colony	Total No. of Individuals	Sex	
		Male	Female
1	10	0	10 (nymphs)
2	9	0	9 (nymphs)
3	2	0	2 (penultimate nymphs or adult)
4	4	0	4 (1 adult; 3 penultimate nymphs)
5	5	0	5 (penultimate nymphs)
6	11	0	11 (penultimate nymphs)
7	67	1 (nymph)	66 (nymphs)
8	105	5 (nymphs)	100 (nymphs)
9	232	14 (13 nymphs; 1 adult)	218 (2 nymphs; 216 penultimate nymphs)

In two colonies, flying insects (a honeybee, *Apis mellifera*, and a wasp, *Angiopolybia pallens*) were caught in the web complex. In both cases no spiders approached the struggling insect. By the end of the observation period, the bee was still trapped in the web, but the wasp had freed itself.

Examination of colony composition showed that colonies can both be dominated by either nymphs or penultimate nymphs. Colonies of this species are founded by masses of nymphs (Lubin 1980). Therefore, colonies dominated by nymphs, such as colonies one, two, seven

and eight (Table 1), may be in the early stage of development, with larger colonies such as seven and eight showing the transition between founding and established; colonies dominated by penultimate nymphs are believed to be older and more established. However, colonies with a small number of penultimate nymphs, such as colonies three to six (Table 1), could represent colonies near the end of their lives, with many of the occupants either dead or having already dispersed.

A study of the colony composition of two temperate *Philoponella* species, *P. oweni* and *P. arizonica* (Smith 1997), showed that penultimate nymphs emerged in early April to early June. However, in *P. republicana*, penultimate nymphs were present later. Also, males tend to be shorter lived than females and would disappear from the population in these two species over the summer period; however, for *P. republicana*, males started to show up in the population. They may be waiting to gain maturity and mate with the females in the colony. However, our results seem to indicate that males are found in larger colonies, suggesting that they may select these colonies to have a greater chance of reproductive success, as there are more females to mate with in larger colonies than in smaller colonies.

The largest colony (Colony 9) was disturbed each day for five days and any changes in colony structure noted. Disturbance consisted of dusting the entire colony with talcum powder. This served to highlight the web structure for description and coat the sticky catching silk on the spiral of the webs, thereby directly affecting the ability of the spiders to catch prey. Observations on the web structure were taken the next day. After each such disturbance, on the following day the dusted webbing was cut down and discarded either to the side of or below the web complex. On the first day, the tangle retreat was constructed in the centre, surrounded by orb webs. Subsequent disturbances caused an increase in web area and in the number of orb webs, with more members of the colony building webs and a gradual reduction in the number of individuals in the tangle retreat. On the third day, the shape of the diagonal webs changed to almost a spiral structure, which was maintained into the fourth day. The colony originally was orientated in a north-south direction; however, on the fourth day the web accidentally was com-

pletely destroyed and the next day was rebuilt in the east-west orientation.

Orb-weaving spiders respond to a decrease in food supply in a number of ways, including relocating webs and spinning larger webs; however, communal spider species respond differently, by changing the distance between the orb webs in the colony (Smith 1985). In Smith's 1985 study, a tent was built around colonies to exclude prey to allow study of the effect of prey exclusion on the distance between orb webs. It was found that when the tent was removed, the colony would move to another site. In the present study, the persistence of this colony at this site after continuous disturbance and total destruction, despite the time taken to repeatedly rebuild webs, may indicate that this site was ideal in terms of availability of attachment sites as well as prey levels. It is also possible that the level of disturbance may have been insufficient to trigger a response to cause the colony to relocate.

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# Eleventh Report of the Trinidad and Tobago Bird Status and Distribution Committee: Records Submitted During 2013

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The Trinidad and Tobago Bird Status and Distribution Committee (previously known as the Trinidad and Tobago Rare Birds Committee) was established in 1995 to assess, document, and archive the occurrence of rare or unusual birds in Trinidad and Tobago and thus provide reliable long-term monitoring of our rarer species. The Secretary of the Committee represents Trinidad and Tobago on the South American Classification Committee (SACC) of the American Ornithologists' Union (AOU).

The Committee has now assessed all records submitted during 2013. In all, 90 records were adjudged, representing 54 different species. One additional species has been added to the Official Checklist of Birds of Trinidad and Tobago, bringing the running total to 473 species at the end of 2013. Of the submissions assessed, in only six cases did the Committee find the identification inconclusive. The records presented below follow the nomenclature and taxonomic order of the AOU's Classification of the Bird Species of South America, December 2013 (Remsen *et al.* 2013).

The Committee comprises the following members: Martyn Kenefick (Secretary), Geoffrey Gomes, Floyd Hayes, Bill Murphy, Kris Sookdeo and Graham White. Archived records, including photographic submissions, numbered 1,027 at the end of 2013, are held at 36 Newalloville Avenue, San Juan, Trinidad. Previous reports of this committee were prepared by Hayes and White (2000), White and Hayes (2002) and Kenefick (2005, 2007, 2008, 2009, 2010, 2011, 2012 and 2013).

The list of species considered by the Committee, together with the Official Checklist of the Birds of Trinidad and Tobago and details of all records accepted by the Committee, can be accessed from our new website at <http://rbc.ttfnc.org>. We urge finders to document and report their sightings to us.

## RECORDS ACCEPTED

A flock of six **White-faced Whistling-Ducks** (*Dendrocygna viduata*) was photographed flying over the Caroni Rice Project on 29 August, 2013 (FA, FO, MRo). All sightings of this species in Trinidad and Tobago in recent times have been between the end of May and mid-October.

An immature/female **American Wigeon** (*Anas amer-*

*icana*) was photographed at Lowlands, Tobago (NG, MK, GW). It was found initially on 16 November, 2013 and remained until 20 November, 2013 at least. There have been six documented sightings of this species in Trinidad and Tobago in the last 18 years, all from Tobago.

Two immature/female **Green-winged Teal** (*Anas crecca*), in the company of Blue-winged Teal (*A. discors*), were seen and photographed on 16 November, 2013 at Lowlands, Tobago (see plate). They were present until 20 November at least (NG, MK, GW). Whilst still extremely rare in Tobago, this is the third record of this migrant from continental North America. The species has not been recorded from Trinidad.

An immature/female **Ring-necked Duck** (*Aythya collaris*) was found at Lowlands, Tobago, on 10 December, 2013 (MKe). Additionally, there were undocumented reports of a flock of 10 at the same location on 16 November, 2013 (NG, pers. comm.).

A flock of 28 **American Flamingos** (*Phoenicopterus ruber*) were photographed on 1 May, 2013 feeding on the tidal mudflats at Orange Valley (NL). This is the fourth highest group total ever found in Trinidad, the largest being 137 in August 2003.

Up to three **Jabirus** (*Jabiru myzateria*) were found and photographed on 27 July, 2013 in the agricultural fields and freshwater marsh surrounding Kernaham Settlement, Nariva Swamp (FA *et al.*) (see plate). Two birds were still being reported into early November. It was also reported that a third bird was shot soon after arrival.

Single adult **Gray Herons** (*Ardea cinerea*) were seen and photographed feeding on the tidal mudflats at Orange Valley on 28 January, 2012 (NL) and between 26 December, 2012 and 5 January, 2013 (many obs). Further sightings were made on 2 December, 2013 (NL) which remained until 22 December, 2013 at least (MK). It is not possible to categorically state how many birds were involved. This is a well-watched site, and there were no reports of the species during the intervening 11 months of each year. The recent increase in documented records of this species may have more to do with awareness of identification criteria by local birdwatchers than it does with a change in species status.

An adult **Cocoi Heron** (*Ardea cocoi*) was photographed beside the Richmond River in Tobago on 24

March, 2013 (MKe). This is the fourth record for Tobago in this century, all found in February or March.

An adult **Whistling Heron** (*Syrigma sibilatrix*) was photographed in cattle fields beside Turure Farm Road on 15 October, 2013 (KM) (see plate). Despite searching on subsequent days, the bird was never relocated. Native to the llanos and Orinoco Basin of Venezuela, this is the first record for Trinidad and Tobago.

An adult **Scarlet Ibis** (*Eudocimus ruber*) was photographed at the freshwater lakes at Lowlands, Tobago, on 4 April, 2013 (AR). This is the first documented record for Tobago in at least 18 years.

A flock of seven **Glossy Ibis** (*Plegadis falcinellus*) was seen flying over the Caroni Rice Project on 27 October, 2013 (FM, AS, SR). In Tobago, a particularly confident individual fed beside a roadside ditch at Bon Accord on 16 November, 2013 and was still present at the end of November at least (NG, MK, GW) (see plate). There are unconfirmed reports that it was subsequently shot. This is the first record for Trinidad's sister isle in many years. Whilst documented in seven of the last 13 years, the origin of these individuals remains uncertain. They are abundant in Venezuela, and our birds may well be engaging in post-breeding dispersal. They also migrate south in autumn from their North American breeding sites and could conceivably reach Trinidad from there. Moreover, the Committee has one documented photograph of a bird banded in southwestern Spain (Kenefick 2009).

A **Black Vulture** (*Coragyps atratus*) was observed soaring over Speyside, Tobago, on 28 September, 2012 (MB). With only two such documented sightings in Tobago in the last 18 years, these were probably birds that had wandered over from Trinidad.

An adult **Black-collared Hawk** (*Busarellus nigricollis*) was photographed over Rousillac on 1 January, 2013 and again on 30 November, 2013 (KS). The lack of birdwatcher coverage in this swamp, as well as a previous sighting by the same observer in the same area in November 2011 (Kenefick 2012), suggests that this bird may be resident. There has been only one other documented record of this species from Trinidad and Tobago in the last 18 years.

An immature **Snail Kite** (*Rostrhamus sociabilis*) was photographed on 1 May, 2013 on the Caroni Rice Project; it may well have been the same individual seen on 20 July (CS, FO, NL). Despite an abundance of suitable habitat, this rare wanderer from the South American mainland has been documented in Trinidad and Tobago on only nine occasions since 1995.

The only documented report of **Crane Hawk** (*Geraospiza caerulescens*) during the review period was of an adult flying over scrubland north of Piarco Interna-

tional Airport on 25 June, 2013 (FA).

An adult **White-tailed Hawk** (*Geranoaetus albicaudatus*) was observed in the Kernaham area of Nariva Swamp on 31 March, 2013 (GW) and photographed on 9 July, 2013 (KM). An individual has been documented from this area in three of the last six years. It is a well-watched site, so it is unlikely that a single bird could have remained undetected throughout the intervening period. The species is resident in both Venezuela and Guyana. This is the sixth documented occurrence of the species in Trinidad and Tobago in this century.

An **American Coot** (*Fulica americana*) was photographed on one of the lagoons at Lowlands, Tobago, on 15 March, 2013 (MKe). This is the fifth documented sighting in Trinidad and Tobago in the last 18 years, all from southwestern Tobago.

A **Double-striped Thick-knee** (*Burhinus bistriatus*) was photographed at Kernaham Settlement, Nariva Swamp, on 27 July, 2013 (FA) (see plate). Additionally, and for the second consecutive year, at least two birds were seen at Millenium Lakes Golf Course from 2 August to early October 2013 at least (LJ). There have been eight documented records of this species in Trinidad and Tobago in the last 18 years, of which six have been found during the period of late July-early September.

Adult basic-plumaged **Black-headed Gulls** (*Chroicocephalus ridibundus*) were found at Store Bay, Tobago, on 15 March, 2013 (MKe) and amongst the high tide gull roost at Orange Valley, Trinidad, on 23 November, 2013 (NL). Individuals have now been found in seven of the last 13 years, unsurprisingly all but one sighting being from the main gull roosting site on each island. All records have occurred between late November and mid-March.

A first-summer-plumaged **Franklin's Gull** (*Leuco-phaeus pipixcan*) was found at Orange Valley on 10 January, 2013 (JC, AJ), and at the same location, a bird in first-winter plumage was photographed on 29 November, 2013 (NL). Found almost annually in Trinidad and Tobago in recent times, there have now been 13 documented records of this species in the last 18 years.

An adult **Kelp Gull** (*Larus dominicanus*) was found amongst the high tide roost at Orange Valley on 13 December, 2013; it remained until 18 December (NL) (see plate). This is the third sighting of this austral gull in Trinidad, all unsurprisingly from the West Coast.

A first-winter-plumaged **Lesser Black-backed Gull** (*Larus fuscus graellsii*) was photographed at Store Bay, Tobago, on 27 February, 2013 (MKe). Whilst recorded year-round in Trinidad, this is the first documented record for Tobago in the last 10 years.

For the second year running, a **Striped Owl** (*Pseu-*

*doscoops clamator*) was photographed on the roadside between Parlatouvier and Bloody Bay, Tobago, this time on 15 June, 2013 (FM) (see plate). There is anecdotal speculation that the individual reported in 2012 was shot. This species remains by far the most localised and difficult to see of the Tobago speciality species.

Two **Fork-tailed Palm-Swifts** (*Tachornis squamata*) were found hawking insects over the golf course at Lowlands, Tobago, on 15 March, 2013 (MKe). Whilst very common in Trinidad, recent reports from this site in Tobago in successive years may herald a true range expansion for the species.

An adult female **Ringed Kingfisher** (*Megaceryle torquata*) was photographed beside the Bon Accord sewage lagoons on 15 March, 2013 (MKe). There have been only three documented sightings in Tobago of this common Trinidad resident, all at this location, the most recent having been a male in December 2008.

Single juvenile **Aplomado Falcons** (*Falco femoralis*) were photographed in the vicinity of Kernaham Settlement, Nariva Swamp, on 14 August, 2013 (CC) and 10 November, 2013 (MK, GW). These records support the established pattern of sightings being made during the latter months of each year that coincides with the passage of their migrant shorebird prey.

Two **Brown-throated Parakeets** (*Aratinga pertinax*) were found feeding on 3 January, 2013 in the Aripo Livestock Station (CM). Whilst a number were reported towards the end of the 1990s, this is the first documented sighting in this century. This species is widely found in coastal Venezuela; however, there has to be a question mark over the provenance of these birds, which are often kept in captivity.

A belated sighting of **Small-billed Elaenia** (*Elaenia parvirostris*) at Orange Valley on 11 May, 2012 (NL) brings that year's total to an unprecedented 12 individuals. By contrast, only one was found during 2013 at the Aripo Livestock Station on 20 May (NL).

A **Slaty Elaenia** (*Elaenia strepera*) was photographed feeding in a fruiting *Trema* tree along Blanchisseuse Road on 13 February, 2013 (FM, AS). This is only the second record for Trinidad and Tobago. The previous sighting was from Brasso Seco in July 1998. This species breeds in Bolivia and northwestern Argentina, with a post-breeding dispersal northwards.

The true status of **Variiegated Flycatcher** (*Empidonax varius*) in Trinidad is under review. It was previously considered to be a rare austral migrant; however, during 2013, seven individuals were found as follows: Talparo on 2 February (FM, AS); Aripo Livestock Station on 23 May (FM, AS); Mexico Road on 31 May

(FO); Asa Wright on 29 June (FM, AS); Cat's Hill on 25 August (FM, AS); Brasso Seco on 27 October (FO); and Talparo on 12 November (MK).

Adult male **Summer Tanagers** (*Piranga rubra*) were photographed at Gran Couva on 14 February, 2013 and 23 December, 2013 (both NL). This winter visitor from continental North America is now found almost annually.

Since their arrival in 2004, the resident population of **Grassland Yellow-Finch** (*Sicalis luteola*) had been restricted to the Aripo Livestock Station, east of Arima. On 15 June, 2013, three birds were found in cattle fields along Turure Farm Road, Valencia, some 7 km away (KM), with at least 10 showing up there on 16 October, 2013 (MK). There are also undocumented reports of several birds seen in fields adjacent to Piarco International Airport.

For the sixth consecutive year, several adult male **Lesson's Seedeaters** (*Sporophila bouvronides*) were singing on territory at a suspected breeding site in southern Trinidad in August 2013 (KS). Sadly, on at least one occasion bird catchers replete with cage and decoy birds were seen in the area.

It is suspected that **Yellow-bellied Seedeaters** (*Sporophila nigricollis*) are now breeding at several locations on the southern slopes of the Northern Range. Farther west, a small flock comprising at least three males and several females was found on Chacachacare Island on 11 August, 2013 (KS).

Single **Bay-breasted Warblers** (*Setophaga castanea*) were photographed on 19 February, 2013 at Gran Couva (NL), 3 March, 2013 at Wallerfield (FM, AS), and 6 March, 2013 (MKe, FO). Prior to 2013, there were only eight documented records in Trinidad and Tobago of this North American migrant.

An adult male **Blackburnian Warbler** (*Setophaga fusca*) was photographed at Fond Pois Doux Road, Paramin, on 8 December, 2013 (KM, FO). Whilst a common winter visitor to neighbouring Venezuela, this is only the third documented sighting for Trinidad and Tobago in the last 18 years.

An adult male **Cape May Warbler** (*Setophaga tigrina*) in full breeding plumage was found and photographed in a private garden at Lambeau, Tobago, on 7 April, 2013 (IE, BE) (see plate). This is the fourth documented occurrence in Trinidad and Tobago since 1995 of this North American migrant.

An adult male **Lesser Goldfinch** (*Astragalinus psaltria*) was photographed on the slopes of Mount St. Benedict on 10 June, 2013 (LJ). First recorded for Trinidad and Tobago in February 2005, all sightings of the species have been from this one site.

## ADDITIONAL RECORDS

Acceptable records were received for a further 22 sightings of the following species whose status has already been established: **Hook-billed Kite** (*Chondrohierax uncinatus*), **Great Black Hawk** (*Buteogallus urubitinga*), **Rufous Crab Hawk** (*Buteogallus aequinoctialis*), **Black Hawk-Eagle** (*Spizaetus tyrannus*), **Crested Caracara** (*Caracara cheriway*), **Scaly-naped Pigeon** (*Patagioenas squamosa*), **Mottled Owl** (*Cicca-ba virgata*), and **Black-whiskered Vireo** (*Vireo altiloquus*).

## INTRODUCED SPECIES

### ESCAPED CAGE AND AVIARY SPECIES

During the review period, reports were received of **Red-and-Green Macaws** (*Ara chloropterus*) at the Pitch Lake, a **Red-shouldered Macaw** (*Diopsittaca nobilis*) from Chaguaramas, a **Black-headed Parrot** (*Pionites melanocephalus*) from Gran Couva, a **White-eyed Conure** (*Psittacara leucophthalmus*) from Carli Bay, at least two **Village Weavers** (*Ploceus cucullatus*) from the Caroni Rice Project, and an adult **White Hawk** (*Pseudastur albicollis*) from the forest above Englishman's Bay, Tobago.

### INCONCLUSIVE RECORDS

Submissions of documentation for the following species were deemed inconclusive: **Purple Heron** (*Ardea purpurea*), **Zone-tailed Hawk** (*Buteo albonotatus*), **Ornate Hawk-Eagle** (*Spizaetus ornatus*), **Common Greenshank** (*Tringa nebularia*), **Lesser Elaenia** (*Elaenia chiriquensis*), and **Short-crested Flycatcher** (*Myiarchus ferox*).

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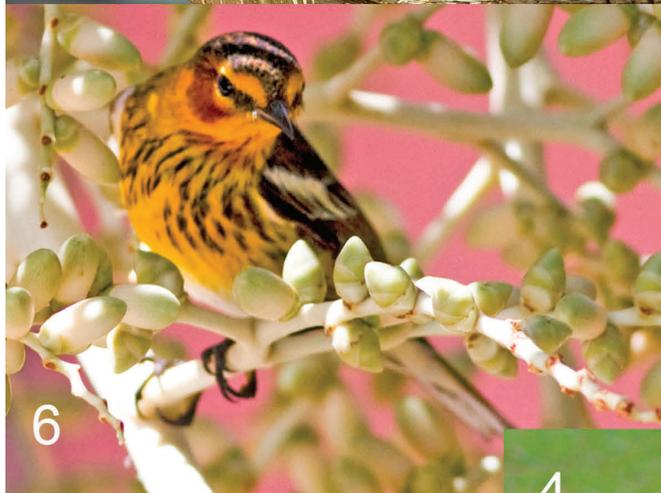
### Legends to Plate

1. 201388a Kelp Gull – Nigel Lallsingh – December 2013
2. 201353c Jabiru – Fayard Mohammed – August 2013

3. 201377a Glossy Ibis – Graham White – November 2013
4. 201358a Double-striped Thick-Knee – Lawrence James – August 2013
5. 201378a Green-winged Teal – Graham White – November 2013
6. 201337b Cape May Warbler – Ian Ellis – April 2013
7. 201360a Whistling Heron – Kamal Mahabir – October 2013
8. 201345a Striped Owl – Fayard Mohammed – June 2013

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# A.M. Adamson (1901-1945): Entomologist and Travelling Naturalist. Some Correspondence and a Bibliography, with Special Reference to Trinidad and Tobago

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## ABSTRACT

Scottish son of the Manse and graduate of the University of St. Andrews, Scotland, Martin Adamson travelled the world during his relatively short career, with appointments in the United States, the Pacific, and the Caribbean. His interests in natural history were broad, including the fauna of the Pacific Islands, but the need for a permanent job with paid work led him to Trinidad, where he specialised in economic entomology. He became an expert in a number of applied aspects of entomology in the tropics as well as in tropical agricultural education.

**Key words:** entomology, termites, agriculture, Imperial College of Tropical Agriculture, Pacific Islands.



**Fig. 1.** Professor A.M. Adamson. Courtesy of the Department of Life Sciences, The University of the West Indies, Trinidad. This picture accompanied Adamson's obituary in *Tropical Agriculture*, 23.

he also made important contributions to the knowledge of tropical insects, especially termites, as well as to agricultural education in the former British tropical colonies. However, Adamson was an all-round naturalist, interested not only in insects and terrestrial environments, but also in marine and freshwater habitats. He wrote, at various times, about watching dragonflies, freshwater crabs, aquatic caterpillars, tree frogs, and prawns. Many of his letters are preserved in the archives and Special Collections of the University of St. Andrews, Scotland, and

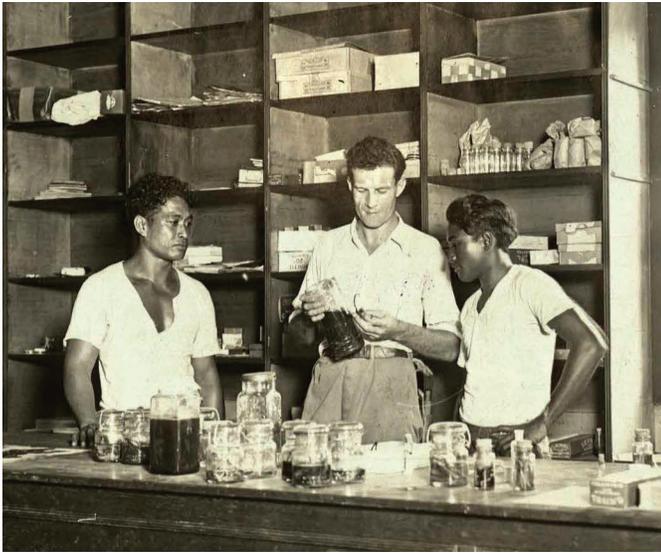
## INTRODUCTION

Martin Adamson's life was a short one, but he packed an enormous amount of work into it on both the Pacific invertebrate fauna and economically important tropical insects, especially those in the West Indies. He was an important naturalist in the tropics, a member of the Pacific Entomological Survey, and later Professor at the Imperial College of Tropical Agriculture, Trinidad, in charge of entomology and zoology. One of the early workers on biological control in Trinidad,

copies of these are available in the Alma Jordan Library, The University of the West Indies (UWI), St. Augustine, Trinidad. These letters, which are correspondence with his former professor D'Arcy Wentworth Thompson (DWT) (note 1) and, to a lesser degree, with David Burt (note 2), form the basis of the paper.

## Brief biography

Martin Adamson was born in Scotland on 17 October, 1901. He spent his early life with his parents and brothers in Ayrshire, his home being St. John's Manse, Ardrossan where his father, the Rev. R.M. Adamson, was minister of the church from 1892 to 1937. After school at Ardrossan Academy and with a bursary from Ayrshire County Council, he crossed the country, moving from the Firth of Clyde to the east coast to become a student at St. Andrews University. He graduated with an M.A. in 1922 and a B.Sc. in 1923 with First Class Honours in Natural Science with chemistry and natural history as his principal subjects. After graduation Adamson held a research Fellowship at St. Andrews, where from 1924 to 1926 he was Assistant in Zoology in Professor Thompson's department. In 1933 he married Florence Jacobson of San Francisco, graduate of the University of California and Columbia University in New York City, a psychologist and sociologist who worked in social and welfare work. They had a son named Alper. Martin Adamson died in San Francisco at age 44 on 24 December, 1945, where he was being treated for a tumour. He was described as someone with "exceptional personal charm...[and with



**Fig. 2.** Dr A.M. Adamson and assistants. September 1929. Marquesas Islands. ms 9300, photograph of Alistair Martin Adamson, Records of Scottish West Indian Links collection. Reproduced courtesy of the University of St. Andrews Library.

a]...quiet presence...[who displayed]...kindliness, simplicity and utter sincerity” (Anon. 1946).

### Travelling naturalist

Adamson was a naturalist at heart. His “first love was marine biology” (Anon. 1946). Later he wrote that he was “engaged in my favourite occupation of looking through a microscope at pond water” (Adamson to Burt letter 37781/43, no date). Early in his career he likely was disappointed not to win a place as zoologist on the R.R.S. Discovery Expedition to the Antarctic in 1925.

After leaving Scotland, Adamson journeyed round the world, taking up appointments in California and visiting other parts of North America as well as the Pacific Islands and finally Trinidad and obtaining, en route, a Ph.D. from the University of California, Berkeley (UC Berkeley) (note 3). In 1933, ten years after earning his B.Sc., he was appointed Senior Lecturer in Entomology, later Reader and finally Professor at the Imperial College of Tropical Agriculture in Trinidad.

### California

In August 1926 Adamson arrived at Berkeley, California, as a Commonwealth Fund Fellow to work with Professor Charles A. Kofoid (1865-1947) on systematic studies of some dinoflagellates that comprise part of the marine plankton (Kofoid and Adamson 1933). During this period he travelled widely, to the Pacific, Alaska, and Mexico as well as within the United States. He wrote to Burt, “You may be surprised at my doing systematic work but I hope not scornful...The dinoflagellates are

an interesting group...I think it would be good to spend some time on systematic work,” (Adamson to Burt 13 January, 1927). At UC Berkeley he met E.P. Mumford, another Commonwealth Fellow, who was to play a part later in Adamson’s career. The dinoflagellate work completed towards the end of 1927, Adamson was looking for another job. “What I should like most would be a job at home with one of the Fisheries Boards,” he wrote, and was hoping for a new post “fairly soon” (Adamson to Burt 26 October, 1927). Soon afterwards he joined the Pacific Entomological Survey.

### The Pacific Entomological Survey and the Marquesas Islands

The Pacific Entomological Survey was formed in 1927 and was funded for a 5-year period ending on 31 December, 1932, through a cooperative agreement among the Hawaiian Sugar Planters’ Association, the Association of Hawaiian Pineapple Cannerys, and the Bernice Pauahi Bishop Museum. The activities of the survey and the personnel are given in the various reports.

Adamson wrote to his former professor, informing him of this appointment and adding, “I am much interested in insects... I am learning some entomology and rejoicing in charts of the Pacific.” He left for Honolulu early in 1928, his headquarters being at the Bernice Pauahi Bishop Museum, where E.P. Mumford was Director of the survey (note 4). However, he spent most of his time either in the field collecting or at the offices of the Hawaiian Sugar Planters’ Association, where the collected material was sorted and identified.

Adamson encountered problems while working with Mumford and by 1929 wrote, “things are going badly wrong... a fungus is eating the skin between our toes... Mumford is ill...impossible to get good food here... [but]...never felt better re general health,” (Adamson to DWT 1 May, 1929). Mumford, it seems, was difficult, and although Adamson’s years on the survey were enjoyable and interesting, they were “very difficult ones!” Mumford was a “hindrance to the work – ill health psychological and physical, total incompetence and lack of knowledge... an intense desire for achievement,” (Adamson to DWT 19 June, 1933), and it seems that he tried to direct Adamson away from his entomological work.

Collecting during that period focused on French Polynesia, primarily on the Marquesas Islands. Adamson spent January 1929 to April 1930 living on these islands; during this time made extensive collections of both insect and non-insect groups on seven of them. He also collected insects in Tahiti and Mo’orea. As his funding reached its end, he sent specimens to specialists worldwide. The results of his research were published in a vari-

ety of scientific journals, primarily through the *Bulletins* and *Occasional Papers* of the Bishop Museum (note 5). Adamson's work is described in a series of papers (Adamson 1932, 1935a, 1935b, 1936a, 1939, and Mumford and Adamson 1932).

Following the completion of his work on the Pacific Entomological Survey and before he left for Trinidad, Adamson spent time at UC Berkeley (Neal Evenhuis to RB 12 January, 2014) working on his doctorate and writing.

### **The Imperial College of Tropical Agriculture, Trinidad**

The UWI was established in 1948 with the first campus at Mona, Jamaica. A second campus was formed at St. Augustine, Trinidad in 1960 based upon the former Imperial College of Tropical Agriculture (ICTA), the latter becoming the Faculty of Agriculture at the new institution. ICTA was the recognised centre for the training of Diploma (the equivalent of a degree) and postgraduate students in tropical agriculture from 1922 until 1960, although it never awarded degrees. The students came mainly from countries in the British Colonial Empire. This arrangement continued until the founding of the UWI in Trinidad.

ICTA was established on 30 August, 1921. The opening ceremony was held in October 1922. Brereton (2010), in her historical account, refers to the original name of the institution as the West Indies Agricultural College; the name was changed in 1924 to indicate that the college was concerned with the development of agriculture throughout the Colonial Empire and not just in the West Indies. The main objectives were research, with generous staff-to-student ratios to allow for this, and the teaching of agriculture. There also was postgraduate training in tropical agriculture for the Agricultural Services of the Colonies. Research was concerned mainly with problems relating to cacao, sugar, bananas, and citrus fruits, including pests and diseases as well as plant genetics and soils. The cost of the work was met by contributors from commercial firms (note 6) and by the British Government. The old Government Yaws Hospital, constructed on the site of a former sugar plantation, was used as the first building. A new building for the science departments was completed by 1926. The Trinidad Herbarium, established in 1887, was transferred to the college site in 1947, and the journal *Tropical Agriculture* began publication in 1924.

The college was, "A very British Institution: British staff, many British students ... a very British ethos," (Brereton 2010). Campbell (quoted by Brereton 2010) described it as "a social enclave of English civilisation

surrounded by black Creole and Indian villagers." The last Principal, prior to the college becoming the Faculty of Agriculture of the University College of the West Indies in Trinidad, was G.A.C. Herklots (from 1953-1960), himself a noted naturalist who published several books on birds and botany, including the birds and plants of the West Indies (note 7).

Adamson's predecessor at the college was Henry A. Ballou (note 8), who was also Commissioner of Agriculture for the Leeward and Windward Islands and who was "more active...[in this]...than in the work he did at the same time as Professor of Entomology" (Adamson to DWT 12 January, 1934).

Adamson applied for the post of Senior Lecturer and sent details to his father in Ayrshire. His father wrote to Professor Thompson to inform him of these developments, "Salary £550 with allowances and rises...climate good...leave is frequent...there is a small but not negligible chance of me getting it. If I did...start in the autumn," (R.M. Adamson [father] to DWT 3 June, 1933). References were supplied by D'Arcy Thompson and Lucien Berland (note 9). The latter wrote that Adamson was "an excellent entomologist, remarkably gifted, and that he will certainly apply the finest scientific spirit in all the research one might entrust him with," (Berland to Thompson, letter 9284 13 May, 1933). Adamson was successful in securing the position, and although he found it hard after his time in Honolulu, he started work in Trinidad in October 1933 as Senior Lecturer in charge of the department of Entomology and Zoology.

Adamson found the, "richness of the fauna and the tremendous opportunity for work in fields that have not ever been explored" to be the real attraction and challenge (Adamson to DWT 18 May, 1935). Writing about his first impressions, he noted that the experience of "settling down... [was]... very slow, and somewhat difficult...[but there were]...great hopes of building up a strong department" (Adamson to DWT 12 January, 1933 – note 11). He developed the department rapidly, appointing staff, improving the collections, and establishing a research base. He was rewarded by the college with a Readership in 1935 and with the title of Professor in 1938. By 1936 there were "2 new Indian boys for routine work, one extremely clever Chinese girl – Technical Assistant, 3 other lab. assistants...[and]... [Ronald Gordon] Fennah" (note 10) (Adamson to DWT 18 February, 1936).

Despite his "complete ignorance" (Adamson to DWT 12 January, 1933 – note 11) of economic entomology in the tropics, Adamson began by running a course on insect pests of tropical crops to postgraduate students, and F.W. Urich (note 12) lectured to the younger Diploma

students. Adamson found the laboratories and equipment adequate but noted that the “library is weaker in Zoology than in other subjects, but there is a little money to spend,” (Adamson to DWT 12 January, 1933). He was disappointed to find that the preserved “collection of all kinds of animals is extremely poor in quantity and worse in quality, many of the specimens being without locality labels, and almost all of the pinned insects covered in mould... the fauna is so rich here that I hope to build up a good collection,” (Adamson to DWT 12 January, 1933). Anxious to improve on the library and museum, he applied for and received a grant of “£200 for metal insect cabinets, an extra technical assistant, and I (*sic*) almost sure of a special grant of £100 at least for books,” (Adamson to DWT 1 July, 1934). He built up the zoological museum by making collecting trips to different parts of Trinidad; many of his early expeditions were in the company of Urich, who also taught at the college and who knew the country well. Adamson then completely reorganised the “rather antiquated entomological collections at the college,” which were to be housed in “fireproof steel cabinets of the most modern construction,” (Anon. 1946).

Once he had become established and familiar with the island of Trinidad, Adamson and colleagues began to take students on field trips. Adamson appreciated the advantages of field work: “Field trips for senior students - bus for 24 and motor launch marine expeditions to the coral reefs on the NE corner of the island and to the deep rainforest at 2000 feet.” He found the field trips to be “extremely successful in stimulating an interest in biology and promoting the best kind of relations between staff and students,” (Adamson to DWT 10 April, 1945). The students and staff visited the Toco Coral Reef, the Arena Forest, the Aripo Caves, and Mount El Tucuche, amongst other places.

While working in Trinidad, Adamson served as secretary to and entomologist with the Plant Quarantine Station Committee of the British West Indies. He also was appointed as one of two technical officers in charge of the Plant Quarantine Station at the college in St. Augustine (Adamson 1940a), the other officer being a mycologist. Adamson wrote that they “must not let any insect pest through” (Adamson to DWT 30 September, 1934), although initially they were concerned only with insect pests of sugar cane and cacao. After the quarantine station had been in operation for a year, Adamson was able to report that for “sugar cane and cacao only, no serious insect problem to deal with - but great difficulty to get plants to grow well in green houses - preaching air conditioning,” (Adamson to DWT 18 May, 1935).

Adamson’s research soon got under way, and his range

of interests was wide. He was one of the early workers in Trinidad on biological control. He wrote to Thompson, “I have started some work on thrips - urgent local problem - defoliate the cacao trees” (Adamson to DWT 12 January, 1934). Through an arrangement with G.S. Cotterell, an entomologist in the Gold Coast (Ghana), Adamson’s department imported a parasitic wasp as a biological control agent (Adamson 1936b). He wrote that he was “busy on a most interesting project - the introduction of a minute Chalcid wasp, *Dasyscapus* [*D. parvipennis* Gahan], a parasite of the cacao thrips, from the Gold Coast to Trinidad... if it goes well I may save the cacao planters many thousand of dollars a year,” (Adamson to DWT 30 January, 1936). He succeeded in rearing eight generations of the parasite and then wrote, “I think we shall succeed in establishing the parasite here,” (Adamson to DWT 30 January, 1936). However, although established, it did not bring about any immediate economic control of thrips. Adamson and his colleagues were also interested in varieties of cacao resistant to attack by thrips, which the researchers thought could be used as a potential method of control (Callan 1943b) (note 13). The control of insect pests by restricting their spread also was an important part of Adamson’s work. That topic required knowledge of the geographical distribution of insects, so he took an interest in that subject as well (Adamson 1941a).

Early during his time at Trinidad, Adamson turned his attention to termites, which became a major interest of his. He wrote, “I am spending all my spare time on termites,” (Adamson to DWT 15 October, 1938). By 1937 he had collected 1000 samples from across the island and had written a preliminary report (Adamson 1937), and a second fuller report followed three years later (Adamson 1940b). He was helped in the identification of the termites by Alfred Edwards Emerson (1896-1976) from the University of Chicago. Adamson wrote about laboratory techniques in dealing with living specimens (Adamson 1941c), built up a major collection and became a specialist on their habits and general biology (Adamson 1938, 1940c, 1941b, 1941c, 1943 and 1948). At the time of his death, he was preparing an important work on termite biology; on which he had become a recognised authority.

Adamson continued to work at ICTA during the Second World War. There are records of his collecting zoological material in 1940, 1943, and 1944, but by 1945 his ill health was causing serious concern. According to him, life was “not so pleasant as before the war but work at my college has changed little, except for increase in numbers of students,” (Adamson to Burt 22 May, 1945). Life on the island during the war was, however, “considerably changed by the US military bases, unemployment became acute, but conditions for the poor improved,”

(Adamson to Burt 22 May, 1945).

During 1945 Adamson became seriously ill and had to take time off work. He wrote letters from hospitals in Baltimore and San Francisco, where he was undergoing tests, examinations, and treatment. His last letter to St. Andrews University is dated 8 November, 1945: "Tumour right clavicle area – responded to X-rays – complication thrombo-phlebitis – on sick leave from Trinidad," (Adamson to DWT 8 November, 1945). He died the following month.

Following Adamson's death, his work continued to be published (Adamson 1946, 1948) and his interests and some of his work was carried forward by Callan (1943a, 1943b) (note 13). Professor T.W. Kirkpatrick (note 17) succeeded Adamson at the college.

The zoological material Adamson collected is scattered throughout the world. The main part of his termite collection is in the termite collection at the American Museum of Natural History in New York (Kumar Krishna and James Boone to RB 16 February, 2014). Other entomological material of Adamson's is housed in the Essig Museum of Entomology at Berkeley, California (note 14). Other invertebrates, including insects and shells collected during the Pacific Entomological Survey, are at the Bernice Pauahi Bishop Museum in Honolulu (note 15). Much of the material Adamson collected in the Caribbean is housed in The University of the West Indies Zoology Museum (UWIZM) at the St. Augustine campus in Trinidad. At time of this writing, 41 specimens collected by Adamson are listed in the museum's database. Staff at the UWIZM are currently in the process of cataloguing the collections; with many thousands of insect specimens still to catalogue, it is highly likely that other specimens collected by Adamson will be found. Most of the Adamson material currently in the UWIZM database was collected in either Trinidad (32) and Tobago (1) or Barbados (7), and almost all material has been identified to species level. Regarding the Trinidad material, most specimens were collected from Manzanilla (3), the Maracas Valley (11), and Toco Reef and district (6), with a few species from Macqueripe Bay, Tacarigua, Port of Spain, St. Augustine, and the Gulf of Paria. All specimens were collected between 1935 and 1944. The material includes molluscs, cnidarians, crustaceans, insects, echinoderms, and vertebrates, an indication of Adamson's breadth of interest and his desire to cover the animal kingdom, not just insects of economic importance, for teaching purposes. The collection includes marine gastropods and bivalves in the Mollusca, and amongst the insects is an interesting collection of 11 specimens of Odonata, mostly identified to species (note 16 and Tikasingh 2003).

Adamson also sent material he had collected to St.

Andrews University, "preparing some land snails and some large insects to send you – I asked if you would like a collection of some West Indian and Hawaiian corals," (Adamson to DWT 10 April, 1945). The museum collection at St. Andrews University is currently being catalogued and a database prepared, and thus Adamson's material cannot readily be identified at present.

## CONCLUSION

Remarkably gifted and a first-class naturalist, Martin Adamson worked in several parts of the world and was a successful researcher and teacher. As an educator in tropical agriculture, he was a pioneer – thorough, hard-working, and dedicated. He set high standards for himself and for others. His research interests focused on entomology, especially pests of commercial crops. His research areas included termites, biological control of pest organisms, and the geographical distribution of agricultural pests and diseases, as well as the fauna of some of the Pacific Islands. Had he lived longer, he would have become internationally recognised, with honours, as an outstanding entomologist, zoologist, and academic.

## ACKNOWLEDGEMENTS

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## NOTES

1. Sir D'Arcy Wentworth Thompson FRS, eminent mathematical biologist (especially morphogenesis), classics scholar, and author of the seminal book, *On Growth and Form* (1917). Born Edinburgh 1860, died St. Andrews 1948. Came to the University of St. Andrews via Dundee, where he was Professor of Natural History. 64 letters Adamson to Thompson, ms 9223-9325, ms 9577-21551, in the D'Arcy Wentworth Thompson collection. Burt (note 2) writes about Thompson at: [www-history.mcs.st-andrews.ac.uk/Extras/Burt\\_Thompson.html](http://www-history.mcs.st-andrews.ac.uk/Extras/Burt_Thompson.html): <http://www.bing.com/search?q=David+Burt+zoology+Columbo+St+Andrews&qs=n&form=QBRE&pq=david+burt+zoology+columbo+st+andrews&sc=0-26&sp=-1&sk=-#>
2. David Raitt Robertson Burt, an associate of Thomp-

- son, graduate of St. Andrews and member of the zoology staff at St. Andrews at the time Adamson was a student. Moved to take up the post of lecturer in charge of zoology at University College, Ceylon (1924) and later the Chair of Zoology there (1940). This college received university status in 1942. Burt returned to St. Andrews in 1947. Adamson corresponded with him occasionally, from 1925 to 1945; these letters are also at St. Andrews (45 letters to D.R.R. Burt ms 37781/ in the D'Arcy Wentworth Thompson collection). Adamson wrote to Burt to thank him for specimens sent to St. Andrews from Ceylon: "What a fine lot of insects and other things you have sent us! Badly in need of some of the things, especially mosquitoes – everything arrived in perfect condition," (Adamson to Burt 22 June, 1925).
3. PhD dissertation, 1935, from Berkeley, California, entitled, "The affinities and origins of the fauna of the Marquesas Islands," (Dean Smith, Bancroft Library, Berkeley, to RB 2 December, 2013).
  4. E.P. Mumford was put in charge after the death of the first survey director, Charles Fuller Baker.
  5. Ten publications from the survey are numbered. Other publications based on material collected by the survey are unnumbered but are treated in the Index to the survey. A link to all the publications is at <http://hbs.bishopmuseum.org/pubs-online/pes.html>
  6. *Nature*, 143: 468 (18 March, 1939).
  7. Herklots (1902-1986) was Principal from 1953 to 1960. His books include *The Birds of Trinidad and Tobago* (1961) and *Flowering Tropical Climbers* (1976).
  8. Henry Arthur Ballou (1872-1937) C.B.E., Commissioner of Agriculture for the West Indies and Professor of Entomology at the Imperial College of Tropical Agriculture, Ballou worked on insects from the Caribbean and was a prolific author of papers on insect pests from the various islands.
  9. Berland was in the Entomology Department at the Museum National D'Histoire Naturelle, Paris, in the 1930s, although his specialty was the Arachnida, in particular spiders. Adamson collected spiders on the Marquesas Islands that were later identified by Berland.
  10. Ronald Gordon Fennah (1910-1987) was in the Agricultural Advisory Department at the Imperial College of Tropical Agriculture. He investigated food-crop pests in the Windward and Leeward Islands, in particular on varieties of sugar cane resistant to a frog hopper.
  11. Actually 1934.
  12. F.W. Urich was a good all-round naturalist with an unrivalled knowledge of Trinidad and its fauna, but he did not publish a significant amount of work. By the time Adamson arrived in Trinidad, Urich had reached retirement age.
  13. On or before 1940, Adamson was joined in Trinidad by Callan, as a lecturer. At St. Andrews are three letters from Dr Edward McCallum Callan (Callan ms 9323, 45118, 45119), mainly regarding the death of Martin Adamson.
  14. Essig Museum of Entomology – see [essig.berkeley.edu](http://essig.berkeley.edu)
  15. The Bernice Pauahi Bishop Museum in Honolulu holds the Pacific Entomological Survey insect, mollusc, and other zoological material (Neal Evenhuis to RB 12 January, 2014).
  16. The University of the West Indies Zoology Museum, Department of Life Sciences, St. Augustine, Trinidad. For a history of the collections, see <http://www.bing.com/search?q=zoology+museum+UWI+TRINIDAD&qs=n&form=QBRE&pq=zoology+museum+uwi+trinidad&sc=0-15&sp=-1&sk=-#>
  17. Thomas Winfrid Kirkpatrick (1896-1971) had worked on mosquitoes in Egypt for the Anti-Malaria Commission, Ministry of Agriculture, and then in East Africa on insect pests of coffee. He wrote the book *Insect Life in the Tropics* (Kirkpatrick 1957).

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## Dr Elisha S. Tikasingh: Life Among the Parasites

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Dr Elisha Tikasingh

Dr. Elisha Tikasingh is well known for his work on arboviruses (arthropod-borne viruses). He has described Nariva virus and was a co-describer of Restan virus both viruses were new to science. Dr. Tikasingh's greatest achievement however was the development of antibody reagents used in the identification of arboviruses.

He is also a stalwart member of the Trinidad and Tobago Field Naturalists' Club joining in the mid-1960s. He served in many roles in the Club, including serving as a member of the Management Committee during the 1970s, and as Chairman of the Centenary Celebrations Committee in 1991. He has given lectures at our Club meetings and written several articles for the Club's Journal. He has been its Editor for 15 years. This biographical article is taken from two interviews conducted in Trinidad in February and May 2014, transcribed by Jo-Anne Sewlal. The full interview is archived at the St. Augustine Campus, The University of the West Indies (U.W.I) and with the Trinidad and Tobago Field Naturalists' Club.

Born in 1927 in the village of St. Julien which is outside of Princes Town, Elisha Tikasingh and his family moved

from village to village because of his father's job as a Catechist in the Presbyterian Church. He went to primary school at the Palmyra Canadian Mission (C.M.) School and when it closed, he attended Reform C. M. School. At that time his family was living in Mt. Stewart and the daily trek to school involved a five mile hike to and from school barefooted on the hot asphalt road. After his father's death in 1940, his family moved to San Fernando where he attended Naparima College to do his Senior Cambridge. At that time one had to pay tuition fees to attend secondary school, but his entry into the school was due to the privileges allowed to children of church workers of the Presbyterian Church to attend their secondary schools for free. His mother would not have had the money to pay the tuition fees.

Shortly after the successful completion of the Cambridge School Certificate Examinations in December 1947, he got a job teaching at Fyzabad C.M. School, and taught there for about two years before going off to do his Bachelor's degree at Eastern Nazarene College in Wollaston, Massachusetts, U.S.A, at the suggestion of a friend, who said that one could work and study at this College. He was financially able to leave, thanks to his mother's thrifty nature, who saved his earnings as a teacher. Almost immediately after his arrival in college, he started earning money by washing pots and pans in the school's kitchen. His usual routine involved working in the summer and paying off for the Fall semester, borrowing part of the money for the spring semester, returning to work in the summer to repay the loan of the Spring semester and have enough money for the next Fall semester.

When he took his first undergraduate course in biology he knew that was his calling as he thoroughly enjoyed the subject. In the final year of his B.Sc. degree he was given a teaching assistant job at the College and was free from manual labour for a change. From there, with a partial scholarship from the Jessie Smith Noyes Foundation, he enrolled at Boston University, where he graduated with his M.A. in Biology. He chose the area of parasitology inspired by a paper he wrote in his undergraduate studies on the life cycle of the hookworms which fascinated him. He was awarded his Ph.D. in Zoology in 1960 from Oregon State University specializing in his favourite discipline, parasitology. At Oregon State University, he was made a Teaching Fellow which involved assisting with tutoring undergraduate laboratory courses. The stipend was suffi-

cient to live very, very modestly during the semesters but he still had to find work during the summers. However, his Major Professor, Dr. Ivan Pratt, supervising his Ph.D. research suggested that he spend at least one summer at a marine biological laboratory or inland field station to study invertebrate biology as many invertebrates are marine based or found in inland lakes and ponds. In order to spend a summer doing further studies he needed to have money. However, his Major Professor was able to arrange a scholarship from the National Science Foundation and he spent two summers at the Friday Harbor Laboratory of the University of Washington where he took courses in Advanced Invertebrate Zoology and Advanced Invertebrate Embryology. During his time there one of his professors, Dr. Dixy Lee Ray, who later went on to become the governor of the state of Washington, he remembers fondly, not only for being an excellent teacher or her annual salmon barbeque for her students, but she was also responsible for his dissertation topic. During a dredge from a boat in Puget Sound, Washington a number of animals were brought up including sea cucumbers. Dr. Ray introduced the students to the parasitic gastropod *Entoconcha* found in holothurians. *Entoconcha* was first described from the Mediterranean Sea and the idea that it had such a wide distribution appealed to Tikasingh. However, during his research he discovered that it was not *Entoconcha*, but something new to science. He ended up describing a new genus and two additional species of endoparasitic gastropods: *Comenenteroxenos parastichopoli* Tikasingh, 1961 and *Thyonicola americana* Tikasingh, 1961. He admits that he was beginning to like marine biology having spent two summers at a marine laboratory.

After graduation in June 1960, he spent the summer in Alaska working on King Crabs for the U.S. Fish and Wildlife Service. He returned to Trinidad in October 1960 and was awarded a Rockefeller Foundation Fellowship to study arboviruses at the Trinidad Regional Virus Laboratory (TRVL) which was quite fortunate as they had no post for a parasitologist. He worked there for about a year and a half after which he was appointed as a Lecturer in Microbiology, Faculty of Medicine, U.W.I. (Mona).

During the 1930s and 1940s work on the yellow fever (YF) virus was conducted at the Rockefeller Foundation Laboratory (RFL), New York and in the field in Latin America which resulted in the isolation of a number of other unknown viruses. However, not wanting to distract from their research on the yellow fever virus, the other viruses that were isolated were put in deep-freezers by the RFL for later studies. However, the development of a yellow fever vaccine by Dr. Max Theiler, which was used during World War II on soldiers, brought an end to the research on this virus. In the early 1950's work on the

viruses which were in deep-freezers were started and the Rockefeller Foundation then opened up laboratories in Johannesburg, South Africa; Poona, India; Belém, Brazil; Cali, Colombia and Port of Spain, Trinidad, the goal was to study arboviruses in each of the country they established. These laboratories also isolated a number of viruses new to science, as well as determined the ecology of some of the viruses.

The Trinidad Regional Virus Laboratory which was the forerunner of CAREC (Caribbean Epidemiology Centre) was established in 1952. It was well known for its research in the area of arboviruses and would attract visiting researchers from all over the world to Trinidad. When Tikasingh started working there in 1960, the laboratory was already established, and was coming towards the end of the exploratory stage which ended in the mid 1960's. It was also about the same time that the entomologist Dr. Thomas Aitken was due to be transferred to Belém, Brazil. This impending move resulted in Tikasingh understudying him. With this in mind, Tikasingh was put to work studying mosquitoes which are the vectors of arboviruses. The transition from parasitic gastropods to mosquitoes also involved sending him to University of California, Berkeley or a year to study entomology. Here he was offered to do an advanced degree but declined the offer in that he already held a Ph.D. and this visit concerned his job rather than personal advancement.

In 1961 the Rockefeller Foundation transferred the administration of the laboratory to the Department of Microbiology, Faculty of Medicine, U.W.I, Mona, Jamaica, as the medical school in Trinidad did not exist as yet. However, for administrative purposes, the laboratory had to sometimes deal with U.W.I, St. Augustine. Under this arrangement Tikasingh was made a lecturer and the Director, Dr. Leslie Spence, was assigned the post of senior lecturer.

Though Tikasingh is known for his involvement with research at Bush Bush Forest in the Nariva Swamp located on the eastern side of Trinidad, when he first returned to Trinidad he had no idea where it was located. Not wanting to show his ignorance to senior colleagues he found out from one of the technicians at the TRVL. The Bush Bush Forest Station was established in September, 1959 by the TRVL and Tikasingh recalled spending many nights in Bush Bush Forest by himself although the caretaker lived a short distance away. One of the most haunting sounds he ever heard at night was the call of the Common Potoo.

This interest in Bush Bush stemmed from the fact that in 1959 the yellow fever virus was isolated from a wood-cutter who had visited Bush Bush forest about two weeks before getting the fever. The TRVL suspected that Bush Bush was the "home" of the virus in Trinidad and moved

their activities from northeast Trinidad. Previously they had worked in the Rio Grande and Melajo Forests where they had isolated Manzanilla and Oropouche viruses, new to science at that time. In these forests and Bush Bush, TRVL had isolated 19 viruses new to science.

Although his current work on arboviruses was far from his doctoral research “Endoparasitic gastropods of Puget Sound Holothurians”, he thoroughly enjoyed his work and regarded it as fun, getting to go into the forests and swamps catching birds, trapping for mammals, collecting mosquitoes to test for the presence of viruses with his colleagues. But life while working at the TRVL did not involve much socializing outside of work. However, Tikasingh who was not married at the time would meet regularly with Dr Brooke Worth for dinner on weekends.

In his book entitled, “A Naturalist in Trinidad”, Dr. Brooke Worth talked about list-making, noting the former entomologist Aitken as a truly pathological list-maker. However, Tikasingh recalls that it is this personal quality that made him a great collector and which resulted in a good collection of arthropods of medical importance, plants, birds, mammals, amphibian and reptiles. The wild animals were collected to process for virus isolations. However, Tikasingh suggested that intensive collecting of rodents for viruses over a period of time may have been responsible for its population crash in Bush Bush Forest at that time.

In 1968, The Rockefeller Foundation funding to TRVL ended as they shifted their priorities from arboviruses towards agriculture in the programme called “Towards the Conquest of Hunger.” This caused retrenchment of staff as funds were not forthcoming. Then the polio outbreak came to save the day, so to speak. Over the years we had the occasional isolate as the virus was still present in Trinidad. Then in December 1971, Dr. Tikasingh recalled the TRVL made two isolates of the polio virus in one day with more reports in the following days. By this time it was regarded as reaching epidemic levels and the Ministry of Health decided on a nation-wide vaccination campaign. Although the government canvassed the population to get vaccinated, which was free of charge, many people opted not to be inoculated. Then in January 1972 when the government announced that Carnival would be postponed for that year, people immediately rushed to be vaccinated!

After the polio epidemic through the efforts of Dr. Eric Williams, the then Prime Minister of Trinidad and Tobago, the Pan American Health Organisation (PAHO) and a group of international scientists a new entity was created, the Caribbean Epidemiology Centre (CAREC) in January 1975. Its mandate automatically broadened to include surveillance of communicable diseases, all viruses and parasitic protozoans. In addition to entomology, Dr Tikasingh started the Parasitology Laboratory. Bacteriology

was a new entity. The epidemiology and surveillance of communicable diseases unit was also attached to CAREC.

However, it was the yellow fever outbreak in 1978-79 that started his involvement with the virus. During this period, the reports of monkey deaths in the Guayaguayare forest were attributed to poisoning. After this was reported in the newspaper Dr. Tikasingh wrote a memo to his boss stating that it should be treated as a yellow fever outbreak until proven otherwise. Yellow fever tends to occur as epizootics every 10-15 years. Because of these deaths, he and his colleagues visited the area and collected mosquitoes from which they isolated the virus. After alerting the Ministry of Health, an immunization programme was started as well as the spraying of insecticides to kill mosquitoes in urban areas.

CAREC has now become the Caribbean Public Health Agency (CARPHA) which is actually a larger institution. CARPHA includes the old CAREC, the Environmental Health Institute which is in St. Lucia. It includes also the Caribbean Health Research Council, the Caribbean Food and Nutrition Institute) and it includes the Food and Drug Laboratory in Jamaica.

Dr Tikasingh retired in December 1987. He has published over 100 scientific articles on arboviruses, parasitology, entomology and natural history in peer-reviewed journals. His publications on arboviruses includes the book “The Hunt for Caribbean Viruses: A History of the Trinidad Regional Virus Laboratory”. He is also the editor of the book “The Natural History of Yellow Fever in Trinidad.” His many awards for his research, include recognition as an Icon of Science and Technology of Trinidad and Tobago from the National Institute of Higher Education, Research, Science and Technology. His most recent award was the degree of Doctor of Science *honoris causa* from the University of the West Indies, St. Augustine in 2013.

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# Things We Don't Know About West Indian Social Wasps

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## ABSTRACT

The known social wasps of the islands of the West Indies comprise 31 independent-founding and 20 swarm-founding species. Within the region, most are found only on the continental islands of Trinidad and Tobago. The present state of our nesting-biological knowledge of these 51 species is very variable. This is summarised in tabular form as a way of drawing attention to aspects that have not yet been studied. In addition, 21 scientific problems of various magnitudes are outlined. Of these, 19 have to do with social wasps in the formal sense (Vespidae: Polistinae in our area), while the other two concern members of the family Crabronidae.

## INTRODUCTION

Social wasps, in the formal sense, comprise three sub-families of the family Vespidae. Like other eusocial insects, they live in durable structured groups, known as colonies, with a reproductive division of labour. Of the approximately 700 known species in the world, 51 species, all in the subfamily Polistinae, are found in the islands of the West Indies: 38 in Trinidad & Tobago (Starr and Hook 2003) and 16 in the Antilles (Richards 1978). They fall into two major groups. In the independent-founding genera (*Mischocyttarus* and *Polistes*, known locally as Jack Spaniards), a new colony is founded by a queen or group of queens without the aid of workers. In the swarm-founders (all other genera, known as maribons or marabuntas), a colony is founded by a group of queens and workers.

Table 1 lists the social wasps of the West Indies and summarises present biological knowledge of them. My purpose here is to draw attention to 21 open questions about the biology and faunistics of these wasps. Where a statement is not referenced, it pertains to an unpublished personal observation.

1. What is the geographic source of Bocas Islands' *Polistes versicolor*?

*Polistes versicolor* is widespread in South America and extends into Central America (Richards 1978). It varies significantly in colouration across this range, suggesting substantial genetic variation. As a rule, in the northern part of its range the yellow marks on the body are more prominent in specimens from the western portion of its range and less so on those from the eastern portion, with an overall darkening effect. *Polistes versicolor* is one of three species of social wasps on the Bocas Islands between Trinidad and the Paria Peninsula of Venezuela. A preliminary examination suggests gene flow into the Bocas Islands from the mainland, rather than from Trinidad. This problem can possibly be satisfactorily solved

through analysis of colour characters. It can certainly be solved through analysis of molecular characters.

2. Why is Tobago's social-wasp fauna so depauperate?

Trinidad and Tobago are topographically and climatically similar, differing substantially only in size; Trinidad is 16 times as large as Tobago. The general trend of the species-area relationship (Spiller and Schoener 2009) predicts that Trinidad will have about 2.5 times as many species as Tobago in a given taxon or guild. Data from a broad range of well-studied groups of plants and animals yield Trinidad/Tobago species ratios between about 2 and 5. The one exception is social wasps, of which Trinidad has 38 species and Tobago just four (Starr and Hook 2003). This case of Tobago exceptionalism calls for explanation.

3. Does Tobago have an endemic species of *Brachygastrina*?

As presently conceived, *Brachygastrina bilineolata* is a very widespread species, whose known range approximates South America north of the Southern Cone (Richards 1978: 172). Wasps matching the description of *B. bilineolata* are found in both Trinidad and Tobago. However, Tobago specimens are somewhat smaller and darker than those from Trinidad and the nearby mainland, suggesting an undescribed species.

4. Why is *Polistes versicolor* so prevalent on Little Tobago?

Three of Tobago's four social-wasp species are reasonably abundant on the main island. These are all swarm-founders, while the one independent-founder, *Polistes versicolor*, is rarely encountered there. On Little Tobago, in contrast, it is the most abundant species. The other species recorded from Little Tobago, *Polybia occidentalis*, is much less common, in contrast to its status as the most abundant species on both the main island and

Trinidad. We have no idea what sets Little Tobago apart in this respect.

5. Why is *Polistes dominicus* absent from Carriacou?

*Polistes dominicus* is present on St. Vincent and quite abundant on Union Island (8km<sup>2</sup>) in the central Grenadines. In contrast, it is absent from Carriacou (34km<sup>2</sup>), which is environmentally similar and just 7km to the south of Union Island. Possible explanations include: a) a subtle environmental difference that makes Carriacou less hospitable to this wasp, b) periodic local extinctions, more recently on Carriacou, without re-colonisation, and c) prevailing winds that make any southward colonization of a new island improbable. The pattern of presence and absence elsewhere in the Grenadines may throw light on this question.

6. What happened to St. Lucia's *Polistes dominicus*?

*Polistes dominicus* was a familiar wasp in St. Lucia within living memory, yet it has now been absent for some decades (various pers. comms.). The most commonly suggested explanation that I have heard – increased application of pesticides – is not believable, given the frequent abundance of *Polistes* spp. in other areas with much heavier pesticide use. To be plausible, any hypothesis must explain why this species is present in St. Vincent but not St. Lucia.

7. Are *Synoeca surinama* and some other species undergoing population collapse?

The global decline in amphibian numbers, suspected by herpetologists as early as 30 years ago, is now an established fact (Wake 2003). The analogous suspicion that something similar is happening to social wasps in some regions is much more recent (Dejean *et al.* 2011). A case in point in Trinidad is that of the familiar djèp tatu, *Synoeca surinama*. At least in the northern part of the island, this once common species is now hardly to be found. Some other species also seem to have become much less abundant than they were just a few years ago. What is needed, both in our region and elsewhere, is a system for field researchers to use to report on species that have become much more or less abundant in recent years.

8. What is the niche separation among Jamaican social wasps?

Jamaica has just three species of social wasps. At least in the Kingston area, *Polistes crinitus*, *P. dorsalis*, and *P. major* are all common in suburban areas, where they often nest together on buildings and other human-built structures. The niche separation between these supposedly very similar species has yet to be addressed.

9. What are the foraging ranges of *Polistes lanio* and *P. versicolor*?

*Polistes lanio* and *P. versicolor* are among the commonest social wasps in Trinidad. Present evidence is that the former prefers more open areas, while the latter is found in more densely vegetated areas, although there is no sharp habitat separation between the two (Kadir *et al.* 2006). What is not known is whether their foraging-flight ranges are a factor in niche separation. To begin with, we have no idea whether either species forages mostly near the nest or further afield. In the one comparable study to date, Dew and Michener (1978) found significant difference in mean flight distance between two co-occurring North American *Polistes* species.

10. What is the niche separation between *Mischocyttarus alfkenii* and *M. baconi*?

This pair of ethospecies is found in Trinidad and probably more widely in northern South America. The two species differ hardly at all physically (O'Connor *et al.* 2011), and preliminary behavioural observations show no differences aside from those leading to distinctly different nest structures (A.A. Scobie and C.K. Starr, unpubl.). Furthermore, colonies of both species are often found nesting in proximity. The niche differences that permit this coexistence will likely be more difficult to discover than in the foregoing examples of coexisting *Polistes* species.

11. Are *Angiopolybia pallens* workers attracted to smoke?

*Angiopolybia pallens* is the most abundant social wasp in closed-canopy forest in Trinidad. It feeds readily on fresh carrion (O'Donnell 1995; Silveira *et al.* 2005), which may be its main protein source. Preliminary observations suggest that *Angiopolybia* comes to carrion baits in especially large numbers when these are close to fire. It makes biological sense that carrion feeders should be attracted to smoke, but it is not experimentally demonstrated that they are.

12. How far away do swarm-founding species move to found?

The maximum potential colony-founding range (i.e. distance from the parent colony at which a new colony can be established) is necessarily much less for swarm-founding social wasps than it is for independent founders. However, this range has been very little studied, and we certainly do not know whether it varies systematically among species. This question has implications for population-genetic patterns and dispersal among islands. Swarming can be induced experimentally by cutting down the nest without damage to the adult wasps.

13. Does *Mischocyttarus punctatus*'s nest form affect its social interactions?

While all other independent-founding social wasps in our area build a fairly compact nest comb, that of *M. punctatus* is extremely elongate, the cells almost standing end to end. This structure presumably serves as a defensive function by camouflaging the nest to resemble a vine. It has been suggested (Starr 1991) that a very elongate comb will affect social life by decreasing the frequency of one-to-one interactions among nestmates. It may also make it harder for the dominant female to maintain a reproductive monopoly. These propositions can be tested through comparison of *M. punctatus* with a sympatric *Mischocyttarus* species with a more compact nest.

14. What is the colony survivorship curve in independent-founding species?

Social-insect colonies go through a regular cycle analogous to the life cycle of individual organisms. The age-survivorship patterns of colonies can be studied in much the same way as those of individual organisms. In independent founders, the founding stage of the cycle begins at colony foundation and ends with the emergence of the first adult offspring (workers). This is presumed to be an especially hazardous period of high colony mortality (Giannotti and Machado 1994b; Reeve 1991), yet this hypothesis has been little tested. Studies of *Mischocyttarus rotundicollis* and *Polistes lanio* in Trinidad show that about half of all colonies do not survive the founding stage. What is not yet known is whether this stage occupies about half of the total cycle or significantly less or more.

15. How bang-bang is the production schedule of offspring?

Theoretical formulations lead to the prediction of an abrupt switch from producing worker brood to reproductive brood (Oster and Wilson 1978). That is, all reproductive offspring will be younger than the youngest worker. However, in North American vespine wasps Greene (1984) found substantial departure from a strict "bang-bang" pattern. In principle, it is possible to devise an index to quantify the middle ground between strict bang-bang and full overlap. In cases where the first males emerge before the first queens (protandry), examination of pupae will allow the comparative use of this index.

16. Is there age-based caste differentiation in independent-founding species?

Polymorphic workers are unknown in social wasps, but this is not to say that all workers in a colony behave alike. Newly emerged individuals are largely quiescent,

and after they become active there may still be differences in their attention to different tasks. In honey bees – which also have monomorphic workers – a well-known temporal division of labour is found among workers, such that individuals shift roles as they age (Michener 1974: Table 12.3; Seeley 1995: 29-31). Nothing comparable is reported from *Mischocyttarus* or *Polistes* (e.g., Giannotti and Machado 1994a; Post *et al.* 1988), yet it seems unlikely that fully mature *Mischocyttarus* and *Polistes* workers retain the same task profiles throughout life. The small size of colonies on their open-comb nests facilitates the observation of the behaviour of workers of different ages. Marking of individuals allows them to be followed through adult life.

17. What are the threat array and sequence in our *Polistes* species?

*Polistes* distinguish themselves by the visual threats that they direct toward intruders at the nest. Under gradually escalating provocation, threat displays tend to originate in a species-characteristic sequence, indicative of differing release thresholds (Starr 1990). To date, these have been studied in five North American and three West Indian species (Starr 1990; C.A. Western and C.K. Starr, unpubl.). Recording the threat and array from a broader range of species can aid in analysing the comparative pattern for the genus as a whole.

18. Is there social facilitation when *Polistes* colonies attack?

If a colony is sufficiently provoked, each adult will either attack the intruder or retreat and flee from the nest. Attacking wasps do not all do so simultaneously, indicating differing individual response thresholds. Nonetheless, it often appears that many wasps attack at virtually the same instant, even without any sudden change in the provocation (R. Bhukal, unpubl.). This suggests visually-mediated social facilitation among nestmates. This would appear advantageous to the colony, but it remains to be demonstrated that it is a real phenomenon. On the other hand, no such social facilitation among fleeing wasps is predicted.

19. What is the schedule of venom expression when stinging?

The venom load and toxicity of many stinging insects has been measured, yielding estimates of the maximum capacity of individual females to deliver pain and/or tissue damage (Schmidt 1990). What is not known is whether a stinging female delivers all or most of her venom at once or only a fraction of it. Wasps are often observed to sting an intruder repeatedly in a single episode, which

suggests that not all venom is delivered in the first sting.

#### 20. Is *Microstigmus theridii* eusocial?

*Microstigmus* (Crabronidae) is a Neotropical genus of 23 known species (Bohart and Menke 1976: 192; Melo and Matthews 1997). Although they are not social wasps in the formal sense, one species is known to be eusocial (Matthews 1991). All species are tiny and build simple hanging nests bound together with silk from the abdominal glands in adult females. The first species to be described, *M. theridii*, commonly has more than one adult female in a nest and so is not entirely solitary. However, it is not known whether it, too, is eusocial.

#### 21. What is the social pattern of *Trypoxylon maidli*?

*Trypoxylon* (Crabronidae) is a worldwide genus of more than 359 species of mud-nesting wasps (Bohart and Menke 1976: 345-49). Most species are solitary, but some members of the *T. fabricator* group commonly have several adult females in a nest (Gobbi *et al.* 1991; Hook 2011; Matthews 1991; Sakagami *et al.* 1990). *Trypoxylon maidli* commonly nests in and on buildings in Trinidad, often with many adults sharing a nest. Nests may persist for years in sheltered locations, and preliminary observations suggest that a given nest can be utilised over a number of years. What is not known is whether cells are reutilised or if there is cooperative brood care among females.

### CONCLUSION

These are of course not the only open questions about West Indian social wasps, nor are they of equal importance or difficulty. However, I believe all to be worthwhile and tractable. It is reasonable to expect that about half of them will be resolved within 10 years, giving rise to new questions.

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	A	B	C	D	E	F	G	H	I	REF
<i>M. collarellus</i>	++	++								62
<i>M. cubensis</i>		+								
<i>M. fitzgeraldi</i>	++	++								
<i>M. injucundus</i>	++	++								
<i>M. labiatus</i>	++	++	++	+	+					31, 34
<i>M. metathoracicus</i>		++								
<i>M. mexicanus</i>	++	++	++							7, 26, 27, 34
<i>M. phthisicus</i>										
<i>M. punctatus</i>	++	++								
<i>M. rotundicollis</i>	++	++			++					
<i>M. socialis</i>		++	+							59
<i>M. surinamensis</i>										
<i>Polistes bahamensis</i>		+						+		
<i>P. billardieri</i>										
<i>P. carnifex</i>		++								9
<i>P. crinitus</i>	++	++						+		61, 48
<i>P. cubensis</i>								+		
<i>P. dominicus</i>	++	++					++	+		
<i>P. dorsalis</i>	++	++								13
<i>P. goeldii</i>		++								
<i>P. incertus</i>										
<i>P. lanio</i>	++	++				++		++	++	13, 19, 21, 58
<i>P. major</i>	++	++								13
<i>P. minor</i>										
<i>P. pacificus</i>		++								13
<i>P. poeyi</i>										
<i>P. versicolor</i>	++	++				++		++		20, 24, 52, 48
<b>Swarm-Founding Species</b>										
<i>Agelaia cajennensis</i>		++						+		8, 38
<i>A. multipicta</i>	++	++						+		16, 38, 71
<i>Angiopolybia pallens</i>	++	++								10, 52
<i>Apoica gelida</i>		+			++					32, 52
<i>A. pallens</i>	++	+			++		++			30, 32, 52
<i>A. pallida</i>		++			+					52, 55
<i>A. strigata</i>		+			+					52

	A	B	C	D	E	F	G	H	I	REF
<i>Brachygastra bilineolata</i>	++	++			++					32
<i>Chartergellus nr. zonatus</i>		+			+					6, 70
<i>Epipona tatua</i>	++	++								42
<i>Metapolybia cingulata</i>	++	++			++					2, 14, 15, 32, 52
<i>Parachartergus colobopterus</i>	++	++		++						68
<i>P. fraternus</i>	++	++			++		++			32, 46
<i>Polybia occidentalis</i>	++	++	++	+	++	++	++	++	+	22, 28, 32, 36, 50, 52
<i>P. quadricincta</i>	++	++								
<i>P. rejecta</i>	++	++			++					32
<i>P. striata</i>	++	++								
<i>P. tinctipennis</i>										
<i>Protopolybia exigua</i>	++	++		+						37
<i>Synoeca surinama</i>	++	++	++	++	++					3-5, 32

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