LIVING WORLD

Journal of The Trinidad and Tobago Field Naturalists' Club

2006

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.

Mission Statement

To foster education and knowledge of natural history and to encourage and promote activities that lead to the appreciation, preservation and conservation of our natural heritage.

Enquiries

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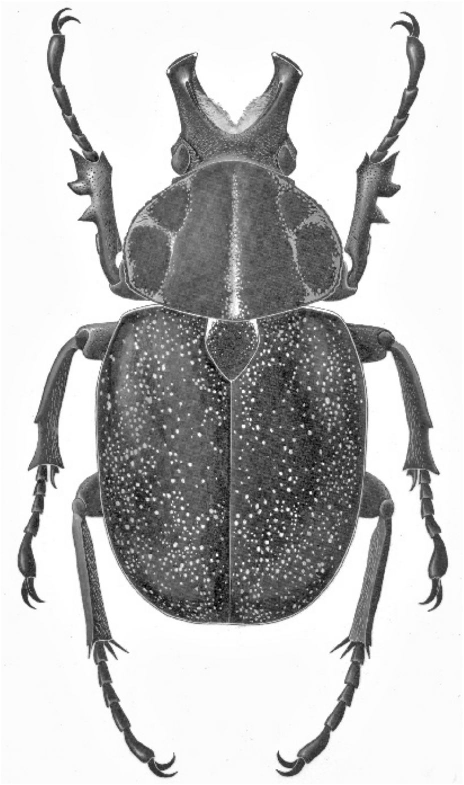

Inca clathrata quesneli Boos and Ratcliffe

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Special thanks to Michael E. Tikasingh for the design and layout of the front and back covers and the sponsors page. We also thank Rupert Mends for proofreading and to Dr. B. Ratcliffe for use of the image of the Inca beetle in the title page.

Editorial

Our Club's Logo

The image of an Inca beetle with the words *Natura maxime miranda in minimis* was chosen as our logo and first published in the Journal of the Field Naturalists' Club of 1892. The reason for choosing this beetle for our logo was not recorded. The Journal ceased publication in 1896, but was restarted in 1956. In re-establishing the Journal, the Editors of that issue wanted to include the logo, but could not find the original woodcut of the image engraved by our first President, H. Carraciolo. A specimen was obtained from the Commonwealth Institute of Entomology from which a new drawing was made by J. S. Kenny for the 1956 issue (p. 27). This drawing was used on the cover or on the title page in all issues of the Journal from 1956 to 2005 and in official documents of the Club. Kenny's original drawing seems to be lost.

In 1985, Julius Boos and Brett Ratcliffe described a new subspecies of the Inca beetle in the Coleopterists Bulletin (vol. 39, No. 4). They named it after Dr. Victor Quesnel, *Inca clathrata quesneli* and noted that this subspecies was found only on Trinidad.

During our centenary year, 1991, a special coloured centenary logo was created depicting three aspects of the environment, with the Inca beetle, which appears to be similar to the Boos and Ratcliffe image, superimposed on it. A circle with the words "Trinidad and Tobago Field Naturalists' Club" and "Founded in 1891" appeared around the art work and under it the words "*Natura Maxime Miranda in Minimis"* inscribed.

Subsequently, around 1994 some aspects of the centenary logo were omitted and the image of the beetle used was either Kenny's original drawing or the one which appeared on the centenary logo. It is time that the Management Committee decide which image of the beetle should be used in our logo.

Nevertheless, the title page of Living World will now include the Boos and Ratcliffe image of the beetle with its identification. This image originated from Dr. Ratcliffe's laboratory and he has given us permission to use it.

The 2006 Issue of Living World

Trinidad and Tobago are two small islands with a growing population. It is also becoming heavily industrialised so there is a constant demand for space. We are pleased to have Professor John Spence as our Guest Editorialist to discuss "Land Usage in Trinidad and Tobago".

In this issue, Charles Collins studied the growth and development rates of two tanagers in Trinidad and showed they were lower than similar sized birds in the temperate zone. He also noted that the chicks gaped silently rather than noisily which could be an antipredator adaptation.

Two of our regular contributors continue with their series: Matthew Cock with skipper butterflies of Trinidad, Group L and David Bass on freshwater macroinvertebrates in the Caribbean, focussing this time on St. Kitts and Nevis.

Victor Quesnel reports on his observations of the reproductive behaviour on the gecko *Thecadactylus rapicauda*.

Knowledge on spiders in Trinidad and Tobago is limited so with this in mind we publish a key to the identification of spider families with colour photos to some representative species.

In this issue there are five Nature Notes. One on nesting behaviour of caimans in the Rupununi Savannahs by Shirley Humphrys. We welcome her to our pages and hope she can continue to contribute on her observations on wildlife in the Rupununi, Guyana. Allan Hook records a species of wasp new to the fauna of Trinidad and Tobago. Matthew Cock points out that Trinidad's Leaf Shoemaker is *Zaretis ellops* and not *Z. itys.* R. G. Cooper notes that because the African Giant rat is becoming a pet animal it may be widely distributed and suggests that we maintain surveillance for its presence. Christopher Starr and Jo - Anne Sewlal discuss heights above the ground as a niche separator in two orb-weaving spiders in Nevis.

There are two book reviews: one by Matthew Cock on the butterflies of the French Antilles and the other on Carol Gould's biography of William Beebe, who established the Tropical Research Station at Simla (Arima Valley, Trinidad) for the New York Zoological Society and where Beebe ended his days. This review is written by Christopher Starr.

Dr. Charles Dennis Adams spent four years in Trinidad and contributed greatly to the knowledge of our flora. Yasmin Baksh-Comeau paid tribute to Dr. Adams in an obituary written for the "Fern Gazette" and we have permission from the Editor of that Journal to reproduce this obituary.

EST

Guest Editorial: State of the Environment

Land Use in Trinidad and Tobago

Since this country consists of two small islands with limited land space, careful planning is essential to ensure that there is a balance between built development and other land uses including conservation under natural forests. Under Town and Country Planning legislation, Parliament has approved plans for general land use but the problem has been to ensure adherence to the plans. In periods of economic "boom", as is presently occurring, the task of balancing development and conservation of the land resource is that much more difficult.

Fortunately this country has a good base from which to plan land use in that there is available a detailed soil survey of the two islands. The soils are divided into seven land capability classes, Class I being the best for agriculture and Class VII being unsuitable for agriculture.

In spite of this excellent basis, land use has so far been abysmal. Some of our best agricultural land has been used for housing and industry and agricultural projects have been developed on land much less suitable for agriculture, such as in Wallerfield. This area is now being developed for the University of Trinidad and Tobago, a technology park and recently it has been announced that a new town is to be developed there. This is more appropriate use for that land. Unfortunately the converse does not occur–that is, the good agricultural land which has been given over to housing does not revert to agricultural use!

In Trinidad the largest area of Classes I and II soils occurs in the valleys on the Northern mountain range and in the area at the foothills of that range. Thus Tucker Valley (in Chaguaramas), Diego Martin, Santa Cruz, Maracas and Caura Valleys, the Aranguez vegetable growing area, Valsayn and Orange Grove possess some of the best agricultural land in the country. Regretfully those areas (except Tucker Valley) are now occupied by intensive housing and other built development. Plans have been announced to start with housing development in Tucker Valley. While the present plans would result in little disturbance of the main area of land suitable for agriculture, this development may represent the beginning of a trend which may in the future result in loss of the entire valley from use for agriculture. There is also the very great risk that with the reduction in sugarcane cultivation significant areas of formerly Caroni (1975) Ltd. land will go into non-agricultural use.

Class I soil type is to be found in River Estate in the Diego Martin Valley, formerly a cocoa experiment station. Over the years it has been gradually given over to housing and other built development. The Santa Cruz Valley was once cultivated in grapefruit and cocoa. In the past, in certain months of the year, there was the beautiful sight of the ripe grapefruit stretching down the valley as far as the eye could see (at that time this country exported over a million crates of grapefruit per annum). Now most of that valley is occupied by housing.

From St. Augustine to Arima, where the soil is good for agriculture, land formerly in cultivation is going into housing. There are few parks or open spaces and no market garden (vegetable growing) areas that should normally abut population centres. The quality of life for the inhabitants of these housing developments is undoubtedly deteriorating. A section of the former Orange Grove Sugarcane Estate (with land suitable for agriculture) has been used to construct houses to relocate persons displaced by the construction of the new airport. Approximately four miles further east of this site is poor agricultural land that could have been used for the housing project.

In the South-West section of Tobago there is land classified as "Very Good" to "Moderately Good" for agriculture and which was once occupied by highly productive coconut estates and cattle. Most of this area has gone into tourism developments–hotels, golf courses, housing and most recently a Sporting complex–the Dwight Yorke Stadium.

A planned housing development at Roxborough Estate in Tobago will replace cocoa at a time when the production of world-famous Trinidad and Tobago cocoa continues to decline.

Some of our agricultural developments also result in improper land use. Thus the growing of rice (to enhance local food production) in the Nariva Swamp in an unplanned way did damage to those wetlands. The growing of christophene on the slopes at the side of the Blanchisseuse Road creates an environmental disaster waiting to happen. Steep slopes should be under permanent forest cover.

Since land that has been built on is never returned to agricultural use, if it is not currently being used for agriculture, it should be utilised for timber trees (a valuable commodity) until such time as it is required for agriculture.

There are other planning decisions that affect use of the land. Thus the construction of a North Coast road from Blanchisseuse to Matelot will encourage illegal logging and agriculture which could destroy the forests as has occurred in the western section of the Northern Range. This not only results in constant flooding but also affects our water supply much of which derives from the Northern Range.

Industrial developments which require large areas of land, such as an aluminium smelter, should be carefully considered in relation to alternative developments requiring less land but giving equivalent economic benefits. Aluminium could be imported and downstream manufacturing developed which probably provides a greater return per unit of energy utilised without the loss of land and risk of environmental pollutants.

While we have the resources from our energy sector, we should also consider claiming land from the sea, wherever this is feasible, to add to our limited land area.

One of our problems is lack of awareness on the part of the population of these issues. This could be corrected by the teaching of geography in schools as a compulsory subject. Modern geography is about the relation of people to their environment and so persons tutored in this discipline will better understand proper land use.

While the knowledge to plan for proper land use is available, and the laws are present, enforcement of such laws is inadequate. With abundant wealth available to government and many citizens at this time, the pressure to circumvent the regulations is great and mistakes in land use that are irrevocable may be made. In this small country with limited land space all planning decisions must take sensible land use into account.

Although agriculture may be of low significance while there is income from oil and natural gas, which are finite assets, the nation's future prosperity will depend on use of renewable resources including agriculture. If a good quality of life is to be sustained in the long-term, the natural environment that is aesthetically pleasing as well as useful must be maintained and this needs proper land-use planning and implementation of the plans. Conservation of the natural environment to preserve biological diversity and to ensure water supplies as well as to prevent flooding is critical to our future well-being.

John Spence
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Cover photo

A male sphecid wasp on its nest, new to the fauna of Trinidad and Tobago, the first collection north of the Amazon river (see page 53)

DR CHARLES DENNIS ADAMS 1920 - 2005

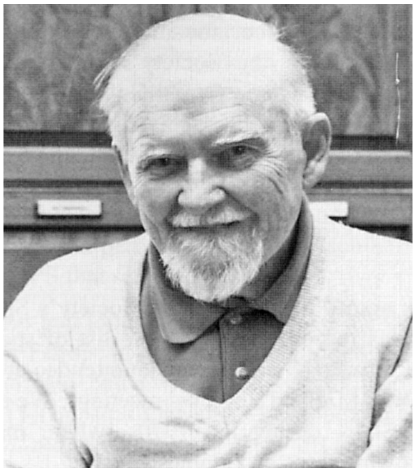
photo: Derek Adams (NHM Photo Studio)
Dennis Adams, April 2000

The field of Tropical Biology, and in particular Caribbean Ecology and Plant Systematics, lost one of its most erudite scholars with the passing of Dr Charles Dennis Adams on the 25th March 2005. Dennis was born on the 23rd March 1920 in Shinfield, Berkshire, England. He attended King's College, University of London from 1937 to 1939. In 1940 he aborted his studies and volunteered for Military Service in the British Army. Moving up the ranks to Commanding Officer in the Weapon Training School in the Royal Artillery Depot, Woolwich, he ended his military career as a Major in the Royal Artillery in 1946. This was a significant period in his life for self discovery and his marriage in 1942 to Elsie, who died in 1986 ending 44 years of a fulfilling and loyal partnership.

Immediately after the war he returned to King's College to resume his university education, graduating with 2nd Class Honours in his BSc General (Botany, Chemistry, Zoology) in 1948 and obtaining 1st Class Honours in a BSc Special (Botany) for which he was awarded the Carter Prize in Botany in 1949. A brilliant scholar, he was now poised to make his contribution to botany. Post-war Britain was grim and depressing, and the opportunity to start a new life and career in one of the Crown Colonies, the Gold Coast (now Ghana), beckoned. A lectureship at the newly established University College of Gold Coast (University of Ghana) marked the beginning of a long and distinguished academic career in tropical plant ecology and taxonomy. His sojourn in Ghana from 1949 to 1959 led to numerous publications on West African vegetation and flora, focusing on pteridophytes and Compositae, establishing many new taxa, combinations and records.

The lure of writing and publishing Caribbean Floras took him to Jamaica to join the University College of the West Indies, Mona Campus (now the University of the West Indies) as a lecturer. The Jamaican era (1959-1976) would establish Dennis' reputation as the esteemed author of the *Flowering Plants of Jamaica* (1972) and other popular books such as *The Blue Mahoe* and *Other Bush* and *Caribbean Flora*. His formal academic career ended as a Senior Lecturer and Reader in Botany at the St Augustine Campus of the U.W.I. from 1976 to 1980.

C.D. Adams the scholar was equally matched by Dr. Adams the lecturer. To many of his students he was a conscientious and gifted teacher who imparted his knowledge with humility, simplicity and clarity. A stickler for organisation and details, nothing escaped his sharp eyes and quick wit. Spelling errors or inaccurate use of terminology were the ultimate travesty in scientific writing! These were perfect attributes for a reviewer, and his expertise was always in demand. While he applauded modern technology, computer jargon made him cringe.

On retirement, he came full circle to his homeland and became an Honorary Associate at The Natural History Museum in London, where flora research continued uninterrupted. He soon became involved with *Flora Mesoamericana*, contributing the accounts of *Asplenium* and *Diplazium* as well as many genera of flowering plants, and several other Caribbean studies involving phytogeography, ethnobotany and conservation. One of the high points of his retirement was a UN/FAO (United Nations/Food and Agriculture Organization) assignment in 1983 to the Maldives where he *"made an extensive survey of the flora and is probably the only authority on the subject"* (Webb, P.A. 1988. *Maldives People and Environment.* Media Transasia Lt. Thailand).

At the personal level he was a very modest and private individual who shunned the limelight. In his spare time he 'taxonomised' his precious stamp collection. Close friends enjoyed his delightful company, with his quick repartee and double entendre. A number of tributes to Dennis were published in 2000 in *The Fern Gazette* (Vol. 16, pts 1-2: 1-10) to mark his 80th birthday.

We extend our deepest sympathies to Dennis' two surviving younger brothers, Michael and John Adams.

Yasmin S. Baksh-Comeau

Reprinted with permission.

The British Pteridological Society Bulletin, 6(4): 344-345.

Growth and Development of the Violaceous Euphonia and Palm Tanager in Trinidad

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ABSTRACT

The growth and postnatal development of Violaceous Euphonia (*Euphonia violacea*) and Palm Tanager (*Thraupis palmarum*) chicks were studied in Arima Valley, Trinidad. Like many tropical passerines, these two tanagers had lower growth rates ($K = 0.462$ and 0.386; $T_{10\text{-}90} = 9.6$ and 12 days respectively) than comparable sized temperate zone species. Palm Tanagers fledged at the age of 18 days and the Euphonias between 17 and 20 days. Both species were poikilothermic at hatching and only became homeothermic at 9-10 days post hatching. Chicks of both species gaped silently which may be an anti-predator detection adaptation. The reduced mobbing by the adult tanagers may represent an adaptive response to increase adult survival and, as a result, long-term reproductive success.

Key words: *Euphonia, violacea, Thraupis, palmarum*, tanager, Trinidad, growth, thermoregulation, behaviour, begging, mobbing.

INTRODUCTION

The postnatal growth and development of nestling birds has been a long-standing interest of ornithologists. The graphical method of characterizing avian growth data and generating summary statistics (Ricklefs 1967) opened the door for broader comparative studies involving a greater diversity of species from around the world (Ricklefs 1968, 1976; Starck and Ricklefs 1998a). Despite the many field and laboratory studies in recent years, some taxa and geographical areas are still under-represented in even the most recent summary of our knowledge of avian growth (Starck and Ricklefs 1998a).

One of the early observations was that "tropical passerine birds, particularly species with small clutches, grow more slowly than passerines in temperate regions" (Ricklefs 1976:179). Although there has been a detailed analysis of this and the relationship of growth rate to other variables such as clutch size and diet (Ricklefs 1976), the available growth and life history data for some predominantly tropical bird families remain rather lean (Stutchbury and Morton 2001). Growth data are available for only 18 of 425 species (4.2 %) of flycatchers (Tyrannidae) and eight of 256 species (3.1 %) of tanagers (Emberizidae: Thraupinae). In the case of the manakins (Pipridae) there are data for only 1 of 52 (1.9 %) of the species and the large and diverse neotropical family Furnariidae (256 species) is unrepresented in the latest compendium of avian growth data (Starck and Ricklefs 1998b).

In the course of field studies of swifts I conducted in Trinidad from 1961 to 1967 (Collins 1963a, 1968a, 1968b, 2002), I was also able to obtain data on the postnatal growth and development of thermoregulation in two tanagers, the Violaceous Euphonia (= Semp, herein), *Euphonia violacea*, and Palm Tanager, *Thraupis palmarum*. Although the statistics characterizing the chick growth of these two species were included in earlier studies (Ricklefs 1968, 1976; Starck and Ricklefs 1998b), the original data on which these were based, along with data on the development of temperature regulation and additional breeding biology observations, were never placed on record and I, belatedly, do so here.

MATERIALS AND METHODS

I was able to follow the growth of four chicks in one Semp nest and seven chicks from four nests of the Palm Tanager. The single Semp nest was located at the lip of a roadside bank in the Verdant Vale area of Arima Valley. Five chicks hatched on 6 August 1962, four of which were followed for 10 of the next 15 days; one chick was collected for natal down analysis (Collins 1962). All four young presumably fledged between 21 August when the nest was last checked, and 25 August when the nest was found empty.

The four Palm Tanager nests were located in two ornamental palms on the grounds of Simla, the William Beebe Tropical Research Station in Arima Valley. One nest, followed from 6-23 May 1963, had only one viable chick; a second chick was found dead in the nest when first checked at which time they were both about 3 days old. In 1964 three nests were followed, each containing two chicks: nest 1 was followed from 6-24 June, nest 2 from 8 July to 1 August and nest 3 from 28 July until 4 August.

Nestlings were weighed with a spring balance obtained from the British Trust for Ornithology. The balance was calibrated in half-gram intervals and weights were estimated to the nearest quarter-gram. Wing and tail measurements were made with a stopped metal wing rule to the nearest 0.5 mm. The summary growth statistics for these data were generated by R. E. Ricklefs (1968) using a graphical curve-fitting procedure (Ricklefs 1967) and the logistic growth model. Included were: the overall growth rate constant K which can be used for interspecific comparisons, the asymptote of the growth curve A and T_{10-90}, an inverse measure of growth rate representing the time for growth between 10% and 90% of the asymptote.

Body temperatures were measured with a fast-registering small bulb mercury thermometer made by the Schultheis Corporation. Readings were taken with the bulb inserted about 10 mm into the cloaca. Cold stress experiments were used in 1964 as part of the investigation of nestling thermoregulatory abilities. These utilized a 20 x 15 x 13 cm (approximately) cold chamber made of foam plastic insulation material approx. 3.0 cm thick (Collins 1968: Fig. 2), which four 6 oz cans of "Skotch Ice" (refreezable liquid) kept at a temperature of approximately 5º C. Nestlings were placed individually in the chamber in the field for a period of 5 min. and their body temperatures were recorded before and after cold exposure. Even though sharp body temperature drops were recorded for very young nestlings, the tests caused no apparent ill effects.

RESULTS

At hatching, Semp chicks had only a sparse covering of 32 natal downs (neossoptiles) confined to the coronal, occipital, spinal and scapular tracts (Collins 1962). The edge of the otherwise dark bill was yellow, the gape was white, the mouth lining bright red and the legs and toes were darkly pigmented. A small egg tooth was noticed only on day 1. The eyes, which were closed at hatching, began to open at day 8 and were fully open on day 14. The dorsal skin progressively darkened during the first 6 days post hatching. Primary wing feathers first erupted through the skin on day 6 post hatching at which time the body contour feathers were still only dark streaks under the skin. By day 9 the contour pin feathers were 1.5-2.0 mm through the skin; both contour feathers and primaries began erupting from their sheaths by day 11. The contour feathers largely covered the body by day 16 but were still ensheathed at their base. By day 3 the still blind chicks gaped vigorously but silently in response to any vocal or tactile stimulus. The chicks developed rapidly and could hop and flutter short distances by day 16. Fledging took place between 16 and 20 days post hatching.

At hatching, Semp chicks weighed an average of 1.1 g. Body mass increased fourfold by day 4 and reached an average of 10.8 g by day 8 (Table 1). The rate of increase slowed thereafter and body weights varied from 13.5 to 14.5 g from days 10-15. The growth rate constant (K) was 0.460 and T_{10-90} was 9.6 days; the asymptote of the growth trajectory was 14.5 g which is the same as the average adult weight (Snow and Snow 1963a). Semp chicks' wing length was 5 mm at hatching and reached 8-9 mm by day 4. Wing length increased rapidly thereafter as the primary feathers emerged and elongated (Table 1). The wing length reached 37.5-41.0 mm (70.8 % of adult length; Snow and Snow 1963a) by day 15, the last day the chicks were handled. The rectrices first emerged on day 10 post hatching and reached a length of 9-11 mm on day 16.

Semp chicks' thermoregulatory capacity was not tested experimentally. However, on the day of hatching, their body temperatures rapidly dropped to 28.5 º C when unbrooded; ambient temperature was probably about 24º C. This would indicate a homeothermy index (H. Visser 1998) of only 0.28. From days 3-8 their body temperature dropped from about 40º C to between 32.7 and 35.8º C during the 5-10 min. period while out of the nest being weighed and measured. During this time H increased somewhat, averaging 0.64 ($n = 12$, range = 0.54-0.73, SD = 0.05) which was still well below a value of $H \geq 0.80$ thus indicating homeothermy had not yet been achieved (Visser 1998). Starting on day 9 the body temperatures only dropped to 38.3-40.2 which was just 0.5-1.2 below the level recorded when they were first removed from the nest. At this time H averaged 0.95 ($n = 16$, range = 0.85-1.01, SD = 0.05). This rapid transition to thermoregulation occurred before the developing contour plumage offered much insulation and when the body mass was about 10-11 g which was 70-77 % of that of adults.

At hatching, Palm Tanager chicks have a moderately dense covering of 173-238 natal downs in 15 tracts and regions, including a newly defined spinal region of the spinal tract (Collins 1962; Collins and Araya 1998). The chicks had a blackish bill with a yellowish tip, ivory white gape and carmine red mouth lining. When gaping the chicks were at first silent and later only uttered a very weak peeping. A white egg tooth, observable on the upper mandible at hatching, was dark coloured but still detectable on day 5 and completely reabsorbed by day 17. The eyes, which were closed at hatching, began to open at 5-6 days and were fully open on day 9. The legs, toes and claws were unpigmented at hatching but started to darken by day 5. Feather tracts were observable by day 4 when the contour feathers were dark streaks under the skin. Primary pin feathers erupted through the skin on day 5 and the secondary and contour feathers on day 7 post hatching. Contour feathers began erupting from their sheaths on day 10. The rectrix pin feathers emerged through the skin on days 8-9

Table 1. Growth of Semp and Palm Tanager chicks. The values presented are: Mean, (range) and [sample size (n)]. ** = no data.

Semp				Palm Tanager			
Age (day)	**Mass (g)**	**wing (mm)**	**Tail (mm)**	**Age (day)**	**Mass (g)**	**Wing (mm)**	**Tail (mm)**
1	1.1 (1.0-1.12 [5]	5 (5.0-5.0) [5]	0 ** **	1	5.5 (5.0-6.0) [2]	8.5 (8.0-9.0) [2]	0 ** **
2	1.8 (1.5-2.0) [4]	5 (5.0-5.0) [4]	0 ** **	2	7.3 (6.75-8.25) [3]	9.5 (9.5-9.5) [3]	0 ** **
3	3.1 (3.0-3.25) 4	** ** **	0 ** **	3	9.6 (8.5-11.0) [5]	11.2 (11.0-11.5) [5]	0 ** **
4	** ** **	** ** **	** ** **	4	12.1 (10.5-13.8) [4]	12.8 (12.5-13.0) [4]	0 ** **
5	4.6 (4.5-5.0) [4]	8.5 (8.0-9.0) [4]	0 ** **	5	14 (13.5-14.5) [2]	15.5 (15.0-16.0) [2]	0 ** **
6	5.9 (5.75-6.25) [4]	10.1 (10.0-10.5) [4]	0 ** **	6	15.8 (15.0-16.5) [2]	18.25 (17.5-19.0) [2]	0 ** **
7	** ** **	** ** **	** ** **	7	18.25 (18.0-18.5) [2]	21.8 (20.0-23.5) [2]	0.5 (0.0-1.0) [2]
8	9.9 (9.5-10.25) [4]	15.75 (15.0-16.5) [4]	0 ** **	8	20.8 (19.8-22.3) [4]	26.5 (25.0-27.5) [4]	0.5 (0.5-0.5) [2]
9	10.8 (10.5-11.0) [4]	19.2 (18.5-20.0) [4]	0 ** **	9	21.9 (20.5-23.8) [5]	30 (27.0-32.0) [5]	1.2 (1.0-2.0) [5]
10	** ** **	** ** **	** ** **	10	23.9 (22.5-25.5) [4]	35.3 (33.0-36.5) [4]	3.1 (3.0-3.5) [4]
11	13.9 (13.5-14.3) [4]	18.7 (23.4-26.0) [4]	2.5 (1.5-3.0) [4]	11	25.9 (24.8-27.0) [4]	39.5 (37.5-40.5) [4]	5.8 (5.5-6.0) [4]
12	** ** **	** ** **	** ** **	12	26.8 (26.0-27.7) [4]	43.8 (41.0-44.5) [4]	8.5 (8.0-9.0) [4]
13	** ** **	** ** **	** ** **	13	27.7 (25.8-30.8) [4]	47.1 (46.0-48.5) [4]	11.4 (10.5-13.0) [4]
14	14.2 (13.8-14.3) [4]	33.4 (31.5-35.5) [4]	6.4 (5.5-7.0) [4]	14	27.4 (27.0-28.0) [3]	49.7 (48.5-51.0) [3]	12.5 (10.5-14.0) [3]
15	** ** **	** ** **	** ** **	15	28.5 (28.0-29.5) [4]	53.9 (53.0-55.0) [4]	16.4 (13.5-18.0) [4]
16	13.5 (13.0-14.5) [4]	39.4 (37.5-41.0) [4]	9.9 (9.0-11.0) [4]	16	28 (27.5-28.5) [2]	57.3 (57.0-57.5) [2]	19.5 (19.0-20.0) [2]
17	** ** **	** ** **	** ** **	17	30.3 (28.0-31.8) [3]	60.8 (60.0-62.5) [3]	24.1 (23.5-28.0) [3]
18	** ** **	** ** **	** ** **	18	29 ** [1]	61.5 ** [1]	23 ** [1]

and erupted through their sheaths by days 11-12. The body was mostly covered by contour feathers, except along the ventral midline by day 13 and was completely covered by day 15. The chicks developed motor skills rapidly. When placed on their side the chicks could right themselves by day 5, turn over by day 6 and begin to grasp things, such as nest material when being removed from the nest, by day 7. They could hold on to and balance on a perch by day 10 and fluttered their wings to help maintain balance on day 16. They gave a "startle" reaction to movements of nearby large objects or sounds by day 17. Fledging was on day 18 post hatching.

Palm Tanager chicks had a wing length of 8.0-9.0 mm at hatching which increased to 15.5 mm on day 5 when the primary pin feathers emerged through the skin. Thereafter, the primaries elongated and the wing length increased rapidly (3.9 mm per day) reaching 61 mm (65 % of the adult length, Snow and Snow 1963a) on day 17 just prior to fledging. The rectrices first emerged on days 8-9 and reached a length of 24-28 mm on day 17 post hatching.

At hatching, Palm Tanager chicks weighed 6.0 g and doubled this by day 4 and weighed 25 g on day 10. Their weight remained in the range of 27.5-28.5 g from days 14-17 prior to fledging (Table 1). The growth rate (K) was 0.386 and $t_{10\text{-}90}$ was 12 days; the asymptote of the growth trajectory was 28.0 g which is only 74% of the adult body weight of 38.6 g (Snow and Snow 1963a).

Like Semp chicks, Palm Tanager chicks had very poor thermoregulatory capacity at hatching. On day 1 body temperatures quickly dropped to 32.2-33.1º C shortly after their removal from the nest. This indicates H = 0.45-0.51. From days 2-9 body temperatures dropped to 35.5-38.6º C with an average H of 0.71 (n = 37, range = 0.36-0.88, SD = 0.14). On days 8 and 9 chicks' body temperatures were higher than expected with H values of 0.75-0.88. This may have resulted from body temperature measurements being taken soon after the chicks' removal from the warm thermal environment of the nest and before enough time had elapsed for much cooling to have occurred. When subjected to 5 min. cold stress tests, days 2-9 chicks lost an average of 4.89º C (n = 15, range = 4.1-6.1, SD = 0.62) to body temperatures as low as 30.9º C. From days 10-17 body temperatures remained higher averaging 40.35º C (n = 15, range = 38.5-42.0, SD = 1.34) and lost only an average of 1.29º C when cold stressed (n = 14, range = 0.0 -3.6, SD = 1.28); one 15-day old chick increased its body temperature by 0.3º C during the test. H values for chicks ≥ day 10 averaged 0.90 (n = 27, range = 0.76 -1.00, SD = 0.07) indicating that homeothermy had been achieved (H ≥ 0.8; Visser 1998). Shivering was first noticed on day 10 at ambient temperatures of 24.6-26.8º C. As noted for the Semp chicks, the transition to thermoregulation was rapid and occurred before the contour plumage offered much insulation and when body mass, on day 10, was about 63% of that of adult Palm Tanagers.

DISCUSSION

Euphonia nests are unique within the tanagers in being domed with a side opening (Skutch 1954, 1989; Isler and Isler 1999); they may be supported by a variety of tree branches, epiphytes and even sprouts on living fence posts. Semp nests in Trinidad are typically found "at the top of a bank overlooking a path" (ffrench 1991). Palm Tanagers, like other *Thraupis* tanagers, build open cup nests but show a distinct affinity for placing their nests in the axils of palm fronds (Skutch 1954; ffrench 1991; Isler and Isler 1999). Faecal material was not removed by adult Semps and the floor of the nest and the nest opening were quite fouled with gelatinous droppings from day 10 to the time the chicks fledged. The Palm Tanager nests were generally clean, the adults presumably having carried away faecal sacs.

The reduced numbers of natal downs on the nestling Semps is not surprising. Little or no natal down is typical for chicks of passerines building domed or closed nests. This contrasts with the substantial number of downs usually found in species building open cup nests. This pattern has been documented previously for tropical flycatchers (Tyrannidae; Collins and McDaniel 1989).

At the approach of adults, both Semp and Palm Tanager chicks begged vigorously exposing the bright red mouth lining framed by the swollen white gape edges. It is notable that in both species this begging was silent or nearly silent. This is in strong contrast to the noisy begging of many temperate zone passerines which make nests and nestlings detectable at substantial distances (pers. obs.). Silent begging has also been observed in White-lined Tanagers (*Tachyphonus rufus*: pers. obs), several thrushes (*Turdus* sp.; pers. obs.), and in previous studies of the Bearded Bellbird (*Procnias averano*) in Trinidad (Snow 1970) and the Cinnamon Flycatcher (*Pyrrhomyias cinnamomea*; Collins and Ryan 1995; Ryan and Collins 1999) and Slate-throated Redstart (*Myioborus mineatus*; Collins and Ryan 1994) in Venezuela.

As noted by Ricklefs (1970) "rates of predation on eggs and nestlings of birds is about twice as high in tropical as in temperate regions." Predation accounted for 82% of all nest failures of the Western Slaty Antshrike (*Thamnophilus atrinucha*) in Panama (Roper 2005) and 80% or more for the Black and White Manakin (*Manacus manacus*; Snow 1962) and three species of thrushes (*Turdus* sp.; Snow and Snow 1963b) in Trinidad. It follows that "antipredator adaptations seem more highly developed in the tropics than in temperate and arctic regions" and thus predation should be considered to be a "strong selective force" (Ricklefs 1970; see also Ricklefs 1969). When nest losses are high "any strategy [like the silent begging noted here] which reduces the percentage loss, even by a little, will greatly increase productivity" (Snow and Lill 1974) and thus be favored by selection. Both experiments (Haskell 1994; Leach and Leonard 1997; Dearborn 1999; Moreno-Rueda 2005) and direct field observation (Perrins 1965; Redondo and Castro 1992) have shown that begging vocalizations in temperate passerines increased the mortality due to predation. Thus, predation is a "selective force that may mold the evolution of begging calls by nestlings" (Moreno-Rueda 2005) and noisy "begging may carry a significant predation cost for nestling birds" (Leach and Leonard 1997). Silent begging by tropical passerines should be viewed as yet another among the many anti-predator adaptations developed in a predator-rich environment. A reduced brood size, requiring fewer provisioning visits each of which might attract predators, could also, in part, be related to the greater array and specializations of tropical predators (Ricklefs 1969, 1970; Snow 1970).

In Costa Rica, Scarlet-rumped Tanagers (*Ramphocelus passerinii*) are active and noisy in mobbing nest predators, such as snakes, and other perceived threats (Skutch 1989). The same is true for the Red-crowned Ant-tanager (*Habia rubica*) in Trinidad (ffrench 1991, pers. obs.). Adult Semps and Palm Tanagers were much quieter. They remained nearby during the time the chicks were being handled but were not particularly active or noisy (2 to 2.5 on a response scale of 1 to 4; Ricklefs 1977); they were somewhat more agitated when larger chicks vocalized during handling. This is in sharp contrast to the intense noisy mobbing, perhaps accompanied by physical attack (4 on the response scale; Ricklefs 1977) described for other tanagers (Skutch 1989) and familiar to field workers studying most temperate zone passerines. Semp and Palm Tanagers were, however, more demonstrative than some other tropical passerines, such as manakins (Ricklefs 1977, pers. obs.) which quietly depart the vicinity of the nest with no defense or vocalizing (1 on the response scale; Ricklefs 1977). Responses, particularly at levels 3 or 4, could endanger the mobbing individual. This could be via a counter-attack from the initial predator or perhaps from another attracted to the commotion; mobbing individuals would expectedly be less vigilant at this time and potentially vulnerable to outside attack. In long-lived tropical species (Snow 1962; Snow and Lill 1974; Johnston *et al.* 1997), risking adult survival and future reproduction by mobbing or nest defense of any one nest, among perhaps many lifetime nesting attempts, would not seem to be optimal for long-term reproductive success. If any action, including predator mobbing could "decrease the individual's chance of survival by even a little" then selection should strongly support opposite behavior which is to say, behavior which would tend to increase life expectancy (Snow and Lill 1974; see also Williams 1966).

Recent field experiments using matched phylogenetically and ecologically similar species provide empirical support for the scenario developed here (the functional constraint model; Ricklefs 2000). South American species,with lower clutch sizes and higher adult survival, decreased food delivery rates to their young when faced with possible predation risk to themselves (Ghalambor and Martin 2001). North American species with larger clutches and higher adult mortality "reacted more strongly to reduce risk to their offspring" (Ghalambor and Martin 2001). Further support is provided by the observations of Roper (2005) which showed that persistent re-nesting, and a reduced re-nesting interval, following nest predation events were important influences on overall reproductive success in a long-lived species. The reduced clutch size of tropical birds may also serve to decrease the energy commitment to any one nesting attempt during a prolonged breeding season (Slagsvold 1984) and also facilitate the observed rapid re-nesting and reduced re-nesting intervals (Roper 2005).

A further analysis of the degree of mobbing and nest defense in tropical vs. temperate passerines and the relationship to different habitats, predator regimes and, particularly, adult survival, would seem to be productive.

All four Semp chicks were in the nest on day 16 but gone, presumably having fledged, by day 20. The exact age at fledging was not determined but it was presumably near the end of the 17-20 day period. In other studies three species of euphonias had a nestling period of 20-20.5 days (Ricklefs 1976). Palm Tanager chicks fledged after a nestling period of 18 days. One day-18 chick left the nest as I was reaching for it and another almost did the same. A third was present in the nest early on day 18 but had fledged on its own prior to my visit around midday.

The growth rate of both Semps (K = 0.460) and Palm Tanagers (K = 0.379) are lower than for similar sized temperate zone passerines (Ricklefs 1976). However, there is substantial overlap in the overall growth rate of temperate species (average K = 0.502, n = 30, SD = 0.071) and tropical species (average K = 0.387, n = 51, SD = 0.079; Ricklefs 1976) as well as substantially differing growth rates among congeneric species. For both temperate and tropical species groups the variation in K is greater among broods than within broods (Ricklefs 1976). The asymptotic weights of Semps (100% of adult weight) and Palm Tanagers (74% of adult weight) are within the range of values for other tropical species; however "tropical and temperate species attain similar asymptotes relative to adult body weight at the end of the nestling period" (Ricklefs 1976).

Several hypotheses have been proposed to explain the generally slower growth rates of tropical passerines, and tested to the extent possible (Ricklefs 1976). Prominent in this discussion is the role of low-nitrogen fruit in the diet of many tropical species and a possible protein deficiency limiting chick growth. However, the evidence does not support this or any one hypothesis to the exclusion of others. The debate continues.

As indicated earlier, both Semp and Palm Tanager chicks are poikilothermic at hatching. They show a rapid decrease in body temperature when unbrooded even at moderate ambient temperatures. These observations, and the cold stress experiments (on Palm Tanagers only), indicate an abrupt shift to homeothermy ($H \geq 80$) on day 9 for Semps and day 10 for Palm Tanagers. The insulative property of the plumage at this stage was still minimal. Thus in both tanager species, and possibly others, this change appears to be related more to the degree of body mass achieved and increased heat production rather than decreased heat loss. The ratio of chick body mass to adult body mass at homeothermy was 0.70-0.77 for Semps and 0.63 for Palm Tanagers; the average for 54 passerines was 0.742 (range = 0.56-1.21, SD = 0.174; Visser 1998).

The data presented here on the growth and development of tanager chicks was collected peripheral to other field studies. Accordingly they are not as complete, in some respects, as desired. Nonetheless, they contribute to the somewhat meager information available on the developmental biology of these species. Additional studies on other tropical birds, even common species, are highly desirable.

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The Skipper Butterflies (Hesperiidae) of Trinidad
Part 14, Hesperiinae, Genera Group L

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ABSTRACT

Details are given of the taxonomy, history, description, identification and biology of the nine genera and 15 Trinidad species of Genera Group L of the Hesperiidae (Lepidoptera). *Decinea lucifer* (Hübner) is a new island record for Trinidad. All 15 species are illustrated as adults. The early stages are illustrated for *Saturnus saturnus saturnus* (Fabricius), *Quinta cannae* (Herrich-Schäffer), *Cynea irma* (Möschler) and *C. diluta* (Herrich-Schäffer) from Trinidad material, and for *Rhinthon cubana osca* (Plötz) from Colombian material, and notes are provided on the early stages of *Saturnus reticulata reticulata* (Plötz). Three genera and three species also occur in Tobago.

INTRODUCTION

Evans (1955) characterises genera Group L as intermediate between Groups J (which I have yet to cover) and O (Cock 2003). More specifically, the morphology of the club of the antennae ranges about one-third of the nudum on the club and two-thirds on the apiculus, to half the nudum on the club and half on the apiculus. The palpi range from a quadrate second segment as in some members of Group J (e.g., *Lerema*) to a flattened second segment as in *Calpodes* (Group O). The termen of the hindwing is convex and not straight or concave as in Group O. All Trinidad species are basically brown in ground colour. Thus, Group L is a convenient arbitrary grouping of genera on limited characters, and unlikely to represent a monophyletic group.

In the new checklist of Neotropical butterflies (Lamas 2004), Mielke's (2004) treatment of the Hesperiidae, does not recognise any groupings below the subfamily level of Hesperiinae. While I agree that this is appropriate given our current knowledge, for practical and historical reasons I have chosen to continue with Evans' Genera Groups at this time. I believe that in due course, increased knowledge of the early stages of the Hesperiidae will make an important contribution to our increased understanding of the classification of Hesperiidae at and below the subfamily level, which is one reason I have taken significant trouble to record these in detail whenever possible.

Evans (1955) recognised 17 genera and 80 species of Group L from the Neotropical Region. Nine genera and 15 species occur in Trinidad, while just three species of three different genera are recorded from Tobago.

To my knowledge only five of these species have been reared in Trinidad until now: *Saturnus saturnus saturnus* (Fabricius), *Saturnus reticulata reticulata* (Plötz), *Quinta cannae* (Herrich-Schäffer), *Cynea irma* (Möschler) and *Cynea diluta* (Herrich-Schäffer). Details are provided on these, as well as details of the life history of *Rhinthon cubana osca* from Colombia. Caterpillars of some species have rather narrow heads. Although *S. r. reticulata* has a 1 mm frontal spike, pupae of other species that I have reared have no frontal spike unlike, e.g., most members of genera Groups K (Cock 2005) and O (Cock 2003). The known food plants of Group L are all Monocotyledons, a mixture of grasses, and Epigynae such as Zingiberaceae, Cannaceae and Marantaceae.

An important recent publication is that of Greeney and Jones (2003), who set forth a classification scheme for the characteristic shelters that caterpillars of Hesperiidae make. I have used this classification for the life history information provided here.

All specimens illustrated are in the author's collection unless indicated otherwise. Similarly, any specimens referred to without attributing a collector or collection were collected by the author and are in either the author's collection or the collection of CABI Bioscience, Curepe, Trinidad. The scale at the bottom of most figures of pinned specimens is in mm. Other conventions and abbreviations follow earlier parts of this series (Cock 2005 and earlier papers). The museum abbreviations can be found in the acknowledgements at the end of the paper.

217. L1/1 *Saturnus saturnus saturnus* (Fabricius 1787)

Figs. 1-6.

The nominate subspecies was described from French Guiana and occurs from Venezuela to the Amazon; a second subspecies, *servus* (Evans 1955), is restricted to southern Brazil.

This species seems particularly common in collections from Trinidad, 34 out of 62 specimens of this subspecies listed in the NHM being from Trinidad (Evans 1955). In spite of this, Kaye (1921, 1940) did not record this species from Trinidad; there are no specimens in his collection in AME, and none of the 34 specimens in the NHM were from his collecting.

Male. Antennae dark, pale under club. UPS brown; head narrowly yellow-tawny around eyes and down centre. UPF brown; basal half of costa tawny; yellow spot in space 1B; yellow hyaline spots in spaces 2, 3, 6, sometimes 7 and occasionally 8. A conspicuous three part stigma UPF: a black streak against cell from above spot in space 2 to above inner margin of spot in space 1; a grey area basal to the spot in space 2, below the first part of the stigma and distal to the third part; and a second black streak, in an arc from basal end of first streak to vein 1 at inner margin of spot in space 1B. UPH brown with faint and indistinct pale discal spots in spaces 3, 4 and 5, which are not apparent in older specimens. UNS of head pale, yellow on palpi; body light brown, legs yellow-brown; abdomen pale with narrow brown ventral and sub-ventral lines. UNS wings lighter brown than UPS; UNF spots as UPF; usually some yellow scales between the UNF spots in spaces 1B and 2, and sometimes in space 3 beyond the spot in space 2; veins of apical portion UNF and all UNH light yellow-brown. Female similar except that the absence of the stigma is striking; in addition the wings are more rounded and less apically pointed; no tawny area along base of costa; F spots paler and that in space 1B smaller. F male and female 14 mm.

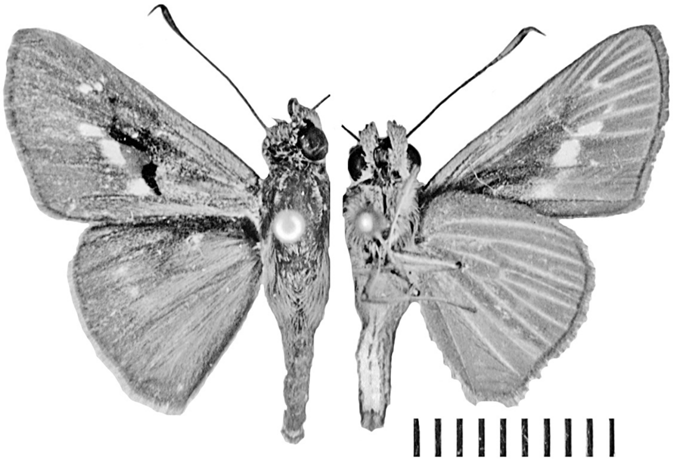

Fig. 1. *Saturnus saturnus saturnus* male; UPS, Point Gourde, 8.x.1995; UNS, Mt. Tabor, 11.iv.1982.

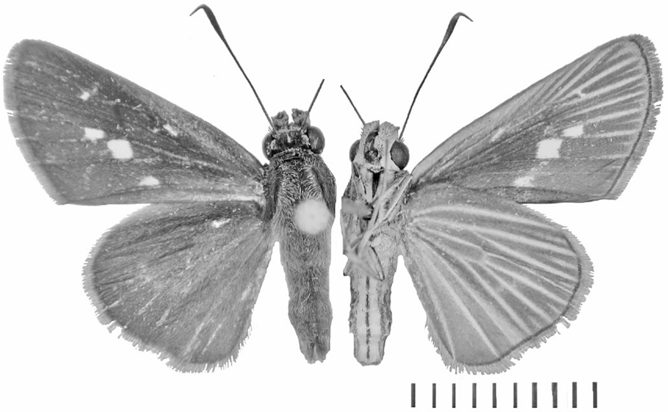

Fig. 2. *Saturnus saturnus saturnus* female; UPS and UNS, North Post, reared from caterpillar collected on *Olyra ciliatifolia*, MJWC ref. 99/10.

Two Trinidad species of *Parphorus* (genera Group J) also have distinctive yellow-brown veins UNS, although these are more yellow in tone, more strongly marked and more contrasting than the light yellow-brown veins of *S. s. saturnus*. Furthermore, *P. storax storax* (Mabille) is smaller (F 11-12 mm); the male stigma is similar, but the spots UPF are more diffuse and less contrasting, forming a more or less continuous line from vein 1 to space 3; the spots UNF are reduced, at most a diffusion in space 1B and a spot in space 3; in the female, the spots UPF are significantly reduced. *Parphorus decora* (Herrich-Schäffer) is intermediate in size (F 13 mm); the UPF spots markings are similar to those of *S. s. saturnus*, but the UNF lacks the spot in space 1B; in addition, the male stigma is restricted to a grey area basal to the spot in space 2, and in both sexes the UNF pale veins are not as extensive.

Saturnus s. saturnus is widespread and quite common in forests throughout Trinidad; it seems to be commoner in the north–44 out of 47 records–and only occasionally found above 1,000 ft. Adults can be found sitting on low (< 1m) vegetation along forest paths, often in sunlit patches. The distinctive striped UNS, and larger size compared to other species with a similar UNS, makes *S. s. saturnus* recognisable in the field in Trinidad.

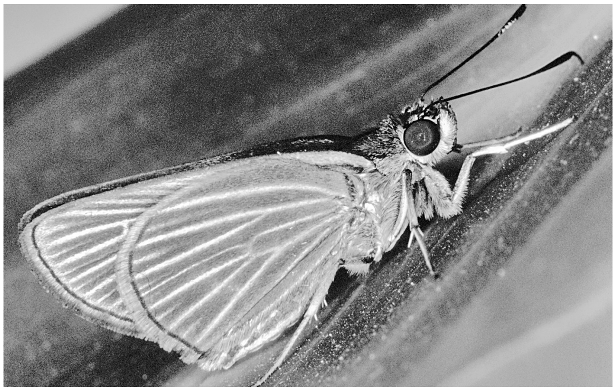

Fig. 3. *Saturnus saturnus saturnus* female; UNS, reared from caterpillar collected on *Olyra ciliatifolia*, North Post, MJWC ref. 99/10.

I have reared this species from caterpillars collected on *Olyra ciliatifolia* at North Post, 16.v.1999 (MJWC ref. 99/10) and Inniss Field, 16.i.2004 (MJWC ref. 04/28). Another caterpillar collected as a fourth instar caterpillar on *O. latifolia* on Lalaja Ridge, 6.v.1995 (MJWC ref. 95/19A) died as a pupa, but is almost certainly this species. Similarly, on 23 March 2003, I found an emerged pupa with associated head capsule on *O. ciliatifolia* behind St. Benedict's (MJWC ref. 03/202). On the same occasion I also found a dead pupa, again with associated head capsule, in a shelter on an unidentified dicotyledenous plant growing amongst *O. latifolia* (MJWC ref. 03/204); there was no associated feeding, and I interpret this as a pupation site, rather than a host plant. S. Alston-Smith (pers. comm.) has reared this species on bamboo, *Bambusa vulgaris* (Bush Bush, x.1999) and *O. latifolia*.

In my rearing (MJWC ref. 99/10), the pupa was formed between two leaves, one on top of the other (Greeney and Jones type 4); the cremaster was attached to a silk bar, and there was a weak silk girdle over the thorax. No white waxy powder on pupa or lining shelter. Pupa 19-23 mm; elongate, smooth, more or less cylindrical; eyes protuberant; slight frontal projection; short, pale brown, erect setae on thorax (in which the silk girdle is lodged), eyes, and ventrally on abdominal segments; proboscis projects 4 mm beyond wing cases, about 2/3 of the length of the abdomen; cremaster rounded, blunt, brown at margin; pupa colour greenish white apart from the proboscis brown where it projects beyond the wing cases.

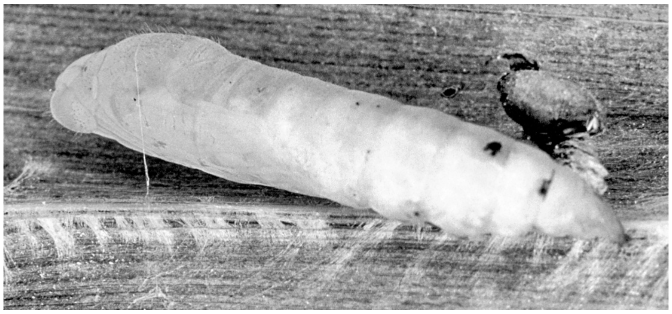

Fig. 4. *Saturnus saturnus saturnus* pupa, Inniss Field, reared from caterpillar collected on *Olyra ciliatifolia*, MJWC ref. 04/28.

The fifth instar caterpillar lives within a simple leaf roll, incorporating the whole leaf. Fifth instar caterpillar 23-29 mm. Head rounded, wider at base, slightly indent at vertex; light brown, with lower part, including mouthparts black, divided sharply in a straight line across the base of the clypeus at the level of the stemmata; a diffuse, broad brown line from vertex, tapering towards stemmata; epicranial suture black; epicranium adjacent to dorsal half of adfrontal area narrowly black; a diffuse dark spot on epicranium, just below the level of apex of clypeus. T1 with black transverse dorsal plate on posterior margin. Body dull translucent green; as the caterpillar matures, pale subcutaneous fat bodies develop except along the dorsal line which therefore appears darker; gonads orange. Legs and prolegs concolorous; spiracles pale, inconspicuous. *Parphorus storax* has similar caterpillars and also feeds on *Olyra* sp(p). However, in this species the upper part of the head of the fifth instar caterpillar is plain light brown, and the black ventral region extends over the stemmata, so that the dividing line is not straight as in *S. s. saturnus*. The pupa is clearly different, having a distinctive T shaped frontal protuberance.

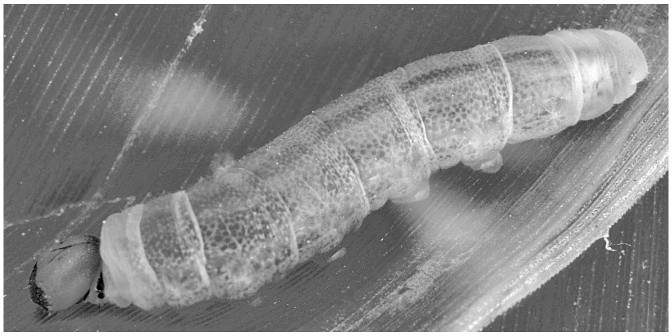

Fig. 5. *Saturnus saturnus saturnus* caterpillar instar 5; North Post, reared from caterpillar collected on *Olyra ciliatifolia*, MJWC ref. 99/10.

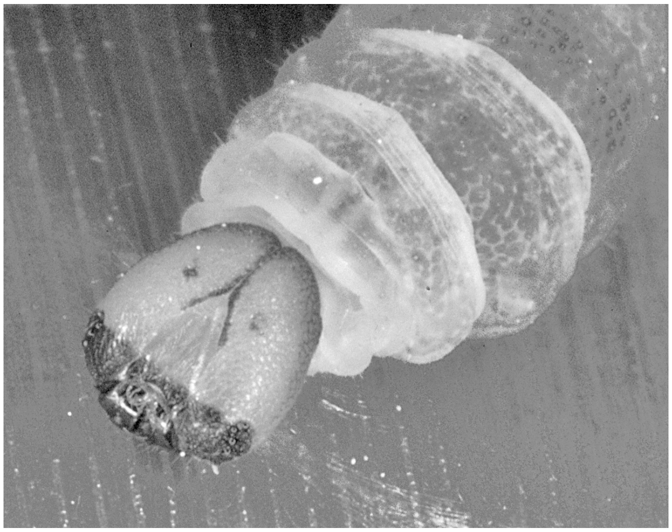

Fig. 6. *Saturnus saturnus saturnus* caterpillar instar 5, detail of head; North Post, reared from caterpillar collected on *Olyra ciliatifolia*, MJWC ref. 99/10.

The fourth instar caterpillar makes a shelter by cutting a notch from the edge of a leaf and rolling the distal portion upwards (Greeney and Jones type 6). Head dark, shiny; dorsal half of epicranium brown. T1 and body as young fifth instar.

218. L1/4 *Saturnus reticulata reticulata* (Plötz 1883)

Figs. 7-8.

This species occurs from Mexico to Uruguay in six subspecies (Evans 1955). The nominate subspecies was described from Venezuela (Laguayra) and is found in Colombia, Venezuela and Trinidad. Evans (1955) treated ssp. *tiberius* (Möschler) as the senior name for this species, which I followed in my checklist (Cock 1982b), but Mielke and Casagrande (2002) point out that *reticulata* is older and therefore has precedence.

Kaye (1914) first recorded this species from Trinidad as *Phlebodes tiberius*, taken in St. Ann's Valley (G. E. Tryhane).

Male. Antennae dark above; shaft UNS weakly chequered; club UNS pale brown. UPF brown with yellow spots; costa tawny from near base to end cell, brighter distally; a variable tawny area basal to stigma in lower space 1B. A three part stigma: space 2 basal to the yellow spot grey with a narrow black border; a small grey spot below this in the upper half of space 1B, also with black margin; a narrow black streak below this, running basal to the spot in lower space 1B to vein 1. UPH brown, the disc slightly tawny, with a trace of discal spots in spaces 3 and 4. UNS of head pale, tawny on palpi; body brown; abdomen pale with narrow brow ventral line, and broader ventro-lateral and lateral lines, tapered distally. UNF dark brown in basal half, paler in distal half; yellow spots as UPF except no spot in space 1B. UNH distinctive: margin (except space 2) and spaces 1B and 1C brown; disc and spaces 1A and 2 to margin yellow-brown; pale discal spots in spaces 3-6, more distinct in 3-4. F 14-15 mm.

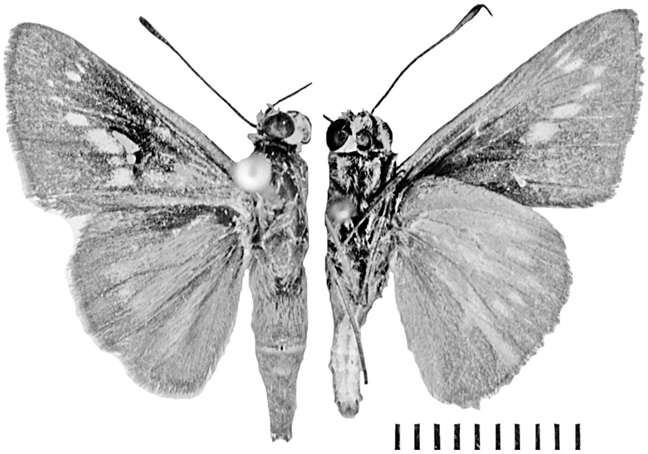

Fig. 7. *Saturnus reticulata reticulata* male; UPS, Lalaja Ridge, 17.xi.1980; UNS, Arena Forest Reserve, 2.x.1982.

Female. UPF brown with white spot in space 1B and white hyaline spots in spaces 2-7 or 8; costa variably tawny from base to middle. UPH brown with diffuse light brown spots in spaces 3-5. UNF no spot in space 1B; dark brown, light brown along costa, yellow-brown at apex and narrowly at margin, extending further towards disc along the veins. UNH brown with pale veins; margin paler at subveins; white spots in spaces 1C-7. F 14-15 mm.

The male due to the yellow spots, UPF three part stigma and distinctive UNH is readily identified, but the female is superficially similar to several females from genera Group J. *Vehilius s. stictomenes* (Butler) is smaller, lacks any yellow colouring, and has elongate spots UPH and UNH, but is most easily separated by the pale veins in the distal half UNF. Several others, such as *Morys* spp. and *Cobalopsis* spp. have a pale spot in space 1B UNF, less pale veins, and often a lilac or purple sheen UNH.

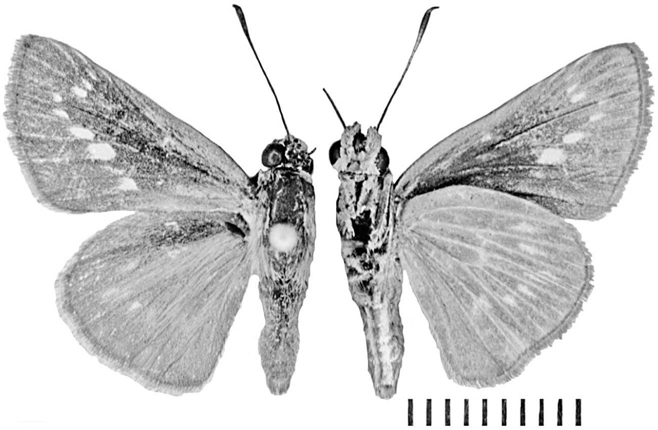

Fig. 8. *Saturnus reticulata reticulata* female; UPS, Parrylands, 2.ii.1980; UNS, Sangre Grande, 25.i.1980.

As with the last, this species seems particularly common in collections from Trinidad, with 20 of the 28 specimens of this subspecies in the NHM being from Trinidad (Evans 1955). This species is widespread and quite common in forests of Trinidad. It seems to be commoner than *S. s. saturnus* above 1,000 ft., and is regularly found on the ridges of the Northern Range. Although it is normally found resting on vegetation along forest paths and clearings, occasionally it comes to flowers such as eupatorium.

I reared this species once, but made only brief notes and took no photographs. I collected a mature larva in a leaf fold on a grass, *Setaria ?poiretiana*, at Sangre Grande, 25.i.1980. The larva measured 25 mm; head black with a brown X on the face; black dorsal plate T1; body dull grey-green, with a thin white lateral stripe and a broad white dorso-lateral stripe, leaving a clear, dark green dorsal line. The pupa was formed between a portion of leaf and the base of the rearing container, suspended from the leaf, supported by the cremaster and a weak silk girdle. The pupa was 25 mm x 5 mm at the widest; a 1 mm frontal spike; thorax and appendages white, abdomen cream; as the pupa matured, the thorax turned dark, but the abdomen stayed cream coloured; spiracle T1 inconspicuous, pale brown; proboscis sheath extending 2.5 mm beyond wing cases; pupa covered with white waxy powder. The date of pupation was not recorded, but an adult female emerged 11.ii.1980.

219. L6/1 *Quinta cannae* (Herrich-Schäffer 1869)

Figs. 9-15.

This common and widespread species is found from Mexico to Argentina, but not in the Caribbean islands (Evans 1955). Kaye (1904, No. 257) included this species in his first list of Trinidad butterflies as *Cobalus cannae*.

Male. Antennae dark, pale below end of shaft and club. UPS brown. UPF brown with white hyaline spots in spaces 2 (excavate on outer margin), 3 and 6-8. The male brand lies above vein 1 UPF and is covered by hairbrushes over the basal half of space 1B and vein 1. UPH brown, sometimes with a visible trace of the UNH discal band. UNS head and body pale brown, lighter on head. UNF spots as UPS; disc and dorsum blackish brown; costa and apex to space 6 dark chestnut; marginal line dark, narrowly lilac before this, fading to brown in older specimens; distal half of spaces 4 and 5 brown before lilac margin; distal half of space 1B paler. UNH variegated brown, chestnut and pale brown, although variable in contrast and extent of markings: marginal line and end of subveins dark; border to margin pale brown with lilac tint in fresh specimens; space 1B brown; remainder of UNH chestnut brown except for orange tinted brown spots in a row from space 1C to space 7, base of space 7 and cell. Female similar, but larger and wings more rounded; white opaque spot in space 1B F; distal half of space 1B UNF whitish brown; spots in spaces 1C to 7 UNH tend to run into each other. F male 16 mm, female 18 mm.

This is not a very distinctive species, but the combination of size, white hyaline spots, and especially the variegated UNH should enable it to be recognised.

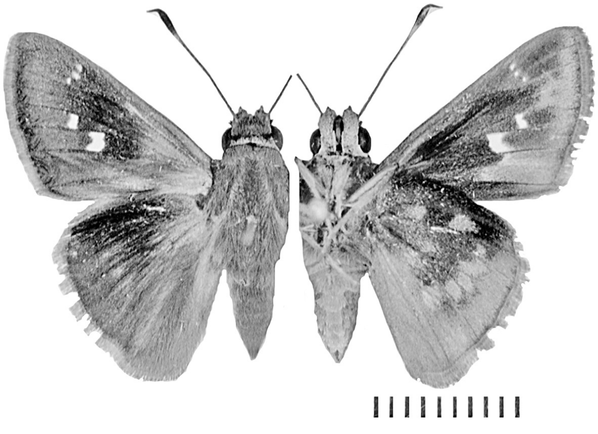

Fig. 9. *Quinta cannae* male; UPS and UNS, St. Benedict's, collected as caterpillar on ornamental *Canna* sp., 6.x.1995, MJWC ref. 95/35.

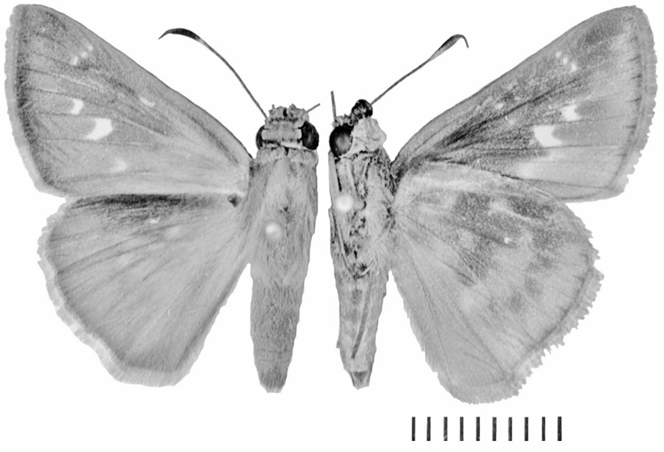

Fig. 10. *Quinta cannae* female; UPS, Curepe, caterpillar on topitambo, 11.ii.1980; UNS, Parrylands, 3.iii.1980.

This species is widespread but occasional in Trinidad, occurring in forests, swamp margins (Cock 1982a), disturbed areas and suburban situations.

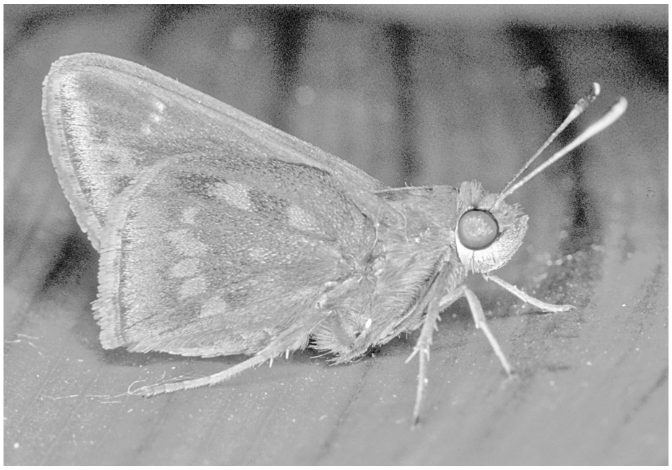

Fig. 11. *Quinta cannae* male; collected as fifth instar caterpillar on ornamental *Canna* sp., St. Benedict's, Pax Guest House, 6.x.1995, MJWC ref. 95/35.

Moss (1949) reared this species from *Carex* sp. (Cyperaceae) and from arrowroot (*Maranta arundinacea*) in Belem (= Pará, Brazil) and illustrates the caterpillar, which is compatible with that described below.

The records of Janzen and Hallwachs (2005) suggest that the normal food plant in Guanacaste Conservation Area, Costa Rica, is *Thalia geniculata*, but they also found it on arrowroot, *Maranta arundinacea*, and once on *Calathea villosa* (all Marantaceae); they do not record it from *Canna* spp. (Cannaceae) although they do record other Hesperiidae from this host.

In Trinidad, I have reared this species from an ornamental *Canna* sp. (St. Benedict's, Pax Guest House, MJWC ref. 95/35; Valencia, iv.1982, no ref. no.) and topitambo, *Calathea allouia* (Curepe, MJWC ref. 80/1). I have not examined *Thalia geniculata* in Trinidad, but it is likely to be a food plant for *Q. cannae*. S. Alston-Smith (pers. comm.) has reared this species also from *Calathea lutea*. The following account is based on the first of my rearings listed above.

The pupal shelter is lined with white waxy powder, and the pupa is also loosely covered especially on the thorax and dorsal surface of the abdomen. Several strands of silk over the front of the thorax hold the pupa in place. Male pupa 25 mm; smooth, no projections, no frontal spike; proboscis extends 6 mm beyond wing cases, almost reaching cremaster; uniformly off-white, slightly yellowish brown; spiracle T1 light brown, slightly projecting.

Fig. 12. *Quinta cannae* pupa; collected as fifth instar caterpillar on ornamental *Canna* sp., St. Benedict's, Pax Guest House, 6.x.1995, MJWC ref. 95/35.

The fifth instar shelter is a simple flap, made by cutting two notches from the edge of a leaf and folding the shelter lid upwards, or sometimes downwards (Greeney and Jones type 9); it is similar to that of *Calpodes ethlius* (Stoll), which also feeds on *Canna* spp. (Cock 2003). Male fifth instar caterpillar grows to 32mm. Head rounded triangular in outline, but narrower than many Hesperiinae, indented dorsally at vertex; ground colour white; posterior margin narrowly black; broad black line from apex of epicranium laterally, widening to stemmata; a broad green-brown patch in centre of face, narrow at vertex, widening to width of base of clypeus and extending over mouthparts. T1 concolorous. Body dull translucent green, with subcutaneous fat bodies giving a strongly grainy texture. Trachea visible through cuticle, and a distinct tracheal line; spiracles pale, conspicuous as the centre of a radiating star of trachea. Anal plate semi-circular, with diffuse pale border and fringe of erect setae. All legs concolorous. Male gonads dorsally in segment A5: green, not very conspicuous. Wax glands not recorded.

The early instars make Greeney and Jones (2003) type 6 shelters (one-cut fold) and type 9 shelters (two-cut unstemmed fold) as shown in Fig. 15.

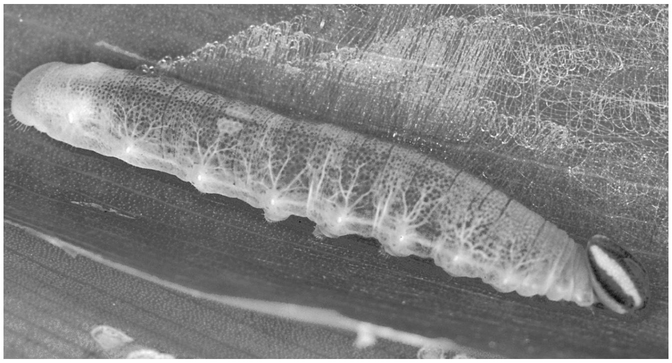

Fig. 13. *Quinta cannae* caterpillar instar 5; collected on ornamental *Canna* sp., St. Benedict's, Pax Guest House, 6.x.1995, MJWC ref. 95/35.

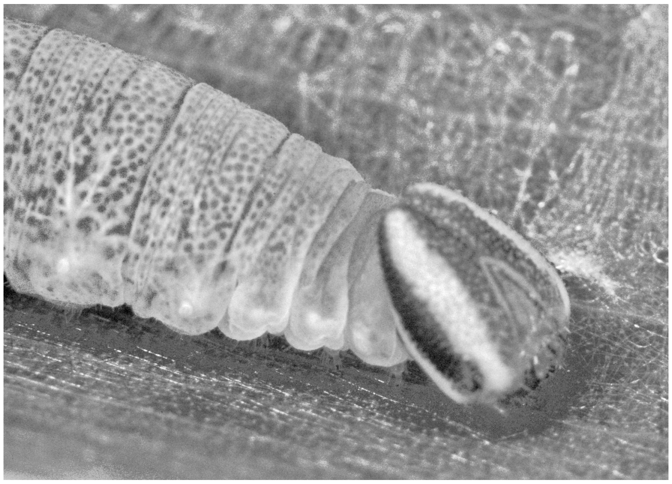

Fig. 14. *Quinta cannae* caterpillar instar 5, detail of head; collected on ornamental *Canna* sp., St. Benedict's, Pax Guest House, 6.x.1995, MJWC ref. 95/35.

Fig. 15. *Quinta cannae* caterpillar; shelters on *Canna* sp., St. Benedict's, Pax Guest House, 6.x.1995. Shelter in centre is type 9, and shelter on right is type 6 (Greeney and Jones 2003).

Cynea Evans 1955

This genus is similar to *Quinta* Evans above, but the antenna are longer (more than half the length of the costa), and the head is usually greenish. Six species are found in Trinidad. *C. anthracinus holomelas* (Mabille) and *C. irma* are plain brown above, while the other four species are brown with white hyaline spots. Identification characteristics are discussed under each species.

The food plants known to me are Marantaceae and Zingiberaceae. In addition to the two Trinidad species, *C. irma* and *C. diluta* treated below, I have reared the mainland species *Cynea cynea* (Hewitson) in Colombia from *Phaeomeria speciosa* and *Alpinia purpurata* (Zingiberaceae, both introduced ornamentals).

220. L7/1 *Cynea anthracinus holomelas* (Mabille 1891)

Figs. 16-17.

In Evans (1955) and hence Cock (1982b), this subspecies is treated as *Cynea anthracinus luctatus* Schaus, but Mielke and Casagrande (2002) point out that this is a synonym of *holomelas* (Mabille). This uncommon subspecies is found from Costa Rica to Guyana to Peru based on ten specimens in the NHM (Evans 1955), and it also occurs in Suriname (de Jong 1983). The nominate subspecies, *anthracinus* (Mabille), was described from Colombia, but appears to be restricted to Guatemala, suggesting the type may have been mis-labelled (Evans 1955).

Male. UPS dark brown, no markings. Brands, two dark streaks, one under the basal portion of vein 2, the other matching above vein 1. UNF brown, unmarked. UNH brown; the margin broadly slightly paler; yellow suffusion in the distal half of space 1C; cilia brown, except margin of spaces 1A and 1B yellowish. F 20 mm.

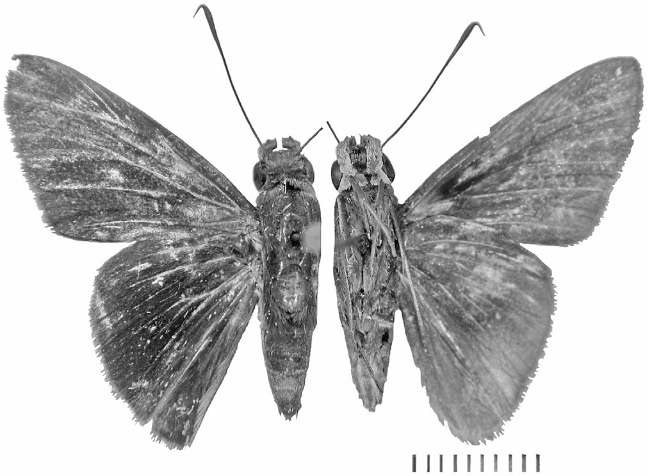

Fig. 16. *Cynea anthracinus holomelas* male; UPS and UNS, Waller Field, 5.xii.1981, June and Floyd Preston (the apparently pale veins, especially UPF, are an artefact as the specimen is rather rubbed).

Female. UPS dark brown; faint indication of spots in spaces 6-8; distal section of vein 1B UPH yellowish. UNF brown; faint spots in spaces 6-8. UNH brown; pale marginal band from space 1A, becoming diffuse and narrow in space 2, and fading out in space 3.

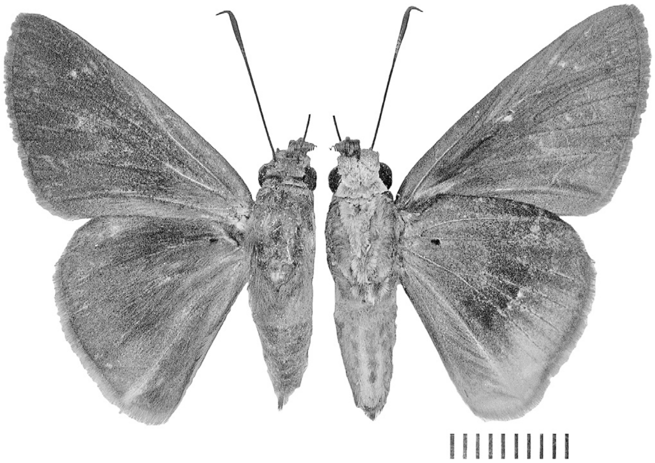

Fig. 17. *Cynea anthracinus holomelas* female; UPS and UNS, Grande Ravine, iii.1995, S. Alston-Smith (specimen in SAS).

Trinidad specimens seem darker than the mainland form of this subspecies, and may represent an island form or subspecies. Thus, Evans (1955) refers to the male as having the "UNH outer third more or less paler, may be pale dots in spaces 2 and 3; UNF may be some yellow scaling at apex", and the female "UNH outer third yellow, inwardly edged with faint whitish spots in spaces 2-5".

This species was added to the Trinidad list on the basis of a male collected in the Waller Field area by June and Floyd Preston, 5.xii.1981 (Cock 1982b). S. Alston-Smith (pers. comm.) has several more recent specimens from Grande Ravine (female, iii.1995), Inniss Field (male, vii.1985), Los Bajos (female, i.1995), Moruga East (male, iii.1998) and Valencia (male, i.1986). Thus, it appears to be absent from the Northern Range, and found predominantly in the south.

S. Alston-Smith (pers. comm.) tells me that the males are highly territorial, patrolling a small area, and returning to the same perch after being disturbed. I have found no information on the food plants or life history.

221. L7/2 *Cynea cyrus hippo* Evans 1955

Figs. 18-19.

This subspecies was described from two males from Trinidad in the NHM (Evans 1955); the specimen labelled type was collected from the Northern Mountains, xii.1938-i.1939 (A. Hall), and the other Trinidad, 1,000 ft, 18.ii.1926 (W. J. Kaye). Subspecies *rhino* Evans occurs in French Guiana and the Amazon, while the nominate subspecies, *cyrus* (Plötz), is restricted to southern Brazil. De Jong (1983) suggests that specimens from Suriname are closer to ssp. *hippo* from Trinidad than ssp. *rhino* from French

Guiana.

Male. Antennae black, slightly paler at base of club UNS. UPS head, thorax blackish brown, with trace of green iridescence on head; UPS abdomen, wings, cilia dark brown. White hyaline spots F in spaces 2 (quadrate, from origin of vein 3), 3 (quadrate, separated by its own width from the spot in space 2), 6-8 (in a row, decreasing in size). UNS head and fore femora grey with slight green iridescence; UNS thorax brown, UNS abdomen pale with narrow brown ventral line. UNF brown, darker basally; the distal half of spaces 1A and 1B light brown; a short bare streak at the base of vein 1 against cell; cilia brown. One of the specimens in the author's collection matches Evans' (1955) description, having the UNH dark brown, with small yellowish spots in spaces 2 and 3. Two other specimens in the author's collection have space 1A to 1C paler, grading to a narrowly light brown tornus; an additional spot in space 5 and a trace of a spot in space 1C displaced slightly basally. F 20-21 mm.

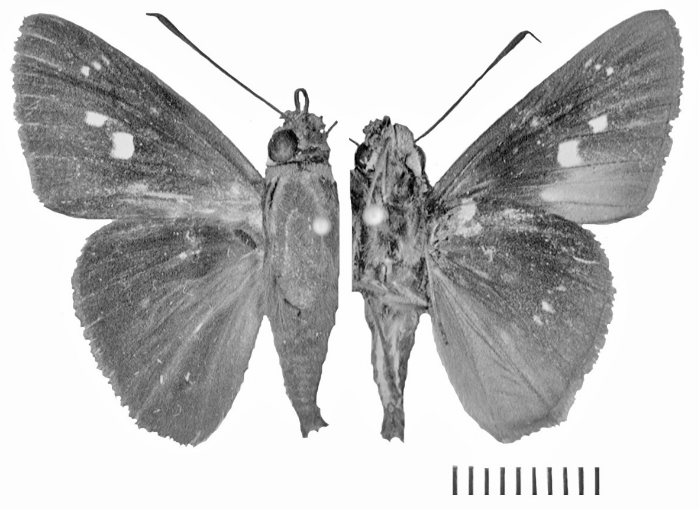

Fig. 18. *Cynea cyrus hippo* male; UPS, Morne Bleu Textel Installation, 2.xii.1980; UNS, Andrew's Trace, 8.x.1994.

Female. Similar to male, but larger and wings more rounded. In addition, a quadrate white spot in space 1B F, against vein 1; UNF paler, the paler area in spaces 1A and 1B more pronounced; UNH as the two paler males described above, but paler, spots in 2, 3 and 5, and a more distinct diffuse spot in space 1C. F 23 mm. The female is recorded here for the first time.

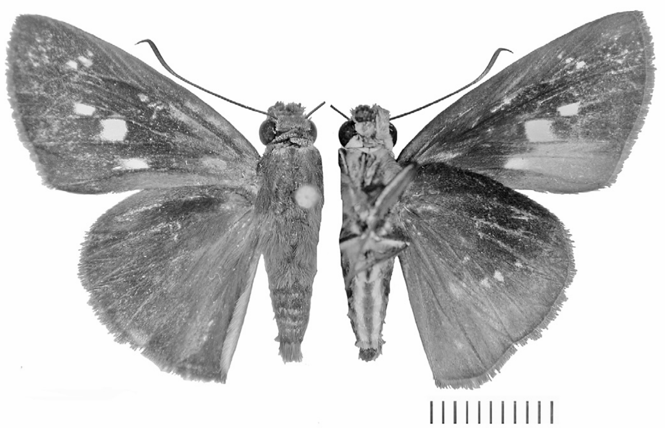

Fig. 19. *Cynea cyrus hippo* female; UPS and UNS, Andrew's Trace, 8.ix.1979.

This species is commonest on the hilltops and ridgetops of the Northern Range. Localities include Morne Catharine (male, 28.i.1980), North Post (SAS), summit of El Tucuche (2 males, 19.vi.1979), Andrew's Trace (female, 8.ix.1979; male, 3.xi.1980; male, 27.xi.1980; male, 8.x.1994), Morne Bleu Textel Installation (male, 3.xi.1980; male, 2.xii.1980; male, 20.i.1981) and Lalaja Ridge (male, 7.i.1980). S. Alston-Smith (pers. comm.) has also collected this species from the lowland localities Tucker Valley, Guapo and Arena Forest. All captures for which I have dates were between September and February. I have no information on the life history or food plants.

222. L7/3 *Cynea irma* (Möschler 1878)

Figs. 20-25.

This species is recorded from Mexico to southern Brazil (TL Colombia) but does not seem to be common anywhere in its range (Evans 1955). Kaye (1921, No. 394) records it from Trinidad as "*Rhinthon melius* (Geyer)", based on a F. W. Jackson specimen from St. Joseph. This was a mis-identification, since *Cynea melius* is similar to *C. irma*, but only found in southern Brazil. There are specimens from W. J. Kaye's collection in AME labelled *Metiscus atheas* (male, Trinidad, vi.[18]98, W. J. Kaye) and *Rhinthon melius* (female, Trinidad, i.1936, A. Hall).

Male. Antennae dark, club pale UNS. UPS dark brown; small pale brown opaque spots in spaces 6-8 UPF; hair brushes in basal portions of spaces 1A and 1B UPF. UNS head, thorax and abdomen grey-brown; a narrow, dark ventral line on abdomen. UNF dark brown basally, except spaces 1A and 1B brown; distal half of spaces 1A and 1B pale brown with a bronze tint; margin of spaces 2-4 lilac-brown, in spaces 2 and 3 separated from dark basal portion by an indistinct narrow, pale spot; apical area narrowly brown, lilac-brown at margin before this, brown patch before this at apex, and basal to brown patch a pale triangle from space 6 to costa at end cell. UNH lilac-brown basally and at margin, divided by a band of deep purple brown, wide at costa, narrowing to space 1C; indistinct, small, pale spots in cell, and along outer border of discal band in spaces 1C to 5; spaces 1A, 1B and dorsal margin of 1C pale brown with bronze tint, paler patch in margin of space 1C. F 17 mm. Female similar to male, but wings more rounded, and no hair brushes UPF. F 17-18 mm.

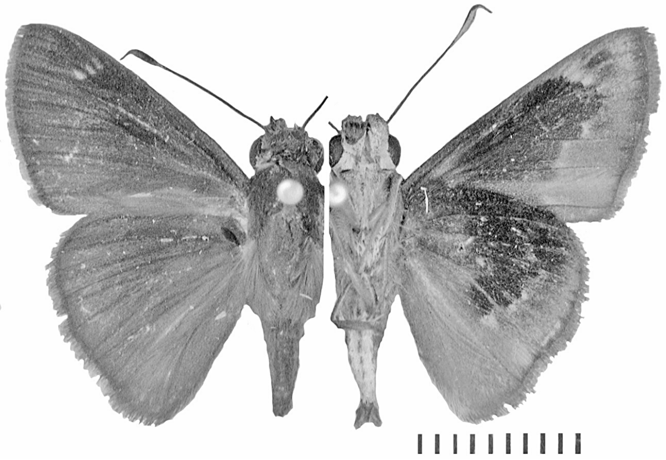

Fig. 20. *Cynea irma* male; UPS, Point Gourde, 16.v.1999; UNS, Las Lomas, Spanish Farm, 17.xii.1980.

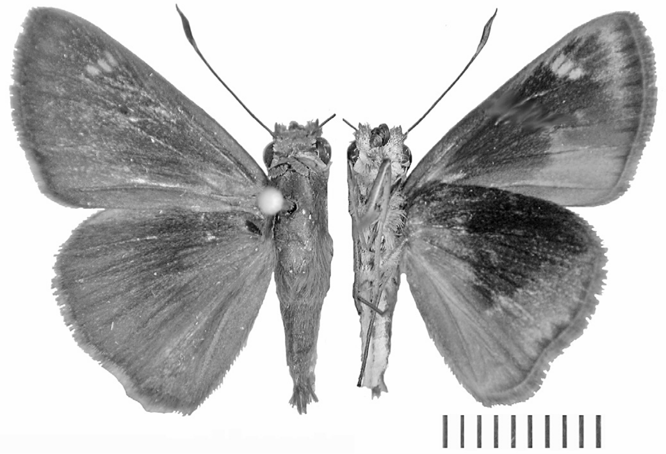

Fig. 21. *Cynea irma* female; UPS and UNS, Point Gourde, 12.vii.1997.

This is a widely distributed and occasional species in Trinidad, usually associated with lowland forest, but occasionally found on the ridges of the Northern Range.

Fig. 22. *Cynea irma* male; UNS, collected as fourth instar caterpillar on *Stromanthe tonkat,* Mt. Tabor, 13.vii.1997, MJWC ref. 97/208.

Host plant records from Janzen and Hallwachs' (2005) database show that *Calathea* spp. and *Maranta arundinacea* (both Marantaceae) are used as food plants in Costa Rica. In Trinidad, however, I have reared this species from another species of Marantaceae: *Stromanthe tonkat* (Mt. Tabor, MJWC ref. 97/208).

Pupal shelter lined with white waxy powder; pupa lightly covered with white waxy powder, densest on dorsum of thorax; cremaster hooked into a silk bar; several strands of silk over thorax. Pupa 25 mm; elongate, smoothly rounded, no projections, no frontal spike; proboscis extends to cremaster; pale light brown; spiracles T1 brown, conspicuous; other spiracles inconspicuous.

Fig. 23. *Cynea irma* pupa, dorsal view with ventral proboscis sheath projecting at right; collected as fourth instar caterpillar on *Stromanthe tonkat,* Mt. Tabor, 13.vii.1997, MJWC ref. 97/208.

Fifth instar caterpillar 35 mm, quite similar to that of *Quinta cannae*. Head rounded triangular, indent at vertex; relatively narrow; marked in black and white; posterior margin narrowly black; a broad black line from apex of epicranium, laterally, over stemmata to mouth-parts; the white area between this line and the posterior margin sullied; epicranial suture black; a black triangle in centre of face, from just below vertex, covering clypeus and extending narrowly onto epicranium, and over mouthparts; a broad, sharply defined pure white line between the lateral black line and the triangle on the face. T1 concolorous with body. Body when recently moulted pale translucent green, the fat bodies giving it a grainy texture. The mature caterpillar is pale translucent brown, with a pink tinge; the grainy texture is pronounced; there is an intermittent slightly darker dorsal line, and two irregular, diffuse and intermittent lateral lines. All legs concolorous; spiracles inconspicuous. Wax glands a series of distinct ventro-lateral patches just below ventro-lateral flange on segments A4-A7.

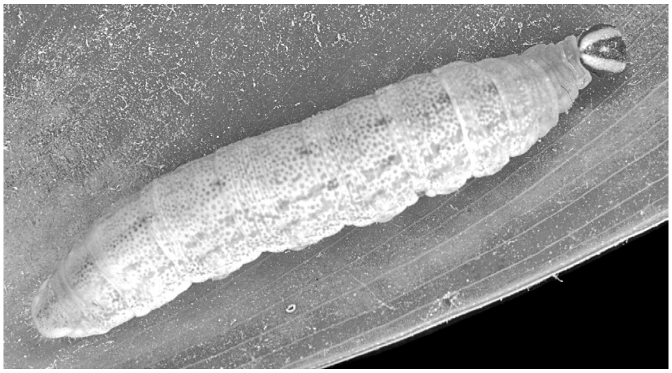

Fig. 24. *Cynea irma* caterpillar instar 5; collected as fourth instar on *Stromanthe tonkat,* Mt. Tabor, 13.vii.1997, MJWC ref. 97/208.

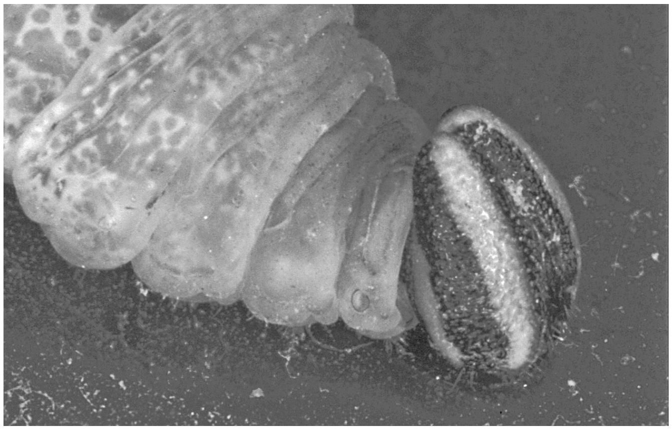

Fig. 25. *Cynea irma* caterpillar instar 5, detail of head; collected as fourth instar on *Stromanthe tonkat,* Mt. Tabor, 13.vii.1997, MJWC ref. 97/208.

Fourth instar shelter 130 mm long; made by eating from near the basal angle, inwards to reach the mid-rib 55 mm from the leaf base, and the distal flap folded over upwards (Greeney and Jones type 6); much of the margin of the other half of the leaf was eaten. Mature fourth instar caterpillar 23 mm; head black, with a small brown streak near the apex of the epicranium; body dull, pale translucent green; T1 concolorous; all legs pale; spiracles pale.

223. L7/8 *Cynea popla* Evans 1955

Figs. 26-28.

This species was described from Trinidad and seems common in Trinidad, Venezuela and Guyana, with scattered records from Colombia, Panama, the mouth of the Amazon and southern Brazil (Evans 1955). There is a male from W. J. Kaye's collection in AME, which he labelled *sylvia / bistrigula* (Tabaquite, 18.i.1921, W. J. Kaye). *Phanis sylvia* Kaye is a synonym of *Morys geisa geisa* (Möschler), (Evans 1955; Cock 1982b). Kaye did not include this specimen or *Cynea bistrigula* (Herrich-Schäffer) in his catalogues.

Male. Antennae dark, with club pale beneath. UPS dark brown, with weak green iridescence on head. UPF white hyaline spots in spaces 2 (under origin of vein 3, narrow or very narrow, normally obliquely angled), 3 (small or very small) and 6 (dot); dark hair brushes at base of spaces 1A and 1B. UNS of head, thorax and abdomen pale brown with dark ventral line on abdomen. UNF brown, basal third darker, spaces 1A and 1B paler distally. UNH brown, spaces 1A to 1C paler; pale spots in end cell and spaces 2, 3 and 5, and sometimes a diffuse trace in 1C and 6. Female similar but wings more rounded. F 15 mm.

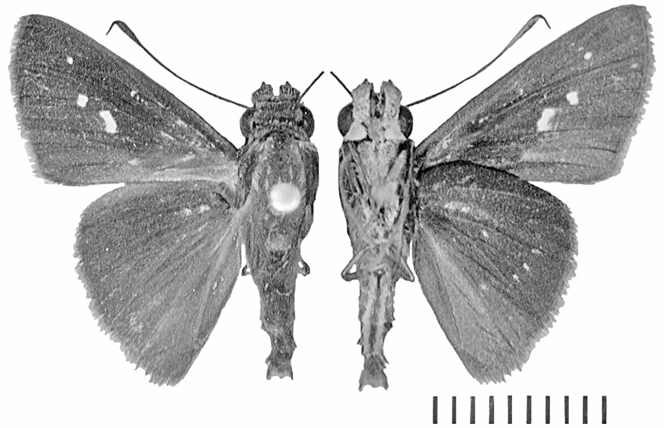

Fig. 26. *Cynea popla* male; UPS and UNS, Lower Morne Catharine, 17.i.1988.

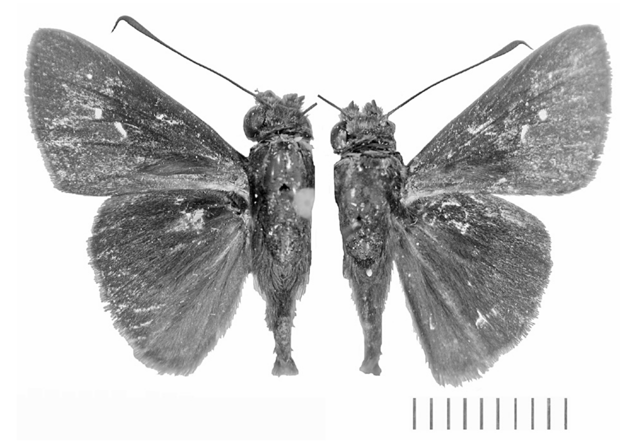

Fig. 27. *Cynea popla* males; UPS, Arena Forest, Nr Parrotts Ride, 8.x.1994; UNS, Parrylands, 26.iii.1980.

Fig. 28. *Cynea popla* female; UPS and UNS, Mt. Tamana, 14.x.1995.

Cynea popla is similar to *C. bistrigula*, but lacks the purple tint UNS of that species, and the oblique spot in space 2 seems diagnostic. This spot is consistently rather narrow, of even width, slightly arced and angled, whereas in *C. bistrigula*, the spot may be wide or narrow, may be of even width or tapered towards the dorsum, and is either directed at right angles to dorsum, or angled slightly outwards. UNH is a richer brown in *bistrigula.*

Kaye (1940, No. 394b) records *Cynea megalops* (Godman) (as *Rhinthon megalops*) from a specimen taken at 1500 ft on El Tucuche, 4.iv.1922 by F. W. Jackson. *Cynea megalops* has the UPS unmarked dark brown, but is unlikely to be a Trinidad species, being recorded only from Mexico, Costa Rica and Ecuador by Evans (1955). I have not found Jackson's specimen in either the NHM or HEC. The only specimen in the NHM from this group which matches the data is a male *S. r. reticulata*, but it is unlikely that this would have been misidentified since the two species are very different. Hence, in Cock (1982b) I treated this record as probably referring to one of the three small *Cynea* spp. from Trinidad: *C. popla, C. bistrigula* or *C. diluta*. However, if the UPS of Kaye's species were plain brown like *C. megalops*, it may be that some other species was involved.

This is a widespread and occasional species in lowland forests of Trinidad, with just a few records from above 1,000 ft. I have no information on the life history or food plants.

224. L7/12 *Cynea bistrigula* (Herrich-Schäffer 1869)

Figs. 29-30.

Evans (1955) records this species from Venezuela to southern Brazil (TL unknown), but not Trinidad.

Sheldon (1936) recorded this species from Tobago, on the basis of a W. J. Kaye specimen taken at Bacolet. I have seen no specimens of *C. bistrigula* from Tobago, but there is a W. J. Kaye specimen of *C. diluta* from Tobago in AME, so it seems most likely that this is the specimen referred to, and the record from Tobago is actually of *C. diluta*.

Cock (1982b) added this species to the Trinidad list, with several records from Parrylands, Arena Forest Reserve and Chaguaramas.

Male. Antennae dark, apiculus brown. UPS dark brown, with weak green iridescence on head; UPF white hyaline spots in spaces 2 (just distal to origin of vein 3, wider towards costa and tapering to dorsum), 3 (small) and 6 (dot); dark hair brushes at base of space 1A, but almost absent in space 1B. UNF blackish brown; distal half of spaces 1A and 1B paler. UNH dark brown with a deep purple wash; absent in spaces 1A, 1B and dorsal margin of 1C; small yellowish spots in spaces 3 and 5, and indistinct diffuse spot in middle of space 1C; the spots may not be obvious in worn specimens. Female similar, but wings more rounded and spot in space 2 F more regular. F 15 mm. The purple wash UNH, and tapered spot in space 2 F should distinguish this species from *C. popla*.

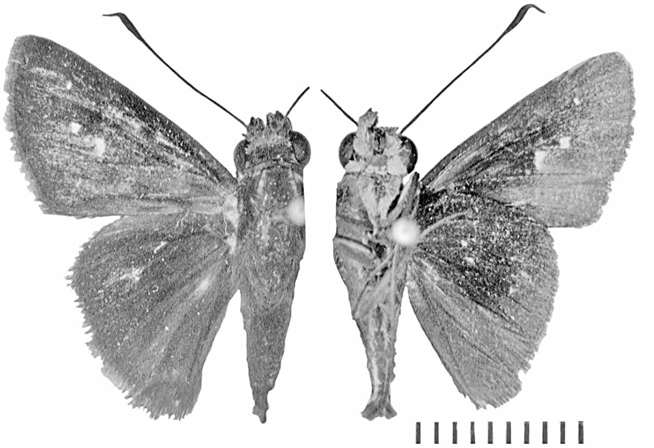

Fig. 29. *Cynea bistrigula* male; UPS, Cuare Valley, 18.i.1980; UNS, Parrylands, 7.xi.1980.

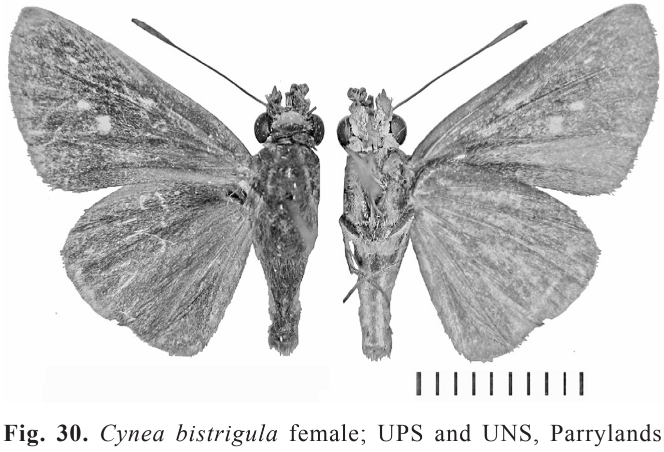

Fig. 30. *Cynea bistrigula* female; UPS and UNS, Parrylands, 26.iii.1980.

This species seems to be scarce in the north of Trinidad, but occasional in lowland forest of the centre and south of the island.

Although *C. bistrigula* was not included in Moss (1949), he did rear this species: there is a male with associated pupal remains in the NHM. It was reared on ground bamboo, which I believe may be the name he used for *Olyra* spp. (see comments under *Orses cynisca* (Swainson) in Cock (2005)). The emerged pupa is light brown; no frontal spike; the proboscis sheath extends to the cremaster; eye (apart from a shiny vertical stripe down middle) and sub-dorsal areas on thorax with erect setae with trapped white waxy powder.

225. L7/13 *Cynea diluta* (Herrich-Schäffer 1869)

Figs. 31-33.

The range of this species extends from Honduras to southern Brazil (Evans 1955). Kaye (1940, No. 394a) records *Cynea cynea* (as *Rhinthon cynea*) from Trinidad, noting specimens from Matura (26.i.1921, W. J. Kaye) and Arima (26.xi.1920, W. J. Kaye). I have not located these specimens; although there is a W. J. Kaye specimen in AME also collected 26.xi.1920 but at P[ort] O[f] S[pain], identified by Kaye as "*Rhinthon diluta*". Since Kaye (1921, 1940) does not otherwise record *C. diluta*, I think he may have misidentified his material as *C. cynea*.

As noted under *C. bistrigula* above, the W. J. Kaye record of *C. bistrigula* from Tobago reported by Sheldon (1936) almost certainly refers to *C. diluta*. In any event, *C. diluta* is a Tobago species on the basis of the specimen in AME referred to under *C. bistrigula* above.

Male. Antennae dark, pale UNS at base of club. UPS dark brown; weak green iridescence on head. F with white hyaline spots in spaces 2 (beyond origin of vein 3, narrow, inner and outer margins more or less concave), 3 (close to spot in space 2 compared to other *Cynea* spp. but separated by at least the width of the spot in space 2, shape similar to spot in space 2), 6 (narrow, at right angles to costa), 7 (small, slightly basal to spot in space 6) and 8 (sometimes reduced to a trace, displaced slightly outward from the spot in space 7); brown hair brushes at base of space 1A and a small one at the base of 1B (variable). Evans (1955) notes that the apical spots F may be reduced or absent. UNF dark brown, paler in distal third; small dark patch at base of space 1B. UNH dark brown, with sometimes a trace of pale spots at end cell and in spaces 1C, 2, 3 and 5. Female similar but wings more rounded, UNH spots more marked. F male 17 mm; female 18 mm. *Cynea diluta* is larger than *C. popla* and *C. bistrigula*, and at least for the Trinidad specimens that I have seen, has two or three apical spots, rather than just one. It is smaller than *C. cyrus hippo*, and the white hyaline spots are narrow, not quadrate.

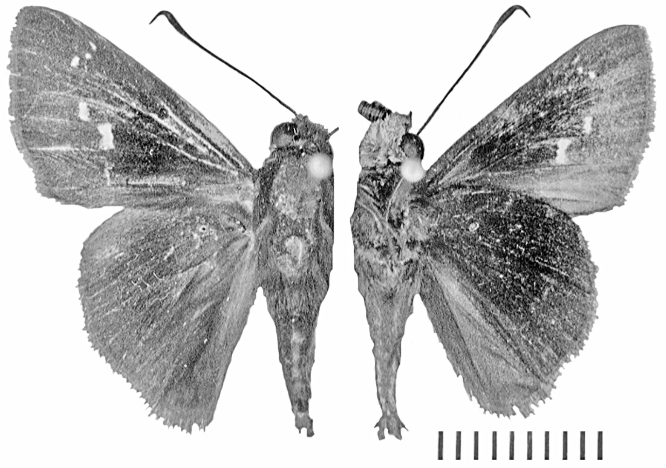

Fig. 31. *Cynea diluta* male; UPS, Andrew's Trace, 9.iv.1980; UNS, Andrew's Trace, 8.x.1994.

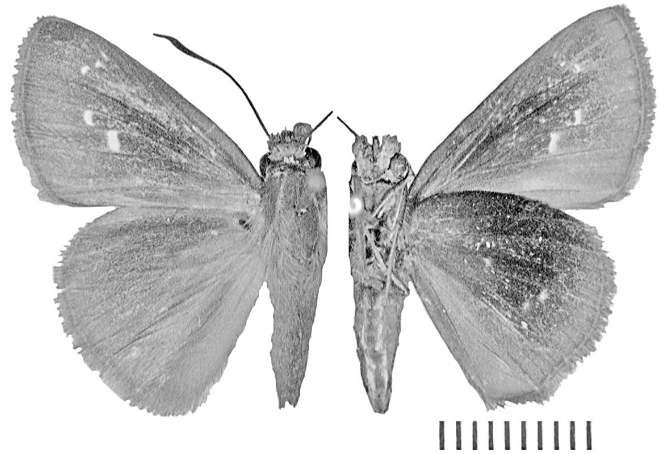

Fig. 32. *Cynea diluta* female; UPS, Trinity Hills, 4.iv.1982; UNS, Port of Spain, 9.x.1995.

This occasional species is most frequently encountered on the forested ridges and hilltops of the Northern Range (summit of El Tucuche, Andrew's Trace, Morne Bleu Textel Road, Lalaja Ridge), with scattered records from Port of Spain, Curepe, Spanish Farm and the Trinity Hills.

In the NHM there are specimens from Guyana, reared on a "wild monocot, ?Zingiberaceae", by H. E. Box, 10.iii.1924 (species XV). I have reared this species once from a caterpillar collected on *Renealmia alpinia*, a large species of Zingiberaceae (Morne Bleu Textel Road, MJWC ref. 94/64), and S. Alston-Smith (pers. comm.) has reared it from a pink ornamental ginger lily (*Alpinia* sp.; Zingiberaceae).

Pupal shelter lined with white waxy powder; some powder on the pupa, particularly on the head and thorax, caught in the erect setae of the eyes and dorsal part of thorax. Pupa 22 mm; elongate, smooth, no projections, no frontal spike; proboscis sheath extends to tip of cremaster;

head, thorax and cremaster brown, appendages light brown, abdomen whitish brown; spiracles T1 light brown and slightly protuberant.

Fig. 33. *Cynea diluta* pupa; collected as fourth instar caterpillar, on *Renealmia alpinia*, Morne Bleu Textel Road, 8.x.1994, MJWC ref. 94/64.

Unfortunately I was unable to make any observations on the living fifth instar caterpillar. The cast caterpillar skin and head capsule are covered with white waxy powder in the pupal shelter, so details are not entirely clear. The cast head capsule is narrow, as for others of the genus; head rugose, with inconspicuous short setae; brown, with a pale brown line from apex of epicranium to stemmata, running just lateral to the clypeus.

Fourth instar caterpillar collected in a simple leaf flap shelter folded under leaf lamina. Fourth instar caterpillar 23 mm when mature; head uniform dark brown; body dull translucent green.

226. L8/1 *Rhinthon cubana osca* (Plötz 1883)

Figs. 34-37.

The nominate subspecies, *cubana* (Herrich-Schäffer), is restricted to Cuba and Jamaica, while subspecies *osca* is found from Mexico to Ecuador, Trinidad and Tobago (Evans 1955). Schaus (1902) described *Thracides biserta* from Trinidad; this is a synonym (Evans 1955).

Sheldon (1936) records this species from Tobago as *Rhinthon chiriquensis* (Mabille), which is a synonym, citing his capture of a specimen at 400 ft. at the back of Agenza, near Speyside. I have not seen this specimen, but there is a female collected by A. Hall from Speyside, ii.1932 in the NHM. Sheldon (1936) goes on to state, "It occurs in Trinidad, from which Mr. Kaye has specimens, as well as in Tobago", yet Kaye (1921, 1940) did not record this species from Trinidad, although there were specimens in his collection, including one labelled *Rhinthon chiriquensis* (a synonym of *R. cubana* – see above). Possibly he confused this species with *Naevolus orius orius* (Mabille) (= *Cydrus naevolus* Godman) (Genera Group J) since one of his *R. cubana* specimens in AME is labelled *Cydrus naevolus*.

The first unambiguous published record of this species from Trinidad is that of Evans (1955), who lists three males from Trinidad. All were captured by A. Hall, two from St. Ann's, xi-xii.1931 and i-iii.1932, and the other just labelled Trinidad, i.1936. I have further records from Arima District, Fondes Amandes, Maraval, N. Hills and Mt. Tabor, and S. Alston-Smith (pers. comm.) has collected it from the north of Trinidad (Andrew's Trace, North Post, Petit Valley), central Trinidad (Mt. Tamana) and southern Trinidad (Inniss Field).

Male. Antennae dark, basal half of club UNS pale. UPS brown, the head with green iridescence. White hyaline spots F in space 2 (large, quadrate, below origin of vein 3), 3 (quadrate with inner and outer margin slightly concave, separated from the spot in space 2 by its own width), 6-8 (small, that in space 6 displaced outwards), and a double cell spot (the lower spot partially overlapping the spot in space 2). UPF a grey brand along middle third of vein 1; brown hair brushes in spaces 1A and 1B. UNS of head and fore femora grey; UNS of thorax and abdomen brown, the abdominal segments each with a pale posterior border. UPH brown; spaces 1A to 5 and cell overlaid with tawny hairs; small semi-hyaline spots in spaces 3 and 5. UNF brown, blackish on disc. UNH brown, with pale spots end cell and spaces 2, 3 and 5. F male 20 mm. Evans (1955) states that there is a spot in space 2 UPH, and UNF a white discal area in space 1B, but neither feature is present in the single specimen in the author's collection. Female similar to male, but not examined in detail.

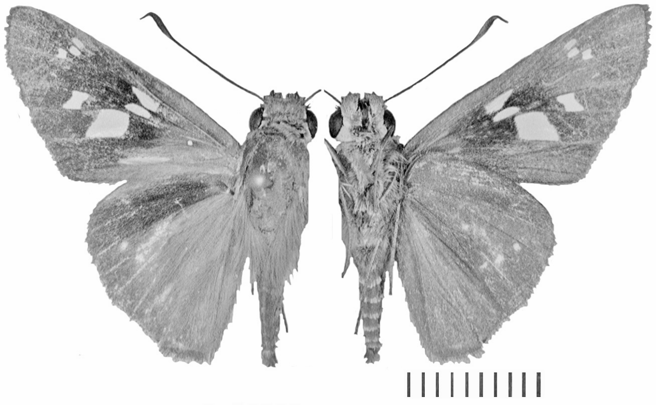

Fig. 34. *Rhinthon cubana osca* male; UPS and UNS, Mt. Tabor, 1000 ft. 22.xi.1981.

In my experience this large species is uncommon in Trinidad, but S. Alston-Smith (pers. comm.) considers it occasional. My only capture (behind St. Benedict's, 1,000 ft., 22.xi.1981) was at 18:00 h, but others have not commented on the time of capture. Hernández (2001) writing about *R. cubana cubana* in Cuba comments, "This is a secretive and easily overlooked skipper, more likely to be found by its larvae than by the infrequently seen adults". Nevertheless, as yet neither I nor S. Alston-Smith has been able to find caterpillars in Trinidad, in spite of regularly checking species of Marantaceae for caterpillars of Hesperiidae.

Hernández (2001) reports *Maranta arundinacea* (Marantaceae) as a food plant in Cuba. Similarly, in Costa Rica, *Maranta arundinacea* is the most commonly used food plant for this species in Janzen and Hallwachs' (2005) database; other food plants include *Canna indica* (Cannaceae), four species of *Calathea*, *Hylaeanthe hoffmannii* (Marantaceae), and *Heliconia latispatha* (Heliconiaceae). I have not reared this species in Trinidad, but have reared it in Colombia (Chinchiná, MJWC ref. 96/106), from caterpillars found on what appeared to be an ornamental *Calathea* sp.; the following notes and figures are based on this Colombian material.

Pupa 27 mm; elongate, tapered posteriorly; eyes slightly protuberant; no frontal spike; light brown, paler on abdomen; T1 spiracles large, brown. Pupa and inside of pupal shelter covered with white waxy powder.

Fig. 35. *Rhinthon cubana osca* pupa; collected as small caterpillar on Marantaceae sp., Chinchina, Colombia, 8.vii.1996, MJWC ref. 96/106.

The fifth instar caterpillar grows to 38mm; head rounded triangular, narrow, slightly indent at vertex; shiny rugose; black, with pale dull green stripe from behind vertex around neck just anterior to posterior margin; a pale white-green stripe from apex of epicranium, antero-laterally to join white mark anterior to ocelli; anterior to this a pale dull green stripe, elongate at each end; adfrontal areas dull green. T1 concolorous with body. Body dull translucent green, irregular subcutaneous yellowish dots and lines; diffuse white line along sub-tracheal flange. All legs concolorous; spiracles pale.

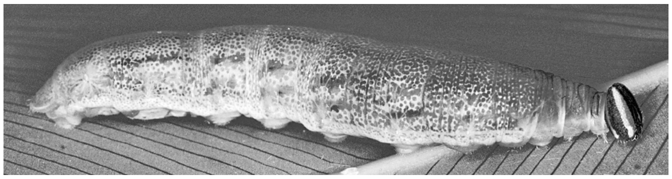

Fig. 36. *Rhinthon cubana osca* caterpillar instar 5; collected as small caterpillar on Marantaceae sp., Chinchina, Colombia, 8.vii.1996, MJWC ref. 96/106.

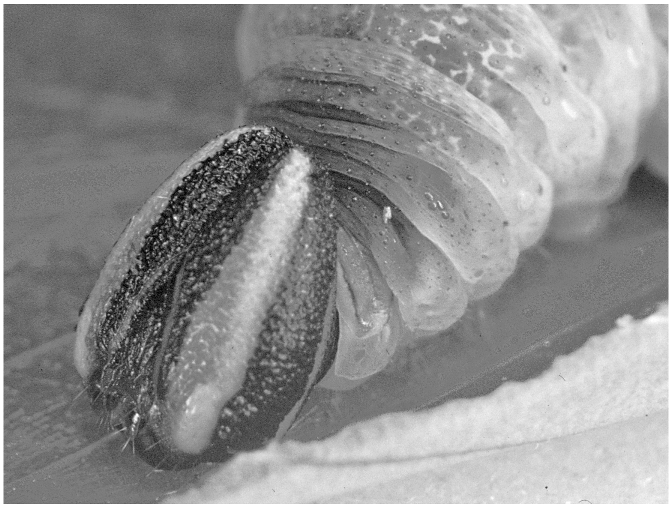

Fig. 37. *Rhinthon cubana osca* caterpillar instar 5, detail of head; collected as small caterpillar on Marantaceae sp., Chinchina, Colombia, 8.vii.1996, MJWC ref. 96/106.

In the earlier instars the head is shiny, black, and the body shiny translucent pale green.

227. L9/1 *Mucia zygia* (Plötz 1886)

Figs. 38-39.

The range of this species is from Mexico to Paraguay (TL unknown), including Trinidad and Tobago, but not the Caribbean islands (Evans 1955). Based on a specimen collected at Maraval, xi.1932-iii.1933 by A. Hall (in AME), Kaye (1940, No. 382c) records this species from Trinidad under the name *M. thyia* Godman, which is a synonym. Sheldon (1938) also uses this name to record his capture of a Tobago specimen from Scarborough; this is probably the male in the NHM from the Sheldon bequest, labelled Tobago.

Male. Antennae dark above; apiculus brown; shaft chequered below; club pale below. UPS dark brown, with an overlay of tawny hairs; cilia slightly paler brown, noticeably paler in spaces 1-2 UPF and 1C to apex UPH. White hyaline spots F in spaces 2 (beyond origin of vein 3; narrow to quadrate, obliquely angled) and 3 (separated from spot in space 3 by its own width); three-part dark stigma, against inner margin of spot in space 2, under basal portion of vein 2, and transversely across lower space 1B. UPH unmarked. UNS of body grey-brown. UNF brown; distal half spaces 1A and 1B paler; costa and apical area, extending as far as vein 2, overlaid with pale ochreous scales, dense along costa, but increasingly sparse apically and to vein 2; traces of paired darker spots in spaces 4-5 and 6-7. UNH overlaid with pale ochreous scales, but almost absent in distal half of space 1B and costa; black spots in spaces 2, 3 and 6, the latter with a slight corona of paler scales. Female very similar, but wings slightly more rounded; white hyaline spots F slightly larger; dark spot in space 6 UNF may be hyaline; and dark spots UNF are stronger. F male, female 17 mm. Evans (1955) notes that the spotting in this species is variable, but the limited Trinidad material that I have examined is relatively constant, at least with regard to the black spots UNH which are diagnostic.

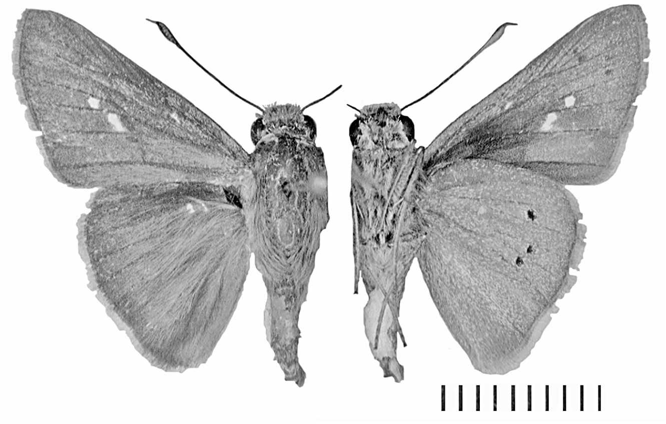

Fig. 38. *Mucia zygia* male; UPS, UNS, Arima, 18.xii.1981.

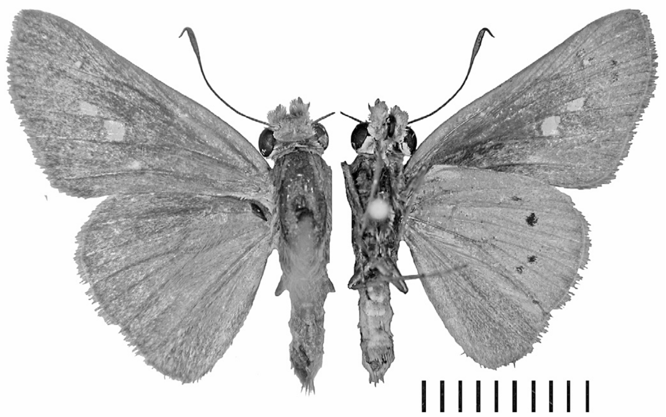

Fig. 39. *Mucia zygia* female; UPS, UNS, Brasso, 1.x.1994.

This species is associated with open disturbed areas in Trinidad, particularly at eupatorium flowers. S. Alston-Smith (pers. comm.) notes that it normally flies very close to the ground, making it easy to overlook, and this behaviour may reflect the use of low growing grasses as food plants. I have seen 14 specimens from the north (Andrew's Trace; Nr. Arima, Demerara Road; La Fillette Bay; Maracas-Caura Ridge; Maraval; North Post; "Northern Mts."; St. Ann's; and Toco). The specimen from Maraval, a female collected xi.1931-ii.1932 by A. Hall and now in AME, could be the specimen on the basis of which Kaye (1940) added this species to the Trinidad list, but the dates of collection differ – see above. I have also seen two specimens from central Trinidad (Brasso and Arena Forest), and two from the south (Vance River, and near Guapo).

I have not located any information on the food plants or life history.

228. L10/1 *Penicula bryanti* (Weeks 1906)

Figs. 40-41.

This species was described from Venezuela, and occurs from there south across the Amazon basin to Argentina (Evans 1955). *Euroto cocoa* Kaye is a synonym described from Trinidad (Kaye 1914) based on a K. St. A. Rogers specimen collected at Maraval River, 29.i.1913.

Male. Antennae dark above; base of club pale below; distal portion of shaft chequered below. UPS dark brown including cilia; black hair tuft over disk of UPH; angular dark brand at base of space 2, and short brands under basal portion of vein 2 and matching on vein 1; pale yellow hyaline spots F in spaces 2 (quadrate, oblique, outer margin excavate), 3 (quadrate, slightly separated from spot in space 2), 4 (partially overlapping spot in space 3), 6 and 7. With more material available, Evans (1955) notes that there may be spots in space 5, and rarely 1-2 cell spots. UNS head pale brown; UNS body brown; UNS abdomen white with a narrow brown ventral line. UNF dark chestnut brown, shading to black-brown on disk and dorsum; trace of spot in space 7; no spot in space 1B. UNH dark chestnut brown, brown in spaces 1A-1C; slightly diffuse pale yellow spots in spaces 2-6. Female similar, but wings more rounded, hyaline spots F slightly larger; faint spot in space 1B UNF; UNF apex and margin, all UNH paler with a lilac suffusion; spots UNH slightly stronger, and visible faintly UPH. F male 15 mm; female 16 mm. The hair tuft on the disk UPH male, and the placement of the spot in space 4 F partially overlapping the spot in space 3 should distinguish this species from similar ones in Trinidad.

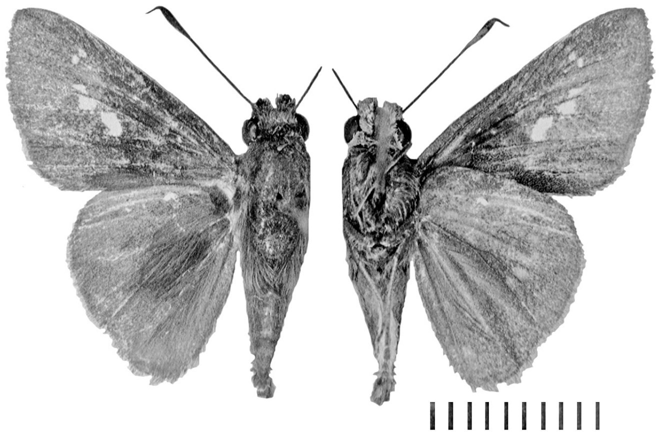

Fig. 40. *Penicula bryanti* male; UPS, UNS, Maracas Valley, 28.xii.1981.

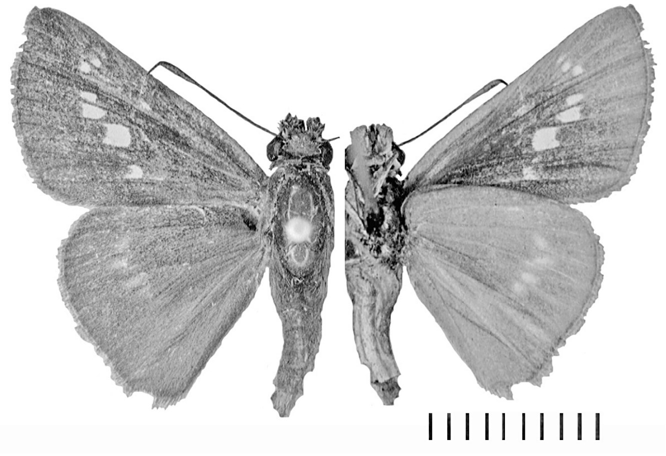

Fig. 41. *Penicula bryanti* female; UPS, UNS, Brasso, 11.x.1993.

I have collected just four specimens of this species, three at flowers of eupatorium: Maracas Valley (male, 28.xii.1981) and Brasso (2 females, 11.x.1993), and the fourth at the edge of the swamp behind Las Cuevas Bay (male, 17.i.2004). These localities suggest that, like *M. zygia*, this species may be associated with open disturbed or grassy habitats. However, S. Alston-Smith (pers. comm.) has collected it from more forested habitats: North Post, Las Cuevas, Guanapo Valley, Inniss Field and Parrylands. The life history and food plants do not seem to have been recorded.

228a. L11/8 *Decinea lucifer* (Hübner 1831)

Figs. 42-43.

This species occurs from Mexico to Argentina (TL Suriname) (Evans 1955), but has not previously been reported from Trinidad (Cock 1982b).

Male. Antennae dark above; shaft chequered below; club pale below; apiculus brown. UPS dark brown with some tawny hairs; cilia brown UPF, paler UPH. White hyaline spots F in spaces 2 (under origin vein 3, large, quadrate, wider against vein 2), 3 (separated from and distal to spot in space 2) and 6-8 (dots in line, that in space 7 may be weaker); no stigma or brands. White hyaline spots H in spaces 2 and 3. Evans (1955) notes that F there may be 1-2 cell spots over the spot in space 2, and often a spot in space 1B, while the spotting H is variable, often including a cell spot and sometimes spots in spaces 4-6; however the single Trinidad specimen I have examined carefully does not show these features. UNF brown shading to black-brown on disk and dorsum; weak spot in middle of space 1B. UNH brown. F male 16 mm. Female similar, but wings more rounded, and there is a small pale spot UPF in space 1B. The white hyaline spots in spaces 2 and 3 H, if present, coupled with the strong spots F in spaces 2 and 3 should serve to identify this species in Trinidad.

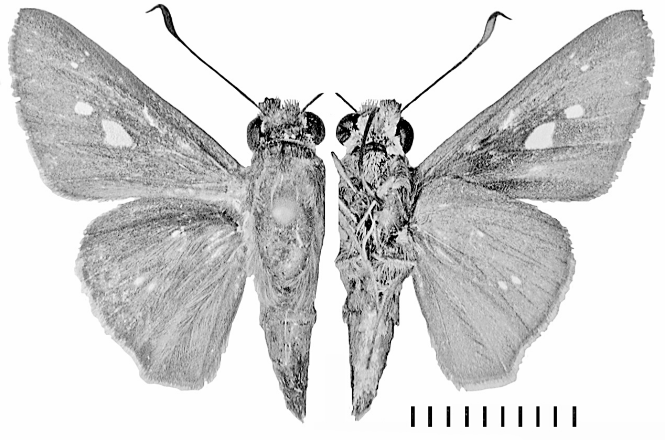

Fig. 42. *Decinea lucifer* male; UPS, UNS, San Rafael, 2.x.1982.

Fig. 43. *Decinea lucifer* female; UPS, UNS, Venezuela, in NHM collection.

I have seen just four specimens from Trinidad: west of San Rafael (male, 2.x.1982); Caltoo Trace (male, iii.2001; S. Alston-Smith, SAS); Palmiste (male, 25.iii.1930, N. Lamont, RSM); and Moreau (male, i.2000, S. Alston-Smith, SAS).

My specimen was taken at eupatorium flowers and, as with the preceding two species, an association with open disturbed grassy habitats may be possible.

Kendall and Rickard (1976) obtained ova from wild-caught females of *Decinea percosius (*Godman) in Texas. They reared these with rather limited success on several species of grass. It may well be that *Decinea* spp. feed on selected species of grass.

229. L15/1 *Orthos orthos orthos* (Godman 1900)

Figs. 44-45.

Evans (1955) treats this species as three subspecies, found from Panama to Argentina; the nominate subspecies is recorded from Panama (TL), Trinidad and Peru.

Kaye (1921, 1940) does not list this species, so two specimens in NHM listed by Evans (1955) are the first record from Trinidad. These two specimens were collected by A. Hall in the 1930s (male, "Northern Mountains", xii.1938-i.1939; female, St. Ann's, i-iii.1932), and Kaye was probably not aware of them.

Male. Antennae dark above, distal part of shaft chequered below, base of club pale below; apiculus bright brown. UPS dark brown; white hyaline spots in spaces 2 (under origin vein 3; variable in width) and 3 (from origin of vein 4; quadrate, variable in size); no apical or cell spots; short brown brands against cell at base of space 2, over and under vein 2 from origin and above vein 1. UNS head grey-brown; UNS abdomen white with pair of sub-ventral brown lines. UNF brown with purple tint to apical area; basal and discal area blackish to dorsum; a large pale, diffuse spot with bronze tint in space 1B under spot in space 2. UNH plain brown, with a purple suffusion, missing in spaces 1A-1C. Female similar but wings more rounded, UPF a pale spot in space 1B under inner margin of spot in space 2, on vein 1, and UNF the pale spot in space 1B more extensive, extending to dorsum. F male 14 mm, female 15 mm. The combination of white hyaline spots in spaces 1 and 2 F, no apical or cell spots F, strong spot in space 1B UNF, and plain UNH with purple suffusion should facilitate recognition of this species.

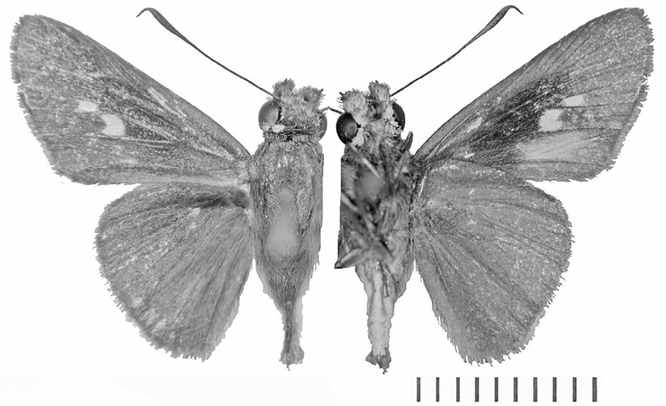

Fig. 44. *Orthos orthos orthos* male; UPS and UNS, west of San Rafael, 2.x.1982.

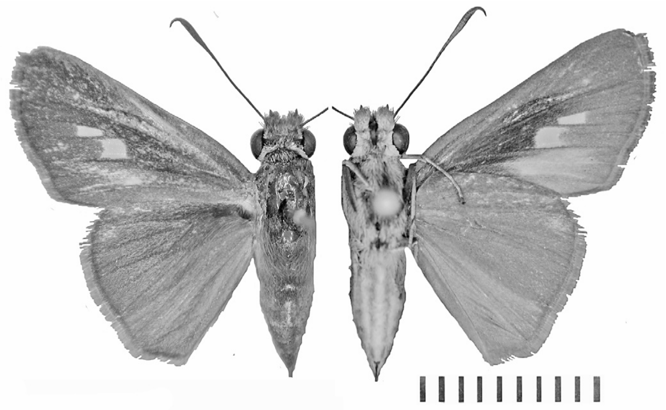

Fig. 45. *Orthos orthos orthos* female; UPS, UNS, Brasso, eupatorium flowers, 11.x.1993.

This species is most often found at eupatorium flowers at forest margins (Morne Bleu Textel Road, Maracas Valley, Cat's Hill, Rio Claro - Guayaguayare Road), but I also have records from more disturbed areas (Brasso, west of San Rafael), and one specimen from my light trap in Curepe (male, 8-14.xii.1981). The life history and food plants do not seem to have been reported, and I have no information.

230. L16/1 *Congo chydaea* (Butler 1870)

Figs. 46-47.

This common and widespread species is recorded from Mexico to Argentina (Evans 1955). A. Warren (pers. comm. 2005) has noted that females in Mexico have two very distinct forms of genitalia, suggesting that more than one species is involved in at least parts of its range. I have not examined the female genitalia of Trinidad material of this species.

Although there is a male collected by A. Hall in W. J. Kaye's collection in AME (Arima District: i-iii.1922) with an identification label as "*Prenes vala* Mabille", which is a synonym of *Congo chydaea*, Kaye (1921, 1940) did not record this species from Trinidad. Accordingly, Evans' (1955) listing of 13 males and 3 females from Trinidad in the NHM is the first record of this species from Trinidad. This material dates back to the 1890s, so it seems most likely that W. J. Kaye saw specimens, and it may well be they are represented under another name in his lists. As noted below, this is a difficult species to characterise, and doubtless this contributed to the confusion.

Male. Antennae dark above; shaft chequered below; club pale yellow-brown at base; apiculus bright brown. UPS dark brown; palpi above tawny; head with tawny spots around eyes; white hyaline spots in spaces 2 (under origin vein 2, curved, excavate on external margin), 3, 6-8 (very small, in a row, may be reduced or absent, especially that in space 8), and cell (close to origin vein 2, may be reduced, but at least a trace present in the specimens before me); there may be a trace of a pale spot in space 1B against vein 1; no brands; UPH may have very indistinct trace of UNH spots visible. UNS palpi pale, tawny distally; UNS head and fore femora pale; UNS thorax grey-brown; UNS abdomen narrowly pale brown with a weak ventral line. UNF brown, darker on disk and dorsum; diffuse pale spot in upper part of space 1B. UNH brown with a scattering of yellow scales, absent along vein 1B and costa; indistinct yellow spots at end cell and in spaces 1C to 6. Female similar but wings more rounded, and spots F reduced. F male 14-15 mm, female 15 mm. This is a rather undistinguished species, but the arrangements of spots, absence of brands in male, and details of UNS colouring and marking may help with identification. Careful comparison with named material, or dissection of male genitalia may be necessary to confirm identifications.

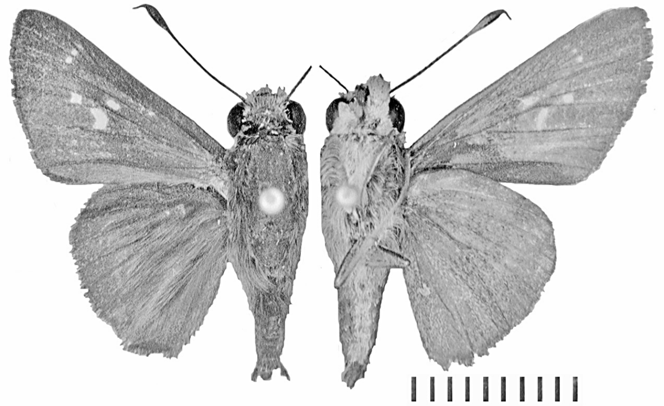

Fig. 46. *Congo chydaea* male; UPS, St. Benedict's, Alton Trace, 11.x.1993; UNS, Valencia Forest, 29.ii.1980.

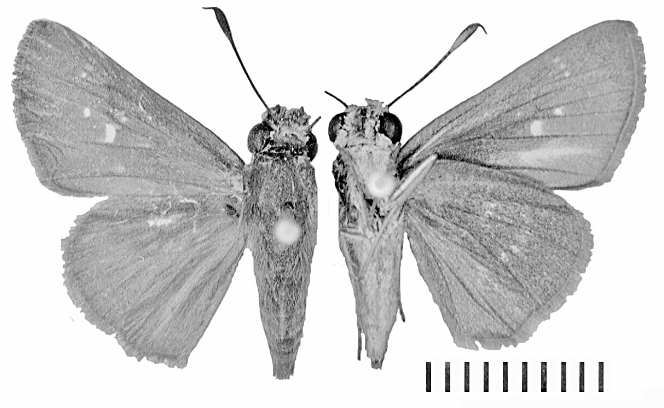

Fig. 47. *Congo chydaea* female; UPS Cunapo South Road, milestone 9.5, 5.ii.1980; UNS, Brasso, 11.x.1993.

This species is widespread in Trinidad; it is usually associated with forested areas and is regularly found on the ridges of the Northern Range. It comes to eupatorium flowers, and I have observed males resting in the last of the sunlight on Alton Trace above St. Benedict's.

Moss (1949) reared this species from *Calathea* (Marantaceae) in his garden in Belem (= Pará), and notes that "the larva is leaden-coloured, the pupa dull brown with a round head". There is also a record from sugar cane in Venezuela (Box and Guagliumi 1954), but given the difficulty of identification of this species, it would be desirable to confirm this record from voucher material or fresh rearing records. Janzen and Hallwachs (2005) list several rearing records in Costa Rica from two unidentified grasses. I have no information on the food plants or life history from Trinidad.

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Once again, I especially thank Mr. Scott Alston-Smith who has read and commented on this paper, and provided additional records from his collecting, and observations and food plant records that have not previously been published.

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Notes on Niche Separation in the Neotropical Social Wasps *Polistes lanio* and *Polistes versicolor* (Hymenoptera: Vespidae)

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ABSTRACT

Nesting and colony productivity of the social wasps *Polistes lanio* and *P. versicolor* are compared at three sites in northern Trinidad, West Indies. Only *P. versicolor* was found nesting at the most vegetated site, while only *P. lanio* was at the least vegetated site. The two species were both abundant at an intermediate site. Where the species co-occur, there is no evident difference in their use of available nest sites. Furthermore, where they co-occur there is no significant difference in colony productivity. However, each species is more productive at the opener, less heavily vegetated site where it is found. As a result, *P. lanio* is significantly more productive, overall, than *P. versicolor*. These data are consistent with the hypothesis that *P. lanio* excludes *P. versicolor* by competition from more productive sites. The basis of this supposed competition remains unknown.

Key words: *Polistes*, niche, social wasp.

INTRODUCTION

Polistes is a worldwide genus of social wasps. The approximately 200 known species (Carpenter 1996a) are very similar in their overall physical makeup, nest structure and social organization (Reeve 1991). In addition, although *Polistes* have been recorded taking a variety of prey as brood-food, it is believed that caterpillars form the main provision of most or all species (Reeve 1991).

In Trinidad, West Indies, seven species of *Polistes* are recorded (Starr and Hook 2003, 2006), with more than one often found nesting in the same sites. Little is known about flight ranges of *Polistes* foragers, although there is reason to believe that they do not usually range far from the nest. Dew and Michener (1978) found mean foraging distances of 48 and 102 m, respectively, in two North American species, while Suzuki (1978) estimated the mean foraging area at only about 120 m^2 (radius about 6.2 m) in a Japanese species. These sparse data suggest that, as a rule, *Polistes* forage close to home.

The two commonest species in Trinidad, *P. lanio* (Linnaeus) and *P. versicolor* (Olivier), both nest abundantly on human-made structures, often together. The two are readily distinguishable by colour differences and size (forewing length of females usually 19-20 mm in *P. lanio*, 12.5-13.5 mm in *P. versicolor*), but are otherwise physically almost identical (Carpenter 1996b). Likewise, the nests are effectively identical except in size (mean side-to-side cell diameter 6.5 mm in *P. lanio*, 5.5 mm in *P. versicolor*). Each species has a very broad geographic range and has been studied extensively in Brazil (Giannotti 1995; Giannotti and Machado 1994a-c, 1997, 1999, Giannotti and Mansur 1993; Giannotti *et al*. 1995, Gobbi 1977, Gobbi and Zucchi 1980, 1985). These similarities raise the question of what ecological factors separate such similar species and allow them to co-exist.

Our purpose here is to examine habitat differences between these two species that may contribute to a niche separation.

MATERIALS AND METHODS

All observation were made during October-November 2000. We utilized three study sites within the same area of Trinidad, each part of the University of the West Indies (UWI). All three sites are in relatively flat lowlands with no sizeable body of water. Although each site is extensive, our attention was restricted to colonies spread over a very few hectares.

1. The medical school at Mt. Hope comprises many large concrete-and-steel buildings and other human-made structures in a relatively featureless grassland with almost no large trees.
2. The University Field Station, about 1 km south of Mt Hope, comprising fewer buildings, many more scattered large trees, and fields for crops and livestock.
3. The University of the West Indies main campus at St. Augustine, about three kilometers east of Mt. Hope, with a great number of steel-and-concrete buildings. It is the most heavily vegetated site, with large trees forming a diffuse parkland forest.

At each site we walked about haphazardly, recording the species and location of nests, whether old or still active. Each nest site on a building was categorized as an eave (on the outside of the building, usually under a short overhang), porch (recessed at least one-half meter from the building's edge, but with broad open access to the outside) or room (inside the building, with narrow access to the outside). Nest substrates were recorded as wood, concrete or metal.

In order to determine whether mature-colony size dif-

Table 1. Relative prevalence and nest situations of *Polistes lanio* and *P. versicolor* at three localities in Trinidad, West Indies. MtH = Mt. Hope, UFS = University Field Station, StA = St. Augustine. Further explanation in text.

Species	**Locality**	**No. of**	**--- Nest site ---**	**--- Nest substrate ---**				
		nests	**Eave**	**Porch**	**Room**	**Wood**	**Concrete**	**Metal**
P. lanio	MtH	60	60	0	0	0	60	0
P. versicolor	MtH	0	0	0	0	0	0	0
P. lanio	UFS	97	97	0	0	86	6	5
P. versicolor	UFS	28	28	0	0	23	2	3
P. lanio	StA	0	0	0	0	0	0	0
P. versicolor	StA	30	30	0	0	0	30	0

fers between species, we collected old (abandoned) and late-stage (with very few adults or with males present) nests of the two species and computed a) number of cells, and b) total production of adults. The second parameter is estimated by dissecting a sample of cells and counting the number of fecal pellets in the base. Each mature larva deposits a single fecal pellet at the time of pupation, so that the number of pellets in a cell indicates the number of adults produced.

We attempted no rigorous measure of foraging distance in either species. However, in order to gain a rough estimate, we opportunistically followed wasps as they left the nest, measuring the distance to the foraging area to the nearest meter by pacing where we were able to follow them.

RESULTS

In Trinidad these two species nest almost exclusively on human-made structures when these are available. We have only occasionally found either of them nesting on vegetation, in no case during the present study.

We found only *P. lanio* nesting at Mt. Hope, only *P. versicolor* at St. Augustine, while both species were abundant at the University Field Station (Table 1), a statistically highly significant difference (X^2 test, $p<0.01$).

All nests in our sample were attached to eaves, although outside of this study we have found these species nesting on porches and in rooms. As seen in Table 1, at the UFS each species nested on wooden, concrete and metal substrates, with no evident preference difference between species (X^2 test, $p>0.05$).

Nest sizes and productivity (as measured by fecal pellets) show an odd pattern in our modest-sized data-set (Table 2). Where the two species nest together, at the UFS, they show no significant difference in either parameter ($p>0.05$). However, it is striking that *P. lanio* did so much better at MtH than at the UFS ($p<0.05$), while *P. versicolor* did much better at the UFS than StA ($p<0.05$; all three comparisons by Kruskall-Wallis one-way non-parametric analysis of variance).

Nine *P. lanio* foragers flew an average of 39.2 m (range 15-87 m) from the nest before alighting on vegetation.

Table 2. Nest sizes and productivity of *Polistes lanio* and *P. versicolor* in Trinidad, West Indies. MtH = Mt. Hope, UFS = University Field Station, StA = St. Augustine. Numbers of cells and fecal pellets are mean±SE. Further explanation in text.

Species	**Locality**	**Cells**	**Fecal pellets**
P. lanio (n=60)	MtH	103.5±11.2	101.9±14.2
P. lanio (n=97)	UFS	55.6±7.0	29.9±6.0
P. versicolor (n=28)	UFS	62.9±10.8	38.0±8.8
P. versicolor (n=30)	StA	28.2±6.1	6.2±2.6

DISCUSSION

The data are consistent with the hypothesis that *P. lanio* tends to nest in areas with fewer trees than those utilized by *P. versicolor*. Given the presumed short average flight distance of foragers, the nesting habitat and foraging habitat are the same. Where the two nest together, nothing is known of any differences in prey preferences.

Exclusive nesting on concrete at MtH and StA, but mostly on wood at the UFS in our samples, is evidently simply a reflection of what was available, not a preference. This is further shown in the lack of any significant difference between species at the UFS.

The data on nest size and productivity (two indices of the same thing) are curious and would bear further study. The pattern in our data is consistent with the hypothesis that a) each species does better at sites with more herbaceous vegetation and fewer trees, hence with greater primary productivity, and b) *P. versicolor* is largely excluded from the better sites through competition from *P. lanio*. However, the basis of any such competitive advantage is unknown.

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A Comparison of the Freshwater Macroinvertebrate Assemblages of St. Kitts and Nevis, West Indies

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ABSTRACT
A survey of macroinvertebrates inhabiting the freshwater habitats of St. Kitts and Nevis was conducted during June 1996, May 1997, and January 2000. Qualitative collections were made by sweeping a dip net through the water column and by hand examination of rocks, plants, and debris submerged in both flowing and standing bodies of freshwater across these islands. These collections yielded at least 90 species, 57 from St. Kitts and 61 from Nevis. Many of the species encountered are being reported for the first time from these islands. Dominant taxa collected included several species of gastropods, decapod crustaceans, odonates, hemipterans, and coleopterans. Generally the macroinvertebrate fauna of St. Kitts and Nevis is sparse, most likely due to their oceanic origins and disturbances of their freshwater environments.

Key words: Freshwater invertebrates, St. Kitts, Nevis, Lesser Antilles.

INTRODUCTION

St. Kitts and Nevis are small Caribbean islands in the Leeward Islands of the Lesser Antilles. St. Kitts is volcanic in origin, rising 1,157 metres above sea level on Mount Liamuiga, and comprises approximately 177 km^2. Its southeast peninsula is much more arid than the forest-covered volcanic peaks. Aquatic habitats include shallow coastal salt ponds, small inland ponds filled with vascular plants, and mountain streams. Nevis is also volcanic in origin, rising 986 metres above sea level at Nevis Peak, and comprises approximately 94 km^2. This smaller island is distinguished by its central, cone-shaped volcanic peak. No permanently flowing water habitats exist in Nevis; only a few temporary streams flow on a seasonal basis. Much of the land surface is relatively porous and underground lava tubes carry water down the mountain slopes, often emerging as springs near the coasts. Standing water comprises all other freshwater habitats of Nevis. Hutton (1976) states Nevis is covered by rock laid down about two million years ago. The two islands are separated by a strait measuring less than four kilometres between the shores.

A limited amount of information regarding the freshwater invertebrates of the Lesser Antilles and other small Caribbean islands is available. Biodiversity surveys have been conducted on some islands including Barbados (Bass 2003a), St. Vincent (Harrison and Rankin 1975, 1976a, 1976b), St. Lucia (McKillop and Harrison 1980), Antigua (Bass 2005), Grenada (Flint and Sykora 1993; Bass 2004), Tobago (Nieser and Alkins-Koo 1991; Bass 2003b), and Trinidad (Hynes 1971; Alkins *et al*. 1981; Alkins-Koo 1990; Nieser and Alkins-Koo 1991). While some invertebrate groups in the Lesser Antillean region have been studied, such as decapod crustaceans (Chace and Hobbs 1969; Hart 1980), odonates (Donnelly 1970), and trichopterans (Flint 1968, 1996; Botosaneanu 2002; Botosaneanu and Alkins-Koo 1993; Flint *et al*. 1999), many others have yet to be surveyed. A general description of freshwater habitats in Nevis and the common groups of invertebrates that inhabit them were provided by Bass (2000), but a species list was lacking and many details were omitted due to the nature of that publication. No such research from St. Kitts has been published.

The objectives of this investigation include: 1) to determine the species of aquatic macroinvertebrates inhabiting freshwater environments of St. Kitts and Nevis; 2) to note microhabitat preferences of each species; 3) to determine the relative abundance of each species; and 4) to compare the macroinvertebrates of St. Kitts and Nevis to each other and to those of other small Caribbean islands.

MATERIALS AND METHODS

Seventeen sampling sites and fourteen sampling sites were established in various freshwater habitats across St. Kitts and Nevis, respectively. These sites were visited and collections were made during June 1996, May 1997, and January 2000. Water temperature was also recorded from each site at the time of collection. Some of those sites were visited more than once.

Several methods of collecting were employed to ensure as many species as possible were captured. Submerged debris, such as stones, leaves, and wood were carefully examined and inhabitants were picked from the substrate using forceps. A dip net (mesh = 0.5 mm) was swept through aquatic vegetation and the water column to capture macroinvertebrates occupying those microhabitats. The microhabitat from where each specimen occurred was noted. Collecting efforts continued at each site until it appeared no more additional species were encountered. These collecting methods were similar to those used on other islands so comparisons of the results could be made (Bass 2003a, 2003b, 2004, 2005). Specimen were preserved in 70% ethanol and returned to the laboratory for further identification. Taxa that could not be identified to the species level were separated into morphospecies for subsequent analysis and the taxonomic name to which they could be identified was used. Sorenson's index of similarity (1948) was used to compare these collections in St. Kitts and Nevis with similar endeavors on other small Caribbean islands.

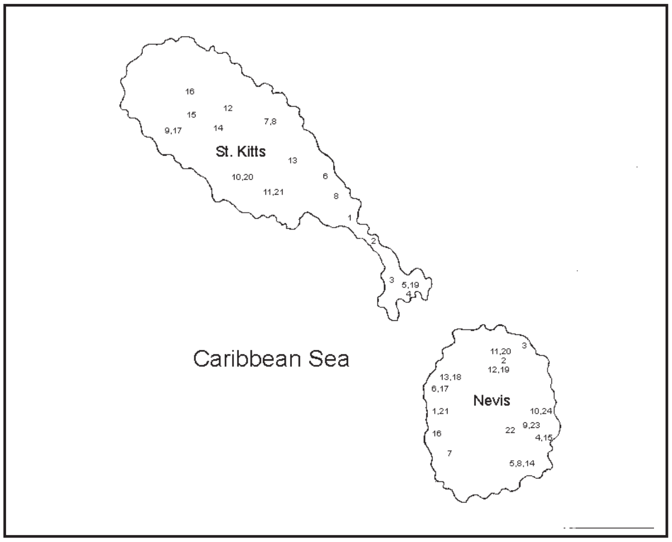

Fig. 1. Map indicating location of collecting sites in St. Kitts and Nevis. Specific locations, dates, and approximate elevations of collections are listed in legend of Table 1.

RESULTS AND DISCUSSION

At least 90 species were recorded from these sister islands – 57 species from St. Kitts and 61 species from Nevis (Table 1). This list is important because it represents the only collections of freshwater invertebrates currently known from these two islands. Insects, especially odonates, hemipterans, and coleopterans, dominated in these collections. Gastropods were also quite common on both islands while decapod crustaceans were frequent occurrences in streams of St. Kitts. Only 27 taxa occurred on both islands.

Porifera

Radiospongilla crateriformis is the only freshwater sponge known to exist on Caribbean islands. This species was initially reported by Bass and Volkmer-Ribeiro (1998) and, in the Caribbean, has been found only on Barbados and Nevis. It was in the form of a light-colored, encrusting growth living on submerged wood debris in Hog Valley Reservoir and Old Spring Hill Pond. All of these sites from where *R. crateriformis* has been reported in the Caribbean basin become dry during periods of extended drought and the sponge survives by forming drought-resistant gemmules until the water returns.

Platyhelminthes

Girardia was the only flatworm encountered, and it was found in only two mountain streams of St. Kitts and a temporary stream of Nevis. The only other reports of this genus in the Lesser Antilles come from Barbados (Bass 2003a) and Grenada (Bass 2004).

Oligochaeta

Only one species of oligochaete, *Allonais paraquayensis*, was collected. This worm existed in the detritus on the bottom of Hog Valley Reservoir in Nevis. This constitutes the first report of *A. paraquayensis* from a Caribbean island (M. Wetzel, personal communication).

Hirudinea

Although *Helobdella triserialis* was collected on both islands, it was limited to standing freshwater environments having dense growths of aquatic vascular plants. Based on observations by Davies (1979), it is hypothesized *H. triserialis* was passively dispersed to St. Kitts and Nevis by egg cocoons attached to macrophytes. It is also possible that aquatic birds carried ingested cocoons between different bodies of water (Davies *et al.* 1982).

Gastropoda

Nine species of freshwater snails were collected from St. Kitts and Nevis. The most abundant of these, *Physella mormorata*, occurred in ponds and streams on both islands. It is interesting that *Tropicorbis albicans* was found at several ponds having dense stands of macrophytes in Nevis, but appears to be absent in St. Kitts. Six gastropod species were collected at only one location. Notably absent from these collections is *Melanoides tuberculata*, an introduced species reported on other small islands of the eastern Caribbean basin (Bacon *et al*. 1978; Bass 2003a, 2003b, 2003c, 2004, 2005).

Pelecypoda

Eupera cubensis was found only in Hog Valley Reservoir and was one of the few species previously reported from Nevis (Bass 2000). Its distribution ranges from the southeastern United States through the Caribbean islands (Thorp and Covich 2001). This small clam is intolerant of salt water and presumably may be transported between bodies of water inadvertently attached to damp feathers of waterfowl such as herons, egrets, or coots.

Table 1. List of freshwater macroinvertebrates, including collecting sites, life cycle stages present, relative occurrence, microhabitats, and proposed trophic relationships in St. Kitts and Nevis during June 1996, May 1997, and January 2000. Life cycle: A, adult; J, juvenile; L, larva; N, nymph. Occurrence: *** abundant, ** common, * uncommon.

Taxa	Collection Sites	Life Cycle	Occurrence	Microhabitat	Trophic Relationship[1]
Porifera					
Radiospongilla crateriformis	N12, N20	A	*	Wood debris	Filterer
Platyhelminthes					
Girardia sp.	SK11, SK12, N24	A	*	Detritus	Predator
Oligochaeta					
Allonais paraquayensis	N12	A	*	Detritus	Detritivore
Hirudinea					
Helobdella triserialis	SK7, N9, N12, N23	A	**	Vascular hydrophyte	Predator
Gastropoda					
Ferrissia beaui	N11	A	*	Detritus	Herbivore
Helisoma sp.	SK7, SK18, N15	A	*	Vascular hydrophyte	Detritivore
Marisa cornuarietis	SK11, SK21	A	*	Rock	Herbivore
Neritina punctulata	N13	A	*	Rock	Herbivore
Neritina virginea	SK1	A	*	Rock	Herbivore
Physella mormorata	SK7, SK9, SK11, SK12, SK14, SK15, SK18, SK21, N1, N5, N8, N9, N10, N14, N15, N20, N22, N23, N24	A	***	Detritus	Detritivore
Planorbella (Seminolina) sp.	SK7	A	*	Vascular hydrophyte	Detritivore
Pyrgophorus parvulus	N13	A	*	Detritus	Detritivore
Tropicorbis albicans	N5, N6, N8, N9, N11, N14, N19, N20, N22, N23	A	***	Detritus	Detritivore
Pelecypoda					
Eupera cubensis	N12, N19	A	*	Sediment	Filterer
Branchiopoda					
Artemia franciscana	SK3	A	*	Sediment	Filterer
Ostracoda					
Chlamydotheca unispinosa	N9, N12	J, A	*	Vascular hydrophyte	
Unknown Ostracoda	SK19	A	*	Detritus	
Decapoda					
Atya innocous	SK14, SK15, SK17, SK21	J, A	**	Detritus	Detritivore
Atya sp.	SK10, SK14, SK15, SK20	J	**	Detritus	Detritivore
Macrobrachium crenulatum	SK14, SK17, SK21	A	**	Detritus	Detritivore
Macrobrachium faustinum	SK10, SK17, SK20, N1, N3, N21	J	**	Detritus	Predator
Micratya poeyi	SK10	A	*	Detritus	Predator
Palaemon pandaliformis	SK1, N13, N18	J, A	*	Detritus	Detritivore
Xyphocaris elongata	N21	J	*	Detritus	Detritivore
Unknown Decapoda (crab)	N18	J	*	Detritus	Detritivore
Ephemeroptera					
Americabaetis sp.	SK10, SK11, SK12, SK14, SK15, SK17, SK21	N	***	Detritus	Collector
Caenis sp.	N10, N12, N15, N19	N	**	Detritus	Collector
Callibaetis sp.	SK7, N1, N2, N5, N6, N10, N11, N12, N24	N	***	Detritus	Collector
Leptohyphes sp. (2?)	SK11, SK15	N	*	Detritus	Collector
Odonata					
Aeshna psilus	N10	N	*	Detritus	Predator
Anax concolor	SK19, N13, N17, N20, N22, N23, N24	N	**	Vascular hydrophyte	Predator
Brachymesia furcata	SK16, N19	N	*	Detritus	Predator
Brechmorhoga praecox grenadensis	SK11, SK12, SK13, SK15, SK16, SK21	N	***		Predator
Dythemis sterilis	SK4, SK18, N10, N24	N	*	Detritus	Predator
Enallagma coecum	SK11, SK12	N	*	Detritus	Predator
Erythemis poss. *vesiculosa*	SK18, N15	N	*	Detritus	Predator
Erythrodiplax sp.	SK21, N2, N4, N6, N10, N24	N	***	Vascular hydrophyte	Predator
Ischnura ramburii	SK5, SK7, SK18, SK19, SK21, N1, N5, N9, N11, N13, N14, N15, N17, N19, N20, N21, N23	N	***	Vascular hydrophyte	Predator
Lestes poss. *forficula*	N11, N15, N17, N20, N23	N	***	Vascular hydrophyte	Predator
Miathyria marcella	SK7, SK9, N5, N15, N17	N	**	Vascular hydrophyte	Predator
Orthemis ferruginea	SK5, N4, N19, N20	N	**	Vascular hydrophyte	Predator

Pantela flavescens	N2	N	*	Detritus	Predator
Tramea abdominalis	SK19, N5, N10, N11, N12, N15, N20, N23	N	***	Detritus	Predator
Hemiptera					
Belostoma subspinosum	N5, N8	N	*	Vascular hydrophyte	Predator
Buenoa sp.	SK6, SK7, N6, N14	N, A	**	Water column	Predator
Centrocorisa nigripennis ?	N4, N10, N11, N13, N23	N, A	***	Water column	Predator
Limnogonus franciscanus	SK6, SK7, SK18, SK19, N13, N14, N15, N18, N21	N, A	***	Neuston	Predator
Mesovelia mulsanti	SK5, SK7, N1, N2, N4, N5, N6, N8, N9, N11, N12, N13, N14, N15, N17, N18, N20, N21, N22, N23	N, A	***	Neuston	Predator
Microvelia longipes	N4, N7, N18	N, A	*	Neuston	Predator
Microvelia sp.	SK6, SK9, SK12, SK19, SK21, N1, N3, N4, N5, N7, N10, N12, N15, N16, N17, N21, N22, N24	N, A	***	Neuston	Predator
Notonecta indica	SK9, SK10, N2, N5, N8, N15, N19, N20, N22, N24	N, A	***	Vascular hydrophyte	Predator
Pelocoris poeyi	SK7, SK18, N4, N5, N1, N12, N13, N14, N15, N20, N21, N22, N23	N, A	***	Vascular hydrophyte	Predator
Rhagovelia elegans	SK10, SK11, SK12, SK14, SK15, SK17, SK20, SK21	N, A	***	Neuston	Predato
Ranatra galatae	N15, N22	A	*	Vascular hydrophyte	Predator
Saldula sp.	N17	N	*	Detritus	Predator
Trichocorixa reticulata	SK1, SK2, SK3, SK4, SK6, SK8	N, A	***	Detritus	Predator
Trichoptera					
Chimarra (Chimarra) sp.	SK11, SK12, SK13, SK14, SK15, N24	L	**	Detritus	Collector
Smicridea (Smicridea) sp.	SK12, SK14, SK15	L	**	Detritus	Collector
Xiphocentron sp.	SK11	L	*	Detritus	Collector
Lepidoptera					
Petrophila sp.	SK15	L	*	Rock	Herbivore
Coleoptera					
Aleocharinae	SK9, SK15, SK17, SK20, SK21	A	**	Detritus	Predator
Copelatus postcatus	SK9, SK17, N10, N22	A	**	Detritus	Predator
Derallus rudis	N9, N14, N23	A	**	Detritus	Collector
Enochrus pseudochraceus	SK10	A	*	Detritus	Herbivore
Eretes sticticus	SK5	A	*	Detritus	Predator
Helochares femoratus	N9, N15, N16, N17, N19, N22, N23, N24	A	***	Vascular hydrophyte	Collector
Hydrobiomorpha phallica	SK7	A	*	Detritus	Collector
Hydrophilus insularis	SK5, SK7, N2, N5, N6, N13 L,	A	***	Detritus	Predator
Laccobius sp.	SK18	A	*	Vascular hydrophyte	Herbivore
Laccophilus subsignatus	SK5, SK6, SK9, SK12, SK18, SK19, N10, N15, N19, N24	A	***	Detritus	Predator
Megadytes sp.	N4, N11, N20	L	**	Vascular hydrophyte	Predator
Paracymus confusus	N1, N4, N6, N17	A	**	Detritus	Collector
Paracymus nanus	SK13	A	*	Detritus	Collector
Scirtes sp.	N5	A	*	Vascular hydrophyte	Herbivore
Thermonectes bacillaris	N5, N6	L, A	*	Vascular hydrophyte	Predator
Tropisternus lateralis	SK7, SK18, SK19, N1, N4, N5, N6, N9, N10, N11, N12, N14, N15, N17, N20, N21, N22, N23	L, A	***	Detritus	Collector, Predator
Diptera					
Ablabesmyia sp.	N2, N12	L	*	Sediment	Predator
Anopheles sp.	N17	L	*	Water column	Collector
Chironomus sp.	SK5, SK16, SK19, N6, N11	L	**	Sediment	Collector
Coelotanypus sp.	N2, N11	L	*	Sediment	Predator
Corynoneura sp.	SK15	L	*	Sediment	Collector
Cricotopus sp.	SK12, SK15	L	*	Sediment	Collector
Culex sp.	N5	L	*	Water column	Collector
Einfeldia sp.	N12	L	*	Sediment	Collector
Goeldichironomus sp.	SK19	L	*	Sediment	Collector
Mansonia sp.	N5, N9, N14	L	**	Vascular hydrophyte	Collector
Monopelopia ? sp.	N11	L	*	Sediment	Predator
Parachironomus sp.	N11	L	*	Sediment	Collector
Odontomyia sp.	SK20	L	*	Detritus	Collector
Paracricotopus sp.	SK21		*	Sediment	Collector
Simulium sp.	SK11, SK21, N24	L	**	Rocky substrate	Collector
Thienemanniella sp.	SK10, SK12	L	*	Sediment	Collector

Trophic relationship[1]–Trophic relationships of insects based on Merritt and Cummins (1996) and non-insects on Thorp and Covich (2001).

Collecting sites: SK1) Salt Pond, Frigate Bay, St. Kitts (2m), 25 June 1996; SK2) Salt Pond, Friars Bay Estate, St. Kitts (2m), 25 June 1996; SK3) Great Salt Pond, Salt Pond Estate (2m), 25 June 1996; SK4) Fleming Estate Pond, Fleming Estate, St. Kitts (2m), 25 June 1996; SK5) Livestock Pond, Fleming Estate, St. Kitts (4m), 25 June 1996; SK6) Muddy Pond, Frigate Bay, St. Kitts (2m), 25

June 1996; SK7) Ottley's Pond, Ottley's Estate, St. Kitts (130m), 25 June 1996; SK8) Golf Course Pond, Frigate Bay, St. Kitts (7m), 27 June 1996; SK9) Wingfield River, Wingfield Estate, St. Kitts (60m), 27 June 1996; SK10) Stone Fort River, Stone Fort Estate, St. Kitts (120m), 19 May 1997; SK11) West Farm Gut, West Farm Estate, St. Kitts (90m), 19 May 1997; SK12) Phillips River, Catchment Area, St. Kitts (290m), 20 May 1997; SK13) Ogee's River Tributary, Catchment Area, St. Kitts (310m), 20 May 1997; SK14) Frankland's River, Catchment Area, St. Kitts (380m), 22 May 1997; SK15) Wingfield River, Catchment Area, St. Kitts (155m), 22 May 1997; SK16) Dos D'ane Pond, Verchild's Mountain, St. Kitts (945m), 24 May 1997; SK17) Wingfield River, Wingfield Estate, St. Kitts (50m), 6 January 2000; SK18) Ottley's Pond, Ottley's Estate, St. Kitts (130m), 10 January 2000; SK19) Livestock Pond, Fleming Estate, St. Kitts (4m), 10 January 2000; SK20) Stone Fort River, Stone Fort Estate, St. Kitts (120m), 11 January 2000; SK21) West Farm Gut, West Farm Estate, St. Kitts (90m), 11 January 2000; N1) Golf Course Ponds, Four Seasons Resort, Nevis (7m), 26 June 1996; N2) Spring Hill Pond, Spring Hill, Nevis (170m), 26 June 1996; N3) Mount Lily River, Camps, Nevis (25m), 26 June 1996; N4) Fothergill's Estate Pond, Fothergill's Estate, Nevis (175m), 26 June 1996; N5) Pond Hill Pond, Pond Hill, Nevis (250m), 26 June 1996; N6) Nelson Spring, Cotton Ground, Nevis (2m), 26 June 1996; N7) Bath Creek, Bath, Nevis (15m), 21 May 1997; N8) Pond Hill Pond, Pond Hill, Nevis (250m), 21 May 1997; N9) Herbert Heights Pond, Herbert Heights, Nevis (360m), 21 May 1996; N10) New River Spring, New River (Road-To-Nowhere), Nevis (90m), 21 May 1997; N11) Old Spring Hill Pond, Spring Hill, Nevis (170m), 21 May 1997; N12) Hog Valley Reservoir, Hog Valley, Nevis (165m), 21 May 1997; N13) Nelson Spring Pond, Cotton Ground, Nevis (2m), 21 May 1997; N14) Pond Hill Pond, Pond Hill, Nevis (250m), 7 January 2000; N15) Fothergill's Estate Pond, Fothergill's Estate, Nevis (175m), 7 January 2000; N16) Boiling Pot, Nevis Museum, Charleston, Nevis (2m), 8 January 2000; N17) Nelson Spring, Cotton Ground, Nevis (2m), 8 January 2000; N18) Nelson Spring Pond, Cotton Ground, Nevis (2m), 8 January 2000; N19) Hog Valley Reservoir, Hog Valley, Nevis (165m), 8 January 2000; N20) Old Spring Hill Pond, Spring Hill, Nevis (170m), 8 January 2000; N21) Golf Course Ponds, Four Seasons Resort, Nevis (7m), 9 January 2000; N22) Zetlands Pond, Zetlands, Nevis (490m), 9 January 2000; N23) Herbert Heights Pond, Herbert Heights, Nevis (360m), 9 January 2000; N24) New River Spring, New River (Road-To-Nowhere), Nevis (90m), 9 January 2000.

Branchiopoda

Artemia franciscana was collected only from a warm, very shallow and somewhat isolated arm of Great Salt Pond on St. Kitts. As implied by the name of the pond, salt water was present, and the presence of *A. franciscana* in that pond indicates its ability to tolerate saline conditions. Horne and Beyenbach (1974) noted the presence of hemoglobin in *Artemia* that allows these beasts to live in aquatic habitats with low oxygen values, which probably occurred in Great Salt Pond. Birds may play a role in brachiopod dispersal as demonstrated by Proctor (1964) when *Artemia* eggs were hatched from feces of ducks.

Ostracoda

Two different ostracods were found during this investigation. *Chlamydotheca unispinosa* was collected from among submerged macrophytes at two ponds in Nevis while an unidentified ostracod was taken from a sediment sample of a pond in St. Kitts.

Decapoda

At least seven species of decapod crustaceans were encountered on these two islands. *Macrobrachium faustinum* and *Palaemon pandaliformis* were the only decapods found on both islands. The atyid shrimps appear to be absent from Nevis due to the lack of running water habitats which they require. One crab was only briefly observed in Nevis, but it escaped before a specific identification could be determined. All of the species collected from St. Kitts and Nevis have been reported from other Caribbean islands (Chace and Hobbs 1969).

Ephemeroptera

A total of four mayfly genera were collected from these two islands, although several of these occurred at more than one site. Three were limited to St. Kitts and three were found only in Nevis, while only one, *Callibaetis*, occurred on both islands. All four of these genera are widespread throughout the Lesser Antilles.

Odonata

Most of the fourteen species of odonates found were present on both St. Kitts and Nevis. Only two species and three species were limited to St. Kitts and Nevis, respectively. The most common odonate collected, the damselfly *Ischnura ramburii*, has been reported primarily in ponds on several other eastern Caribbean islands (Donnelly 1970; Harrison and Rankin, 1976b; Bass 2003a, 2003b, 2004, 2005). All of these odonates are predators that inhabit submerged vegetation and detritus.

Hemiptera

Hemipterans are one of the most frequently encountered aquatic groups of insects in the Caribbean region (Bass 2003a, 2003b, 2004, 2005). Both adults and nymphs are predators in these environments. Eight species were collected in St. Kitts and 11 species were taken from Nevis with six of those taxa being common to both islands. Some of the most common species found include the backswimmer, *Notonecta indica*, and creeping water bug, *Pelecoris poeyi*. The water boatman, *Trichocorixa reticulata,* was limited in distribution to the coastal brackish water ponds in St. Kitts where it occurred in high densities. Other frequently collected hemipterans included the water striders *Limnogonus franciscanus, Mesovelia mulsanti, Microvelia,* and *Rhagovelia elegans*. As on other small eastern Caribbean islands, these water striders had both winged and wingless adults composing the populations. This phenomenon of wing polymorphism and its advantages to hemipterans living in isolated habitats has been well documented (Roff 1990; Schuh and Slater 1995; Thorp and Covich 2001; Bass 2003c).

Trichoptera

Trichopteran larvae are widespread across the Caribbean islands, especially in flowing water habitats (Flint 1968, 1996; Flint and Sykora 1993, Flint *et al.* 1999; Botosaneanu 2002). Although St. Kitts appears to have suitable environments to support many more species, such as in Grenada and Dominica, only three genera were encountered. It is necessary to collect adults via light-trapping, as did Flint (1968, 1996), Flint and Sykora (1993), Flint *et al.* (1999), and Botosaneanu (2002), to collect higher numbers of species, and that method was not used in this study. Therefore, it is expected more species of caddisflies will be reported from St. Kitts, and possibly Nevis, in the future. The reduced number of trichopterans on Nevis is largely due to the limited amount of flowing waters, the preferred habitat for many species of caddisfly larvae.

Lepidoptera

Larvae of *Petrophila* were collected only once. This was in the upper sections of the Wingfield River during May 1997. These larvae are widespread in mountain streams of other small eastern Caribbean islands, including Tobago (Bass 2003b) and Grenada (Bass 2004), so it is surprising this species was not collected in other streams of St. Kitts.

Coleoptera

Sixteen species of aquatic beetles were collected from St. Kitts and Nevis. Although these insects are capable of flight and presumably could exist on both islands, it is interesting to note that most of these species were found only on one island. The most commonly encountered species were the water scavenger beetle, *Tropisternus lateralis,* and the predacious diving beetle, *Laccophilus subsignatus*.

Diptera

Sixteen species of aquatic dipteran larvae were also collected from these two islands. However, nine of these taxa were encountered once with only *Chironomus* being found in more than three collections. *Chironomus* has been reported from several eastern Caribbean islands (Bass 2003a, 2003b, 2004, 2005). It is important to note that the majority of dipterans on these islands belong to a single family of midges, the Chironomidae. It is suspected this family is more common and widespread than currently reported, but midges are very small and much sediment must be carefully examined to adequately determine their abundances and distributions. Helson *et al.* (2006) reports densities of larval chironomids exceeding 100 individuals/m^2 in similar streams of Trinidad.

Island biogeography theory (MacArthur and Wilson 1967) predicts St. Kitts would possess more species than Nevis because St. Kitts is a considerably larger island. However, Nevis has a slightly greater species richness. There are several possible explanations regarding this anomaly. Much of the size difference between the two islands lies with the arid southeastern peninsula of St. Kitts where little freshwater exists. If the area of the peninsula is subtracted, then the remaining mountainous region of St. Kitts is almost the same as the area of Nevis. In addition, there is more development on St. Kitts and this may have negatively impacted freshwater habitats.

Sorenson's similarity index indicates a faunal similarity of 0.46 between St. Kitts and Nevis (Tables 2-3). This is quite high, especially as compared to pair values of other small Caribbean islands (Bass 2003c). However, due to the very close proximity of these two islands, it is likely dispersal between St. Kitts and Nevis occurs in some groups so this result is possible (MacArthur and Wilson 1967). Another nearby island, Antigua, also shares somewhat higher values with St. Kitts and Nevis as well. Generally, as distance increased between the island pairs being compared, similarity values decreased. An interesting exception was Barbados which showed similarity values of 0.17 and 0.18 with St. Kitts and Nevis, respectively. All three islands have similar pond habitats and there is much overlap in species assemblages of those ponds.

Hurricane Lenny, a stochastic event, slowly moved across St. Kitts and Nevis 23-25 November, 1999. Wind

Table 2. Sorensen's index of similarity values comparing the freshwater macroinvertebrate fauna of St. Kitts to that of other small Caribbean islands, including approximate distances to those islands from St. Kitts and approximate island sizes. 0.00 = 0% common taxa and 1.00 = 100% common taxa.

Island	Approximate Distance (km)	Approximate Size (km^2)	Similarity Value
Nevis	4	94	0.46
Saba	49	13	0.02
Montserrat	75	83	0.20
Antigua	93	280	0.18
Dominica	218	751	0.13
St. Lucia	400	616	0.10
Barbados	551	430	0.17
Grenada	575	346	0.10
Tobago	700	300	0.12
Cayman Brac	1,813	37	0.00
Little Cayman	1,840	26	0.07
Grand Cayman	1,956	197	0.01
Guanaja	2,467	69	0.03

Table 3. Sorensen's index of similarity values comparing the freshwater macroinvertebrate fauna of Nevis to that of other small Caribbean islands, including approximate distances to those islands from Nevis and approximate island sizes. 0.00 = 0% common taxa and 1.00 = 100% common taxa.

Island	Approximate Distance (km)	Approximate Size (km^2)	Similarity Value
St. Kitts	4	177	0.46
Montserrat	53	83	0.11
Antigua	70	280	0.25
Saba	80	13	0.03
Dominica	200	751	0.11
St. Lucia	382	616	0.10
Barbados	538	430	0.18
Grenada	560	346	0.09
Tobago	685	300	0.10
Cayman Brac	1,844	37	0.01
Little Cayman	1,871	26	0.11
Grand Cayman	1,982	197	0.01
Guanaja	2,493	69	0.05

speeds measured approximately 215 km/hour and 30 cm of rain fell at R. L. Bradshaw Airport during that period (K. Orchard, personal communication). Large amounts of plant debris washed into streams and stream channels were scoured as a result of the heavy rainfall during that brief period. Evidence of this high discharge and a greatly reduced stream invertebrate fauna from that disturbance was observed in January 2000, six weeks after the hurricane passed. It was also observed that ponds on both islands held larger volumes of water than was present during previous visits, but their invertebrate populations appeared mostly unaffected. Hurricanes are also known to act as a mechanism to transport and re-distribute populations of invertebrates. It is suspected the occurrence of past storms may explain the presence of the sponge, *Radiospongilla crateriformis*, in Barbados and Nevis (Bass and Volkmer-Ribeiro 1998).

Both St. Kitts and Nevis are oceanic islands so their freshwater macroinvertebrate faunas had to colonize these islands from elsewhere. These immigrants must have suitable dispersal mechanisms and be able to tolerate unfavorable conditions encountered while crossing ocean waters (Bass 2003c). No endemic freshwater invertebrates that may have evolved in isolation on St. Kitts or Nevis have been discovered. However, as further investigations are conducted on these sister islands, additional species may be found and some of these might be unique to those islands.

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Reproductive Behaviour of the Neotropical Gecko *Thecadactylus rapicauda* (Houttuyn)

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ABSTRACT
Data were obtained from 46 matings with the times of occurrence being noted for 38 of them. Copulation occurred in all months of the year. Fifteen of the copulations (39.5%) occurred between 0600 h and 1000 h, showing that *T. rapicauda* is not strictly nocturnal. Mating behaviour is described. The male bites the female before mounting. Copulation lasts on average 3 min. 25 sec. and separation is accompanied by violent shaking. Few eggs have been found and egg-laying behaviour is very incompletely known.

Key words: *Thecadactylus rapicauda,* reproductive behaviour*,* hemipenis, eggs.

INTRODUCTION

Thecadactylus rapicauda (Houttuyn) is common in Trinidad and Tobago and well-known to the people of these two islands who call it "woodslave", "twenty-four hours", "mabouia" or "checker-check". It is present in many habitats (Murphy 1997) and particularly in dwelling houses in country areas where it may be seen eating insects attracted by lights. When I moved into my new home near Talparo in June, 1982, a small population was already in residence. It is not the easiest of animals to study for several reasons. It is basically nocturnal and its activity cycle does not match that of humans. Its colour is a pattern of browns, greys and cream which changes with illumination and background and, apart from females with easily visible eggs, the sexes are similar and not determinable unless the lizard is in the hand. It does not invite investigation for its most common "activity" is waiting and the sense that guides action is just as likely to be scent as sight.

On the other hand, its action is not usually rapid and is usually easily followed. Furthermore, it can become habituated to humans, making close observation possible with the near certainty that the observed activity is not influenced by the observer. Over the years, most of the adult individuals in my house have become habituated to my presence and have allowed me to watch them close up, within 0.3 m. My passing to and fro has seldom caused any reaction and there is only one instance in the behaviour I shall describe when my coming on scene may have altered the course of events. The juveniles show avoidence behaviour while growing up but they lose their fear as they mature.

Study site and methods

For the vast majority of the observations presented here, the study site has been my present home in Leotaud Trace, Talparo, Trinidad. The house is a prefabricated one of greenheart timber with a total floor area of about 112 sq. m. It stands on pillars ranging from 56-96 cm tall because of the slightly sloping ground. A level ceiling, also of greenheart timber, 2.41 m above the floor separates an attic from the living area. There are some ill-fitting timbers and the odd knot-hole giving numerous connections for the lizards between the two levels. Lizards are almost never seen on the floor but mostly on the walls and ceiling where the adhesive scales of the feet give them adequate grip (Beebe 1944). Because the species is basically nocturnal, a torch is often required for seeing details. Habituated lizards do not react to this; unhabituated ones react by protruding the tongue and, perhaps, by trying to move away from the illuminated area. I estimate that the total population is about 20.

T. rapicauda is vocal. It makes three distinctly different calls. The one that gives it its name "checker-check" is a loud rattle of clucking sounds which in the literature is designated a multiple-click, or MC, call. The second call is a rasping hiss that I write as "shrrr" and think of as a prickly hiss. The third call is a soft "kek". All three have been heard in connection with reproductive behaviour, but the second is by far the most common. It became a signal to get up and investigate.

This study was begun on 8 December, 1982 and is ongoing. In the descriptions that follow "arm" means "front leg" and "leg" means "hind leg." Dates are given in the form day/month/year.

OBSERVATIONS

Courtship and mating behaviour

In most animals copulation is preceded by a series of movements by both the male and the female that prepare them for co-operation in performing the act. This phase is usually referred to as courtship. In some species it takes a relatively long time. In others, as in *Thecadactylus,* it

Table 1. Actions performed by *T. rapicauda* before, during and after courtship and mating.

	before copulation								copulation							after copulation									
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
01					X	X			X															X	
02				X					X																
03				X					X																
04									X							X								X	
05		X	X	X	X	X		X	X	X				X		X				X	X				
06									X				X	X	X	X				X		X		X	
07																				X	X			X	
08		X	X	X	X				X								X							X	
10																				X	X	X	X	X	
12							X		X		X		X		X	X				X	X				
13																			X	X	X	X			
14							X		X				X	X		X		X	X	X	X			X	
15					X		X		X							X		X		X	X			X	
16										X										X				X	
17				X	X		X	X	X	X			X		X			X		X				X	
18									X								X			X				X	
19		X		X	X	X	X		X	X			X		X	X		X	X	X					
20																X				X	X				
21																X		X	X	X	X				
22											X					X				X	X				
23											X								X	X	X	X		X	
24																			X	X	X				
25																				X	X	X		X	X
26																				X	X				
27																				X	X	X			
33			X	X				X	X	X		X	X			X		X		X	X				
34				X						X										X	X			X	
35									X	X		X	X			X		X		X	X			X	
38	X			X			X		X		X		X	X		X		X	X	X	X	X		X	
41									X	X								X		X	X			X	
42											X									X	X				
43											X									X	X	X	X	X	X
44			X	X	X			X	X		X		X	X		X		X	X	X	X	X		X	
45										X										X		X			X
46										X										X	X			X	
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y

Table 1.
Observations. (Numbers in parenthesis refer to Carpenter and Ferguson 1977).

A. Male protrudes tongue (63).
B. Male bites female's tail (17).
C. Male bites female's flank (128).
D. Male bites female's neck (129).
E. Male mounts female (125).
F. Male wriggles, moves sideways on female's back (108).
G. Female attempts to move forward.
H. Female arches tail.
I. Male opposes his cloaca to hers. Copulation (13).
J. Copulation from female's left.
K. Copulation from female's right.
L. Crossover copulation.
M. Male thrusts. (137).
N. Male wraps tail around female's (132).
O. The female attempts to move forward.
P. Violent tremble accompanies separation (14).
Q. Separation not accompanied by violent tremble.
R. Female moves off.
S. Female's tail arched.
T. Male's tail arched.
U. Male licks hemipenis.
V. Male pursues female (19).
W. Female pursues male (19).
X. Hissing call heard (154).
Y. MC call heard (154).

is relatively short. It seldom happens that all of the possible preliminary movements are made and the inclusion or omission of them has a bearing on the duration of the courtship phase. In *T. rapicauda* the female is relatively passive, whereas the male makes several different movements before copulating. I have seen copulation with some or all of courtship 18 times and part or all of post-copulatory behaviour another 27 times. Table 1 summarises 36 of these observations, the remaining 10 being omitted because they add nothing. From this we can reconstruct the full repertoire of movements during courtship, copulation and the post-copulatory period as follows. Seemingly, following chemical cues (see Discussion) the male approaches the female who may or may not move away at his approach. He bites the female's tail and moves forward on one side of the female. When his head reaches alongside the female's pelvis, he transfers his bite to her flank and then her neck. He crawls on to her back, and briefly wriggles his body from side to side. During this phase the female often tries to move forward. The male restrains her with an arm gripping her near midbody and a leg gripping her near the tail. The female then arches the base of her tail (seemingly as a response to the biting and the rubbing) and keeping one leg pressed to the female's rump, the male slips his pelvis under the female's tail and presses his cloaca to hers. It has been impossible to see if the hemipenis is everted at this stage.

During copulation the male thrusts his pelvis against the female. The thrusts start at the rate of about one per second, and are at first fairly gentle – pulses rather than thrusts. Later the thrusts are much more powerful, last 2-3 sec. and may have the effect of curling the male's body much more strongly. The thrusting seems not to involve prior partial withdrawal of the hemipenis. Throughout copulation the hemipenis is kept firmly within the female's cloaca. The female sometimes tries to move forward but is restrained by the male.

Separation usually comes abruptly and details are hard to see. There is a violent shaking or shivering which lasts a fraction of a second, and then the two are separate. The shaking is sometimes violent enough for one or both of the lizards to fall to the ground as a result; the rattle it produces is audible and recognizable for what it is when heard. After separation the female usually moves off a short distance with a slightly arched tail. The male usually stands still with a strongly arched tail and the reddish hemipenis partially everted. He will then curve around and lick the hemipenis, sometimes for many minutes, either in one uninterrupted session or in several sessions with movements in between. Occasionally, he may chase the female before licking the hemipenis, but in my observations he has always licked his hemipenis. Sometimes the chasing that follows copulation is accompanied by the sound I call a hiss (No. 2 above). This sound is made by both male and female.

It may be assumed that the shaking causes the separation of the two lizards. This may not be correct. To help in deciding the issue, I give descriptions of six different instances: No. 19 (7/5/97). A violent shaking of the pair occurred so quickly it was impossible to know exactly what happened. There may have been 6-9 oscillations and then the lizards separated with the male's hemipenis still partially everted. No. 33 (2/12/01). The male got off the female on her left side, shivered violently without shaking the female and then moved away. No. 35 (14/6/02). The male removed his leg from the female's rump and stood clear of her. He shivered violently shaking the female a little. No. 38 (24/7/03). At parting the male removed his leg from the female's rump while still biting her, shivered, released his bite on the female who then moved away. No. 44 (19/3/05). The male removed his leg from the female's rump and stood a little to her right. Still biting the female, he shivered violently shaking the female at the same time. He released his bite and she moved 20 cm away with a slightly arched tail. On one occasion there was a completely different type of separation and here there may have been some influence from the near presence of the observer. The lizards remained joined for 10 - 15 sec. after first observation. The male then got off the female and turned around to face the opposite direction. He then pulled himself free and ran off hissing. No. 18 (3/12/96). One other separation (No. 8) took place with almost no shaking, the female seeming to slip forward without difficulty.

On four occasions liquid containing white suspended matter flowed down the wall from the lizards during or at the end of copulation. This is thought to be a mixture of semen and urine from the female's cloaca. Ten copulations were timed accurately enough to be meaningful. The mean of these was 3 min. 2 sec. with the range 2 min. 18 sec. - 4 min .

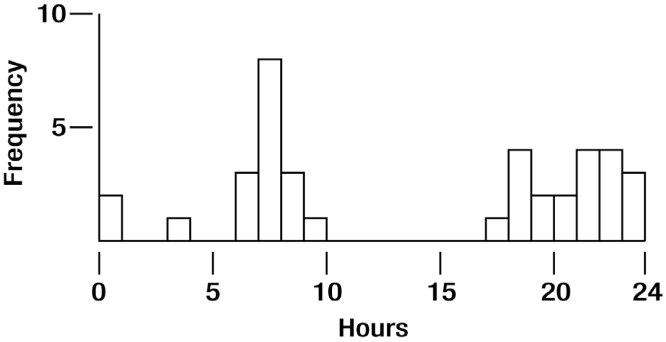

Fig. 1. Distribution of 36 copulations by hour.

Time of copulation

Figure 1 plots copulation as a function of time. There are only 38 observations, instead of 46, because the times at which eight copulations occurred were not recorded. During the period 1000-1800 h no copulation has been observed which is unsurprising for a nocturnal animal. For the next six hours (roughly sunset to midnight) 21 copulations were recorded, which is again unsurprising. Three observations for the next six hours is obviously low, but this coincides with the observer's period of sleep. The 15 observations (39.5%) in the period 0600-1000 h is remarkable for a nocturnal animal and points to a considerable amount of activity in these daylight hours. Figure 2 shows that the lunar cycle does not influence the timing of copulation.

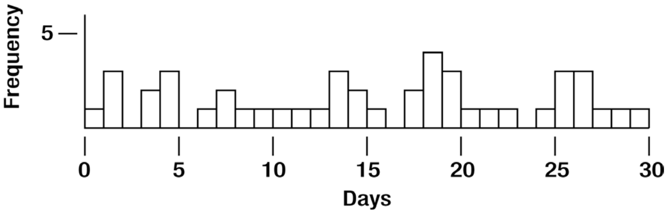

Fig. 2. Distribution of 46 copulations by day through the lunar cycle with Day 1 being the day of new moon.

Table 1 shows that the male usually chases the female after copulation, but there is in fact much variability. In case No. 10 the male bit the female twice while making the hissing sound and before running off. In No. 25 the male made the MC call just seconds after separation and

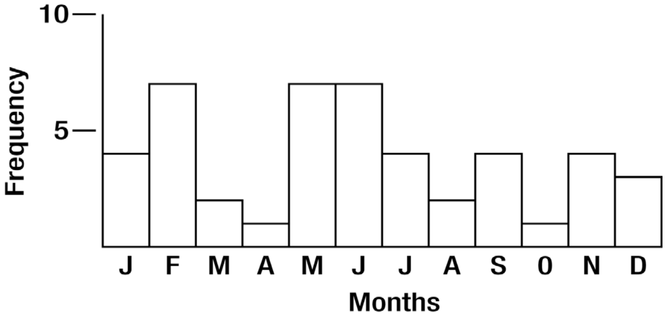

Fig. 3. Distribution of 46 copulations by month.

before licking his hemipenis. This same male, a minute or two later, caught his mate by the base of her tail and gave her a thorough shaking. Copulations 25 and 26 had taken place almost simultaneously with the two couples less than 2 m apart. One of the females ran close to male 25 when she was caught. It was probably his mate, but not certainly so, for I could not accurately keep track of what all four of the lizards were doing at the same time. After copulation 43 the female moved 3-4 m from the site with the male in pursuit. She eventually turned to face the male and tried to bite him. Then she gave the MC call and the male fled. She then uttered two "kek" calls before finally moving away. After copulation 45 the male remained at the site with his body turned around as though licking his hemipenis but I could not actually see this. The female, meanwhile, moved about 2 m off. After about 5 min. the male began tracking her, seemingly by scent, and came face to face with her. He fled behind a small electric oven and the female then gave the MC call. She later moved farther on with the male dallying about 50 cm behind for a while before ceasing to follow.

A failed attempt at copulation is also instructive. A male biting a tailless female on her neck came into view. He was trying to mount the female but kept slipping off as she moved forward. It seemed as though the absence of a tail deprived him of an anchor for his leg on her rump and he never made contact with her cloaca.

Which of his two hemipenes was licked by the male was noted for 22 of the 46 copulations. In 12 it was the left and in 10 the right. This means that on 12 occasions the male copulated from the female's right side and on 10 occasions from the left side. The difference is not statistically significant. ($x^2 = 0.18$, $P = 0.67$).There were only two occasions (33, 35) when the male adopted a "crossover" position, biting the female's neck just right of the mid-line but copulating from her left side.

Breeding Season

Fig. 3 shows that copulation has been recorded for all months of the year, so that there is no breeding season in the ordinary sense of the term. In other words, breeding is continuous.

Only one copulation has been recorded for October but there is other evidence of breeding in that month. On 18/10/02 a female was found on the floor obviously dying from injuries sustained in an accident of 2/10/02. Two hours later she was dead and examination showed she was gravid. The egg measured 16 x 11 mm, was still without a shell but probably close to laying. However, continuous breeding of the species does not mean that the female is always ready to accept the advances of the male. The following observation illustrates this. I heard the sound of a lizard falling to the floor and went to investigate. I found on the floor a dark individual I could recognize as Three-toed Sloth (TTS - named so because of missing fingers on his right hand) and known to be male. On the ceiling was another lizard I could recognize as White Patches (WP - so named for distinctive marks on the tail). TTS quickly ran up the wall and approached WP with the exaggerated, "humped up" stance I had assumed to be defensive. He then bit WP on the flank just rearward of the left arm and held on. WP was then off the ceiling and high up on the wall. He attempted to mount but WP would not co-operate. Together they moved down the wall and then, when near the bottom, up again. WP eventually struggled free and ran to a spot about 70 cm away. The time was 0626 h. I wrote up the observations and then went back to look for them. I found them again close together at the bottom of a nearby door. TTS bit WP, stepped back briefly and then bit her again and held on. He managed to transfer his bite to a point just right of the mid-line and rearward of the right arm. WP arched her tail and copulation followed (No. 33 in Table 1).

Egg deposition

Thecadactylus eggs are hard to find; I have found only one at the study site, on 19/2/90. It measured 14 x 13 mm and was buried in dry soil below the NE corner of the house. This site was searched again on 22/11/01 and 29/6/05. Neither eggs nor eggshells were found. Because I wanted dated eggs for determining the duration of incubation, I built a small retreat shaped like a Nissen hut that I thought might attract them as a laying site. They ignored it. Thinking they might lay in sand I got two circular biscuit tins and filled them with sand. On 26/1/01 I put them in the kitchen against the fridge where they would be seen. No egg was laid in them during the next 10 months. I tried again three years later with two plastic trays placed on the floor of the porch against the west wall on 1/7/05. To 6/2/06 no egg has been laid there.

On two occasions during the year 2005 the attic was searched for eggs but none was found. Eggs of *Gonatodes ceciliae* have been found in large clusters in clefts in limestone boulders in the Heights of Aripo. In searches with Stephen Smith which resulted in these finds no *Thecadactylus* egg was ever found.

Back in 1955 on 12 February four eggs were found in light soil at the base of one tree and one more egg at the base of another tree at the side of Serpentine road, St Clair. On 22 May that year two more were found at the base of a tree in the same area. Although Beebe (1944) collected "dozens of these geckos" the only egg he had was one laid by a captive specimen.

DISCUSSION

Humans evolved in the tropics and they breed all the year-round so it is easy for them to believe that tropical animals breed year round. However, this is not the case. In Brasil the neotropical skink *Mabuya nigropunctata* breeds in the dry season, August - December (Vitt and Zani 1997) while in Trinidad it breeds in the period January - August (Quesnel 2005). The iguanid *Tropidurus plica* also breeds from February to August in Brasil (Vitt 1991). However, *Anolis trinitatis* (Gorman and Licht 1975) and the gecko *Gonatodes vittatus* (Quesnel 1957) in Trinidad breed year-round. The data presented above indicate that *Thecadactylus rapicauda* also breeds year-round. However, continuous breeding of the species does not mean that the female is always ready to accept the advances of the male, as the observation on TTS and WP illustrates.

It is clear from the final outcome that TTS made the correct assessment of WP's physiological condition in his initial bite. Why then did they not mate on his first try? One possibility is that WP may have been a virgin about to experience her first sexual encounter. She may simply have reacted to what was new. If she was not a virgin it may be that a certain amount of learning is required before events proceed smoothly. Van Lawick-Goodall (l97l) gives a vivid description of how different the first sexual encounter of a virgin chimpanzee can be from subsequent ones. Chimps are not reptiles but there may be something common to both in this situation. Anyway, the fact that this "experimental" bite is there in the male's repertoire suggests that the female's physiological state varies in a patterned way in each individual and provides each individual with its own breeding season.

In this species the clutch size is one. Of the four eggs collected on 12/2/55, two hatched on the same day (15/5/55) leading me to believe for a long time that the clutch size is two. This is disproved by the captive female that laid one egg in her vivarium (Beebe 1944) and by the presence of just one egg in the oviduct of the specimen I dissected on 18 October, 2002 (see above). It is likely that the female is unreceptive to the male during the early development of the egg. She would then become receptive as the optimum time for fertilization approached and remain so until the egg had acquired its shell. The 'experimental' bite of the male is his means of determining when this state has been achieved.

WP was described and named on 4/3/01 nine months before she was seen in the incident of 2/12/01 which was described earlier. On three subsequent occasions her post-copulatory behaviour was witnessed in copulations 36 of 2/2/03, 38 of 24/7/03 and 39 of 13/11/03. The last record of her was on 4/2/04 so she had been under observation for a period of 2 years 11 months. Not enough of her copulations were seen to establish a pattern of egg laying (assuming a close connection between insemination and egg laying), but it does seem very possible that the first of her copulations that was seen was actually her initiation to sex.

Table 1 records that the hiss sound was heard at some stage in 21 of the 46 copulatory encounters, one (No. 1) before copulation, three times both before and after and 17 times only after copulation. It is not always possible to know which lizard makes the sound. It is likely that the sounds made before copulation come from a reluctant female. The ones made after copulation can come from either sex. Of the eight calls where one could be sure of the author, two were from females and six from males. Of the two females, one called at separation, the other running away after separation. Of the males, one (No. 18 - see above) hissed on separation, the others all hissed while chasing females.

Animals that do not live in groups (flocks or herds) seem to find close contact with others of their kind stressful, and they avoid it. The fact that 21 of 46 matings generated hissing protests (cries of annoyance) suggests that in this species courtship does not suppress all aggressive behaviour. For the duration of copulation aggression is suppressed, but once that is over aggressive tendencies come flooding back stimulated by the proximity of the protagonists, hence the biting and hissing.

Ten of 22 males copulated from the female's left and twelve of them from the right showing no statistically valid preference for one or the other. Had I learnt much earlier what I recently learnt, that cats like humans are either left or right-handed (pawed), I would have paid much more attention to this aspect of the behaviour of *T. rapicauda.* Yehudah Werner (pers. comm.) has reported that handedness does in fact occur in reptiles. For two reasons, *T. rapicauda* would make a good candidate for the study of this phenomenon in lizards: 1). The hiss that occurs so often at the end of copulation alerts the observer to the fact that copulation may have occurred. 2). The licking of the hemipenis which always occurs after copulation indicates from which side of the female it has taken place. The problem then boils down to collecting enough data on identifiable individuals to obtain a statistically significant result. For me the most surprising aspect of the behaviour is the violent shaking that accompanies separation of the mating animals. At first I considered that this was necessary to liberate the hemipenis from the female's cloaca, but the six variations described earlier argue against this simple postulate. It seems that sometimes the male removes his leg from the female's rump so that he stands to one side. In this case either the hemipenis is already free or it is still locked within the cloaca and stretches as the male gets off. I have found it impossible to see the hemipenis at this time and believe that a stretch of such a length may be impossible. If so, the hemipenis would already be released, so what then is the function of the violent shake? The shake always affects the male but not always the female. It usually (always?) occurs before he stops biting the female so it is an unlikely signal of release. So why does it occur? I have no satisfactory answer. Perhaps the "impossible" stretch is possible. The male of copulation 18 who pulled away without shaking (see above) did seem to be stretching something. Perhaps the shaking does shake loose the inserted hemipenis. This implies spines in the hemipenis such as some snakes have (Bellairs 1960), but it has not been possible to investigate this adequately.

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Reviewers – Living World 2006

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An Identification Guide to the Spider Families of Trinidad and Tobago, West Indies

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Spiders are in the order Araneae in the arthropod class Arachnida. There are about 35,000 known species worldwide (Levi and Levi 2002). They are diverse, adaptable and found on all the continents except Antarctica.

Spiders have two body sections; a cephalothorax and an abdomen. They possess four pairs of legs, all attached to the cephalothorax. Spiders also possess a pair of pedipalps, which resemble small legs, anterior to the forelegs. In females the tips of the pedipalps are simple, while in the male they have a complex structure.

Spiders are placed in two major groups, Mygalomorphae and Araneomorphae, according to the range of motion of the chelicerae. In Mygalomorphae the chelicerae are parallel to each other and exhibit an up-and-down action; tarantulas (Theraphosidae) are the most familiar. However, if they oppose each other and exhibit an open-and-close action, they are placed in Araneomorphae (Fig. 1). Body lengths given refer to adult females: minute <3 mm; small 3-6 mm; medium 6-12 mm; large 12-25 mm; very large >25 mm.

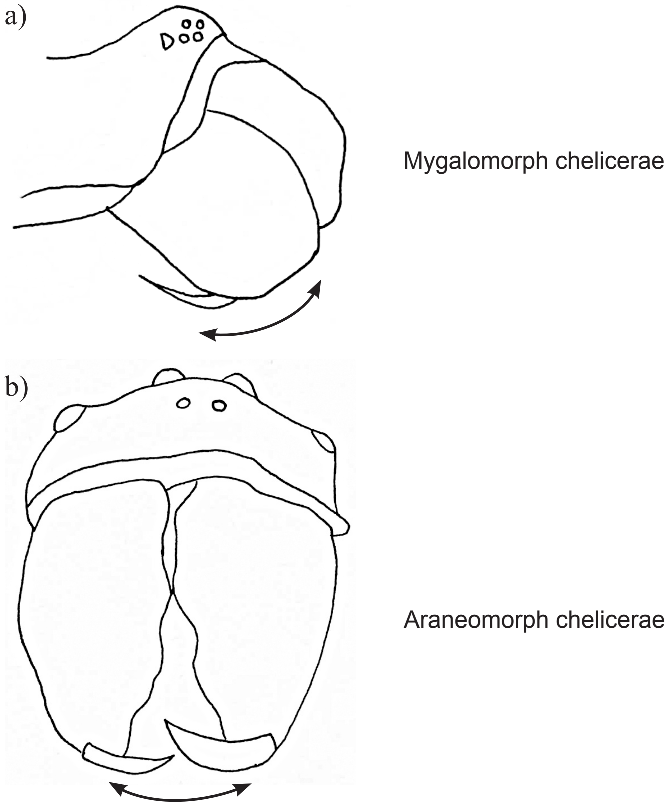

Fig. 1. Diagram of the chelicerae for (a) *Ischnothele caudata* – representative of mygalomorph spiders and (b) *Nephila clavipes* – representative of araneomorph spiders. Arrows show the range of motion of the chelicerae for both spider groups.

Legs are numbered with roman numerals to indicate the exact pair of legs being referred to in the description, starting with those closest to the head (Fig. 2). For example, tarsus IV refers to the tarsus of the hind legs. Another characteristic used to identify families is the number and shape of the spinnerets or silk producing organs (Fig. 3).

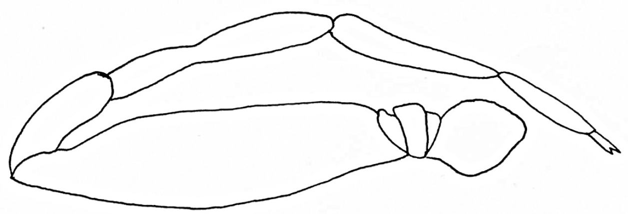

Fig. 2. Diagram of spider leg

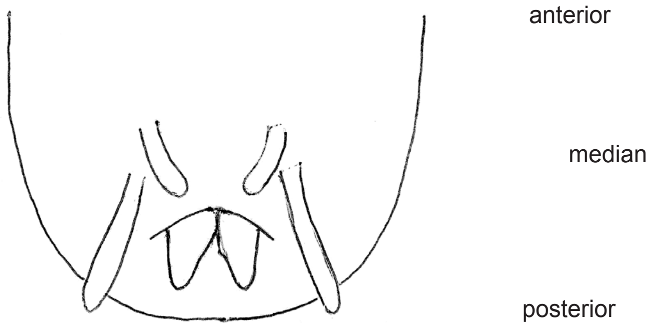

Fig. 3. Diagram of general placement of anterior, median and posterior spinnerets of spider (ventral view of abdomen).

Sewlal and Cutler (2003) and Cutler (2005) listed a total of 42 spider families known to occur in Trinidad and Tobago and an additional 12 that might be found based on their presence in nearby South America. The Table in this paper lists many of the defining characteristics for each family known to occur in these islands compiled from Levi and Levi (2002); Nentwig (1993) and Kaston (1972), some of which can be seen with relative ease using a hand lens

(X10), for example, eye patterns. But not all eye patterns can be used as a defining characteristic since some are repeatedly found throughout many families. Therefore, I have included in the Appendix only the eye patterns of families for which they are characteristic.

Most of the defining characteristics of a family can only be seen under a high magnification (X40). In the following Table these characteristics are marked with an asterisk for example claws and claw tufts (Fig. 4). So it should also be understood that the user will not be able to obtain definite identifications in the field for some families. Also, field identifications should be confirmed by microscopic identifications at a later time. Some of the more common families found in Trinidad and Tobago are illustrated in the Plate.

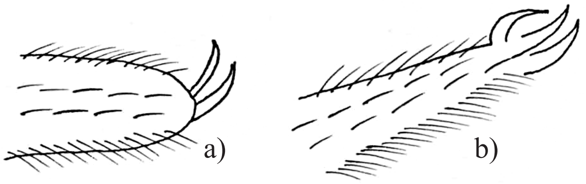

Fig. 4. Enlarged portion of tip of tarsus showing, (a) two claws and (b) three claws.

GLOSSARY

Physical structures:

Anal tubercle – appendage located above posterior spinnerets.

Bipartite – refers to a form of the cribellum which has a parting in the middle.

Calamistrum – a dense row of curved spines on the dorsal side of metatarsus IV.

Cribellum – a spinning plate placed in front of the spinnerets and covered with thousands of silk spigots.

Colulus – slender and pointed appendage found between and in front of anterior spinnerets.

Epigastric furrow – groove joining lung slits on ventral side of abdomen; the epigynum on female spiders is located towards the middle of the epigastric furrow.

Epigynum – a sclerite associated with the reproductive openings of female spiders.

Kleptoparasite – a spider that lives in the webs of other spiders (host) and gets its food by stealing or scavenging from the host spider.

Labium (lower lip) – found under the mouth opening.

Procurved – refers to eye pattern where the eyes at either end of a row are further forward than those in the middle.

Rebordered – possess a thickened edge.

Recurved – refers to eye pattern where the eyes at either end of a row are further back than those in the middle.

Spigot – an opening through which liquid silk is forced through. Each spigot has a valve which controls the thickness and speed of the silk.

Scutum (plural: scuta) – a hard, sclerotized, often shiny plate usually located on the abdomen.

Trichobothrium (plural: trichobothria) – very fine, long hair extending out at right angles from leg which is also sensitive to airborne vibrations.

Web types:

Trapdoor – burrow with a moveable, flat silken lid.

Orb – flat circular web. Silk woven to form a series of concentric circles and divided into sectors.

Space or tangle – consists of a network of silk threads which form no discernable pattern.

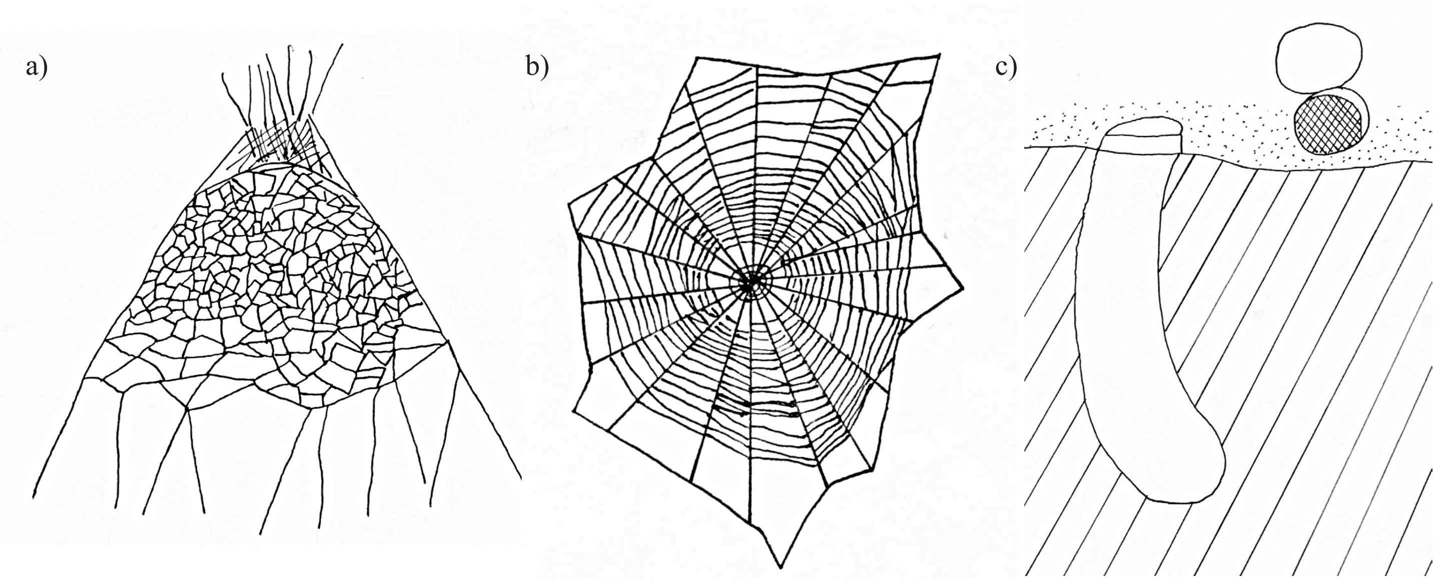

Fig. 5. Diagram of representative web types: (a) domed tangle web of *Physocyclus globosus*, (b) Orb web, and (c) burrow of a trapdoor spider.

Sheet – a mesh of silk threads woven into a flat sheet, the shape of which can vary.
Tube – a cylindrical sheet web.
Funnel – a conical sheet web held in place by numerous silk support threads.
Retreat – this is a web feature but used in this context to aid in identification. It is a silken tunnel sometimes covered with leaves or debris.

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Table 1.

MYGALOMORPHAE

Family	Body Length	No. of Eyes	Spinnerets	No. of Claws	Cribellum/ Calamistrum	Web Type	Distinctive Features
Actinopodidae	Large	8	4 short and blunt	3	No	burrow	Very large bulbous chelicerae. Eyes occupy >50% of head width (Appendix 1).
Cyrtaucheniidae	Large	8	4 long	3	No	burrow	Eye pattern (Appendix 1).
Dipluridae	Minute to very large	8	4	3	No	funnel	Posterior spinnerets are long, may be more than $^1/_2$ length of abdomen.
Theraphosidae	Large to very large	8	4	2	No	Burrow, sheet in some species	Very heavy. Distinct maxillary lobe.

ARANEOMORPHAE

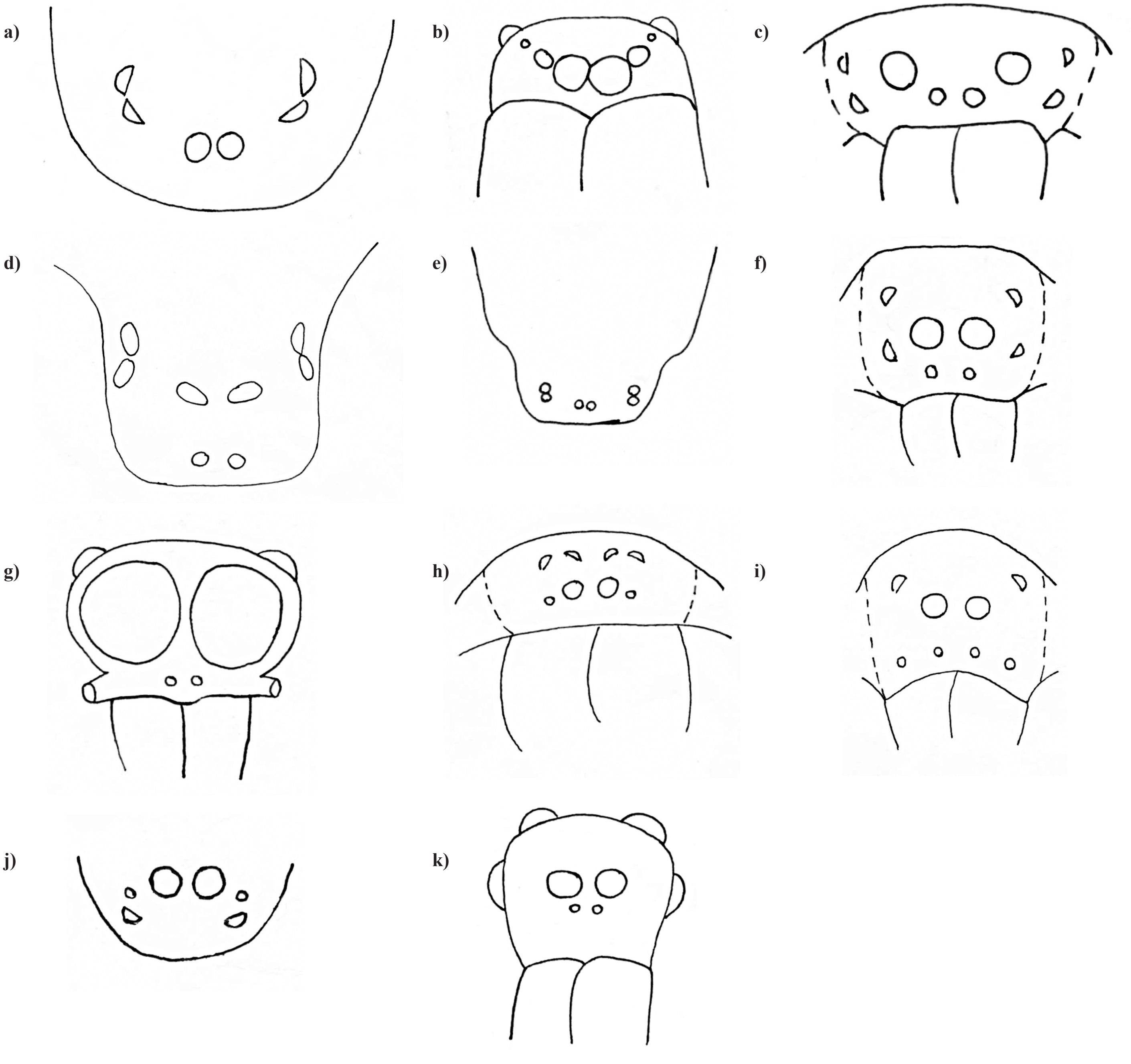
Family	Body Length	No. of Eyes	Spinnerets	No. of Claws	Cribellum/ Calamistrum	Web Type	Distinctive features
Agelenidae	Medium to large	8	6 posterior ones long	3	No	funnel	Webs. *Tarsi with single row of trichobothria that decrease in length towards the end of the tarsus.
Anapidae	Minute	6	6	3	No	orb	In females the last segment of the pedipalps is absent. Possesses armour plates
Anyphaenidae	Medium	8	6	2	No	retreat	Tracheal spiracle between spinnerets and epigastric furrow.
Araneidae	Small to very large	8	6	3	No	orb	*Femora without trichobothria.
Caponiidae	Small to medium	2, 4, 6 rarely 8	6	2	No	retreat	Cephalothorax is orange to pale tan. Abdomen is grey with distinct bluish or greenish tinge.

Clubionidae	Medium	8	6	2	No	retreat	Anterior spinnerets are conical and contiguous. Pale bodied grey to yellow.
Corinnidae	Medium to large	8	6	2	No	none	Many species resemble ants and multillid wasps.
Ctenidae	Medium to very large	8	6	2	No	none	Eye pattern (Appendix 1).
Deinopidae	Medium to large	8	6	3	Yes	orb	Eye pattern (Appendix 1).
Gnaphosidae	Small to large	6	6	2	No	tube	Anterior spinnerets are the longest, cylindrical and well spaced. Eye pattern (Appendix 1).
Linyphiidae	Small to medium	8	6	3	No	sheet	*Femoral spines present.
Lycosidae	Small to large	8	6	3	No	tube in some	Eye pattern (Appendix 1). *Median claw smooth or with single tooth.
Mimetidae	Small to medium	8	6	3	No	none, but occupy webs of prey	*Diagonal rows of spines on metatarsus and tibia I and II.
Miturgidae	Medium	8	6	2	No	retreat	*Leg claws 2 or 3. Legs I longer than IV.
Mysmenidae	Minute	8	6	3	No	orb but can be klepto-parasite	Males have spur on metatarsus. *Females have ventral spot on femur I.
Nesticidae	Small to medium	8	6	3	No	space	*Comb of hairs on last segment of legs IV. *Rebordered labium.
Ochyroceratidae	Minute to small	6	6	3	No	space	Resemble Pholcidae. Mottled purple colouration.
Oecobiidae	Minute	8	6	3	Yes	space	Large hairy anal tubercle.
Oonopidae	Minute	6	6	2	No	none	Eye pattern (Appendix 1). Some species have prominent dorsal and ventral scuta.
Oxyopidae	Small to large	8	6	3	No	none	Eye pattern (Appendix 1). Very prominent spines on legs.
Palpimanidae	Small to medium	8	6 only 2 visible	2	No	none	Legs I thick and held up when walking.
Philodromidae	Small to medium	8	6	2	No	none	Body flattened or elongate. Legs II longest.
Pholcidae	Minute to large	6-8	6	2	No	space	Eye pattern (Appendix 1 shows the eye pattern commonly encountered in this family although other patterns occur). Very long thin legs.

Pisauridae	Medium to large	8	6	3	No	large sheet or dome webs	Some species associated with water surface. Eyes of equal size.
Prodidomidae	Medium	8	6	2	No	none	Chelicerae held far apart.
Salticidae	Minute to large	8	6	2	No	retreat	Eye pattern (Appendix 1).
Scytodidae	Small to medium	6	6	3	No	space	Strongly elevated spherical cephalothorax.
Selenopidae	Medium to large	8	6	2	No	none	Eye pattern (Appendix 1). Flat body.
Senoculidae	Medium to large	8	6	3	No	not known	Eye pattern (Appendix 1).
Sicariidae	Medium to large	6	6	2	No	a few strands of silk which may accumulate with time (not used for hunting)	Eye pattern (Appendix 1).
Sparassidae	Medium to very large	8	6	2	No	none	Colulus absent. *Trilobed membrane at end of metatarsus.
Symphytognathidae	Minute	4 or 6	6	3	No	orb or klepto-parasite	Chelicerae fused. Females have no pedipalps or just basal segment.
Synotaxidae	Small to medium	usually 8	6	3	No	sheet	Elongate body. Long thin spineless legs. Sheet web pattern resembles "chicken wire".
Tetragnathidae	Small to very large	8	6	3	No	orb	Large chelicerae. Epigastric furrow procurved. Femora with trichobothria.
Theridiidae	Minute to medium	usually 8	6	3	No	space	Comb of hairs on last segment leg IV (often reduced in males). *Labium not rebordered.
Thomisidae	Small to medium	8	6	2	No	none	Colulus present. Hold legs crablike and walk sideways.
Theridiosomatidae	Minute	8	6	3	No	orb up at centre to form a cone	Femur I is 3 times thicker than IV. No spines on legs.
Uloboridae	Medium	6 or 8	6	3	Yes	orb	Legs I and II longer than others.
Zodariidae	Small to large	8	>2	3	No	none	Anterior spinnerets are the longest, others may be minute.

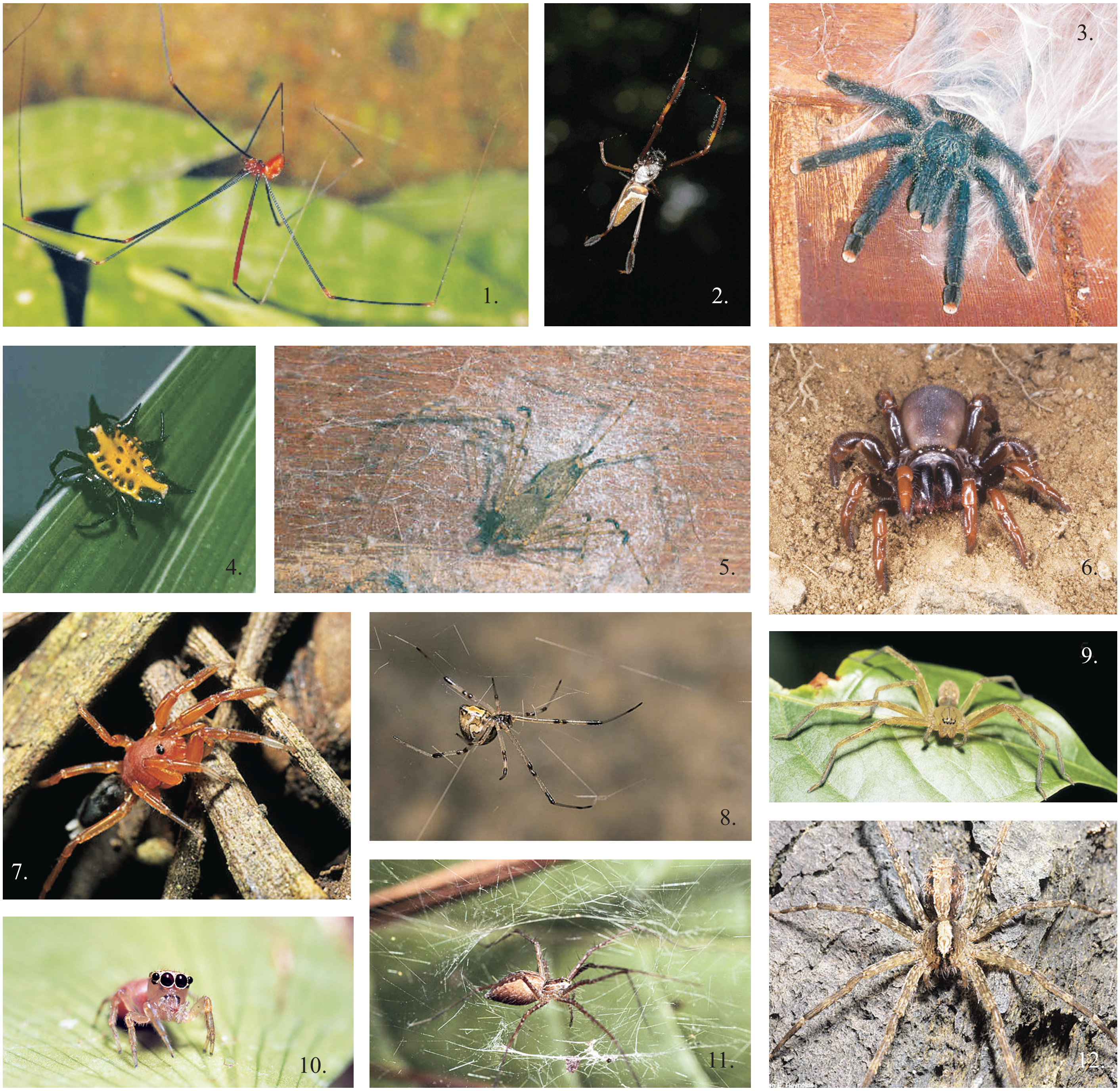
Appendix – Eye patterns of spider families for which they are distinctive features.

Mygalomorphae: (a) Actinopodidae (top view) and (b) Cyrtaucheniidae (top view).



Araneomorphae: (a) Pholcidae (top view), (b) Salticidae (front view), (c) Selenopidae (front view), (d) Senoculidae (top view), (e) Sicariidae (top view), (f) Ctenidae (front view), (g) Deinopidae (front view), (h) Gnaphosidae (front view), (i) Lycosidae (front view), (j) Oonopidae (front view) and (k) Oxyopidae (front view).

Plate – Photographs of representatives of some of the most common families found in Trinidad and Tobago.



1. *Mesabolivar aurantiacus* – Pholcidae (Photo: A. W. Hook)
2. *Nephila clavipes* – Tetragnathidae (Photo: J. Abbott)
3. *Avicularia avicularia* – Theraphosidae (Photo: C. K. Starr)
4. *Gasteracanta craniformis* – Araneidae (Photo: C. K. Starr)
5. *Scytodes longipes* – Scytodidae (Photo: C. K. Starr)
6. *Actinopus* sp. – Actinopodidae (Photo: M. Kuntner)
7. Caponnid – Caponnidae (Photo: B. Reynolds)
8. *Latrodectus geometricus* – Theridiidae (Photo: B. Reynolds)
9. *Olios* sp. (Photo: B. Reynolds)
10. Amycus – Salticidae (Photo: B. Reynolds)
11. Pisaurid in web – Pisauridae (Photo: B. Reynolds)
12. Wandering spider – Ctenidae (Photo: B. Reynolds)

Nature Notes

Trinidad's Leaf Shoemaker is *Zaretis ellops* (Ménétriés), not *Z. itys* (Cramer) (Nymphalidae)

Willmott and Hall (2004) examined museum material from several major collections, and concluded that the genus *Zaretis* comprises six species, four of which are very similar. This group of four similar species includes that known in Trinidad as the leaf shoemaker, *Zaretes* (a mis-spelling of *Zaretis*) *isadora* (Cramer) (Kaye 1921) or *Anaea itys* (Cramer) (Barcant 1970). Barcant (1970) followed the treatment current at that time, i.e. *isadora* is a synonym of *itys*. Willmott and Hall (2004) include Trinidad in the distribution of only one of these four similar *Zaretis* spp.: i.e. *Z. ellops* Ménétriés. I have examined the material in my collection (2 males and 2 females) and A. Hall's collection at the Booth Museum, Brighton (4 males, 6 females, treated as *Z. isadora ellops* and *Z. isadora strigosa*) and consider that all represent *Z. ellops* as characterized by Willmott and Hall (2004).

Zaretis ellops; above female, Symonds Valley, x-xii.1920, A. Hall.; below male, St Anns, xi-xii.1931, A. Hall (For each figure: UPS left, UNS right. Specimens in Booth Museum).

Nevertheless, two other species of the group could occur in Trinidad, *Z. itys itys* and *Z. isadora*. In addition to small differences in wing shape, in both these species, the apical markings forewing UPS are darker, and the basal part of the wings UPS and UNS contrast more with the discal areas. However, these differences are much more marked in *Z. itys*, and I think it most unlikely that this species could have been overlooked by Trinidad collectors.

The detailed biology of the different species needs clarification in light of Willmott and Hall's (2004) treatment of species, i.e. which larval descriptions, illustrations and food plants match which species. Barcant (1970) does not record any food plant for the leaf shoemaker in Trinidad (but see below). However, Margaret E. Fountaine did rear this species (as *Z. isadora*) while in Trinidad (Cock 2004). Unfortunately this is not one of the species which she included in her sketches of early stages from Trinidad (M. E. Fountaine unpublished; M. J. W. Cock in prep.), but she does illustrate a larva (p. 65, No. 235, June 18th 1929) and pupa (p. 66, No. 235a, July 10th 1929) on *Casearia* sp. (as *Casearea* sp.; Flacourtaceae) collected at Belem, Brazil. Since she normally only illustrated each species once in her sketchbooks, by implication she considered the material which she reared in Trinidad to be the same. Local collectors in Trinidad are aware that *Casearia sylvestris* (wild coffee) and perhaps other *Casearia* spp. are food plants (J. O. Boos pers. comm. 2005), but this has not been documented.

Janzen and Hallwachs (2006) have reared *Z. ellops*, *Z. isadora* and *Z. itys* in Costa Rica, and show the early stages of *Z. ellops* and *Z. itys*. All three species feed on *Casearia* spp.: *Z. ellops* prefers *C. arguta* and *C. Nitida,* whereas *Z. isadora* and *Z. itys* prefer *C. arborea.* The larvae and pupae of these two species and those painted by M.E. Fountaine (unpublished) are all similar. Miss Fountaine's paintings are closer to those of *Z. itys* than *Z. ellops*, but the posterier end of Miss Fountaine's caterpillar is more deeply divided and widely flared than for either species illustrated by Janzen and Hallwachs (2006), and so may represent *Z. isadora* as Miss Fountaine labelled them."

Barcant (1970, p.107) gives no food plant for the leaf shoemaker (his "*Anaea itys*"). However, in the previous entry for the flamingo, *Fountainea ryphea ryphea* (Cramer), (Barcant's "*Anaea ryphea ryphea*"), he lists *Casearia ramiflora* (a synonym of *C. guianensis*, pipe wood), which as I have pointed out (Cock 2004) is an error since the normal food plant for the flamingo is *Croton gossypifolius* (Euphorbiaeae). It seems clear now that Barcant's reference to *Casearia ramiflora* was misplaced in his text, and should have referred to the leaf shoemaker.

Willmott and Hall (2004) do not rule out the possibility that *Z. ellops* may be a synonym of *Z. isadora*, recognising that wing shape, colour and markings are variable in these species, and the importance of seasonal variation is far from clear. The fact that only *Z. ellops* seems to occur in Trinidad, supports their separation of this species. Furthermore, detailed observations on life history and field biology may throw more light on relationships within this confusingly similar group of species. For this reason, detailed observations of the life history of *Z. ellops* in Trinidad would be a useful contribution.

I thank Gerald Legg, Booth Museum of Natural History, Brighton, for facilitating my visit to examine A. Hall's collection, and the Natural History Museum, London, for access to the unpublished sketchbooks of Margaret E. Fountaine.

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Observations on Nesting Activity of Caimans at Two Ponds in the South Rupununi Savannah, Guyana

I live in the South Rupununi Savannahs. Average annual rainfall at Mountain Point is about 111 cm, most of which occurs from April-May to September and followed by a long dry season. The vegetation in the area is generally xerophytic. Not far from my house, about 200 m away, are two ponds: one is about 150 m in diameter and about 1.5 m deep and a second larger one is about 355 m in diameter and about 3.5 m deep. About three km away is the Sawariwau River where caimans, Black and Spectacled, are known to be present.

I have been living in this area for 28 years. I have one confirmed sighting of a Black Caiman at my location and I have seen another species, probably a Spectacled Caiman. Although I had noted caimans in the ponds, I had not seen signs of egg-laying. In November, 2000 I found one caiman egg in a sandy depression on the banks of the smaller pond and about 10 baby caimans in the pond, but the parents were not seen.

In November, 2002 about 5:30 pm an adult caiman was seen apparently moving from the larger pond towards a "bush island" which is about 500 m from the pond and about 150 m from my house. The identical observation in time and place was noted on 2 November, 2004. On 5 November, 2005 at about 5:30 pm and at the same spot where the previous observations were made, my dogs began to bark and on checking I saw a white flat object tossed in the air. It was a juvenile caiman and alive. Its narrow head and snout was estimated to be 13 cm, 30 cm trunk (its tail was hidden in the grass) and circumference at 25 cm. It was possible that it hatched in the "bush island" and was heading to one of the ponds.

On the first two occasions I was unable to follow the caiman to its destination. The larger pond is well-populated: 13 pairs of caiman eyes have been "shone" at night! During the dry season the smaller pond becomes dry, but it takes a severe drought for the larger pond to become dry. Since both ponds are well-populated with fish there is a ready and abundant supply of food to support a permanent group of caimans. However, in severe drought conditions as the larger pool dries the fish die and the caimans disappear. A caiman skeleton was found in the bush island several years ago. Re-population of the ponds with fish and caimans can only be by migration from the river when the savannahs are in flood during the rainy season. It would seem that once there are caimans in the pond the migration in November is prior to egg-laying in the shelter of the bush.

Shirley Humphrys
Chaakoiton, Mountain Point
Via Lethem
S. Rupununi, Guyana

A New *Trigonopsis* (Hymenoptera: Sphecidae) Record for Trinidad, West Indies

Trigonopsis is a neotropical genus of rarely encountered sphecid wasps that includes 16 species (Vardy 1978), three of which were known from Trinidad (Callen 1990; Starr and Hook 2003). These secretive wasps are striking in appearance in having a very polished integument, a prognathous and triangular-shaped head bearing long, slender mandibles, a prolonged pronotum, and a petiolate gaster (abdomen). They come in two color forms, metallic blue or black with a red abdomen. These wasps construct mud cells, which are attached to the undersurface of leaves, rock surfaces, and rootlets of fallen trees or rootlets exposed under overhanging dirt banks. Most species provisioned their nests with paralyzed cockroaches, and nests generally consist of a few to several cells. Although many species may be solitary, communal nesting has been documented in *T. cameronii* (Eberhard 1974).

During my recent sabbatical in Trinidad I collected two females of *Trigonopsis cooperi* Vardy on the southern side of the Northern Range of Trinidad. Their label data are as follows: Caura Valley, N10.688˚, W61.371˚, 28.VIII.2004, and Caura Valley, N10.705˚, W61.368˚, 27.I.2005. Elevation at both collection sites were slightly over 200 m. Previously this species was known from only 7 localities in Brazil and Ecuador (Vardy 1978). These two specimens represent a fourth species of *Trigonopsis* in Trinidad, and the first record of this species north of the Amazon River, or a range extension of over 900 km. Voucher specimens have been placed in the Brackenridge Field Laboratory Insect Collection of the University of Texas at Austin and in the Insect Collection of the Department of Life Sciences, University of the West Indies, St. Augustine, Trinidad.

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The Possibility of Naturalisation of the African Giant Rat (*Cricetomys gambianus*, Waterhouse 1840) in the Caribbean

The African giant rat or the Gambian pouched rat, *Cricetomys gambianus* [Rodentia: Nesomyidae] is the world's largest nocturnal rat and native to Africa, many thriving in urban settings. Notes on the behaviour and domestication of this rat have been published (Cooper 1998, 1999, 2000). Females normally produce four litters every nine months with up to six pups in each litter (Cooper 2000). Studies have shown that the rat is physiologically adapted to burrowing habits within cool environments (Knight 1988).

The African giant rat, being predominantly vegetarian, can be destructive to vegetable gardens and will readily eat fruits and bulbs, and is particularly fond of avocado pears, mangoes and guavas (Smithers 1975). Vegetable items, oil-palm nuts and kernels, insects, and vertebrate flesh and scales have been found in the guts of this rat (Iwuala *et al.* 1980). Growth performance of these rodents is high with protein intake of 13% (Ajayi and Tewe 1978). The Caribbean provides a nutritionally ideal habitat for this species.

This rat is highly intelligent and it has been used extensively to sniff out mines in former war-torn countries (Mott 2004). There has also been a growing interest in keeping the rat as an exotic pet, hence facilitating its widespread distribution. Some have inevitably escaped and established themselves on the Grassy Key in Florida and scientists are concerned that they may compete with native species, carry diseases and damage the bird population by eating eggs (Epperson 2005). They could easily interfere with bird nests, as they are particularly good tree climbers (Cooper 1998). Others have discussed the possible spread of diseases like *Angiostrongylus cantonensis*, the rat lungworm which has been detected in the Caribbean (Prociv *et al.* 2000; Sithithaworn *et al.* 1991). Some articles suggest that the emergence of Human monkeypox in the U.S.A. is due to rodents (Di Giulio and Eckburg 2004). A Rickettsiale *Grahamella kaniae* has been found in giant rat blood (Gretillat *et al.* 1981).

Shipping has facilitated the apparent introduction of this species into the Caribbean. Given favourable climatic conditions, vegetation and habitat in the islands, the rat has the potential of rapidly reproducing and encroaching on the natural flora and fauna, including marine and coastal habitats. Discussions with fishermen in Port of Spain, Trinidad, have revealed that the giant rat has indeed been seen on ships and boats (Cooper 2005/6 – personal observation). They characteristically identify the rat by its white-tipped tail and size. The original docking ports for the ships, however, are unknown and would need to be established. Additionally, the current population of this rat in the Caribbean must be investigated.

(Photo courtesy: Mr. A. Bickers)
Cricetomys gambianus, female, aged 2 yr and 9 months, weighing 1.5 kg; 95 cm long from tip of nose to tip of tail.

It is therefore advocated that appropriate screening procedures be set up to monitor the possible naturalisation of this species in the Caribbean. The establishment of strict protocols for the carriage of exotic pets on boats entering Caribbean ports should be enforced. Residents in the Caribbean wishing to keep this rat as a pet should be required to have a licence, which ensures proper vaccination and housing requirements.

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Web Height as a Niche Separator in Two Antillean Orb-weaving Spiders

Choice of foraging site is a critical decision for any sit-and-wait predator. For web-building spiders, which must invest heavily in spinning a web, this decision may be a semi-permanent one. Accordingly, we expect a given species to have fairly characteristic web and web-site features. In a comparison of several web parameters in nine orb-weaving species in Ghana, including one *Gasteracantha* sp. and one *Leucauge* sp., Edmunds and Edmunds (2001) found that each species-pair could be separated according to at least one parameter. Our purpose here is to consider just one parameter, height above the ground.

Leucauge sp. (Tetragnathidae) and *Gasteracantha cancriformis* (Araneidae) are widepread orb-weavers which are locally abundant in the Antilles (pers. obs.). In January, 2006 we found *Leucauge* sp. in abundance in gardens, open areas and lowland forests on Nevis, Lesser Antilles. On the same island *G. cancriformis* was common only in open areas, especially at the edges of secondary forest, where it was interspersed with *Leucauge* sp.

Although the two species differ in size – *G. cancriformis* is strongly sexually dimorphic, so that females are larger than those of *Leucauge* sp., while males are smaller than *Leucauge* sp. males – their webs

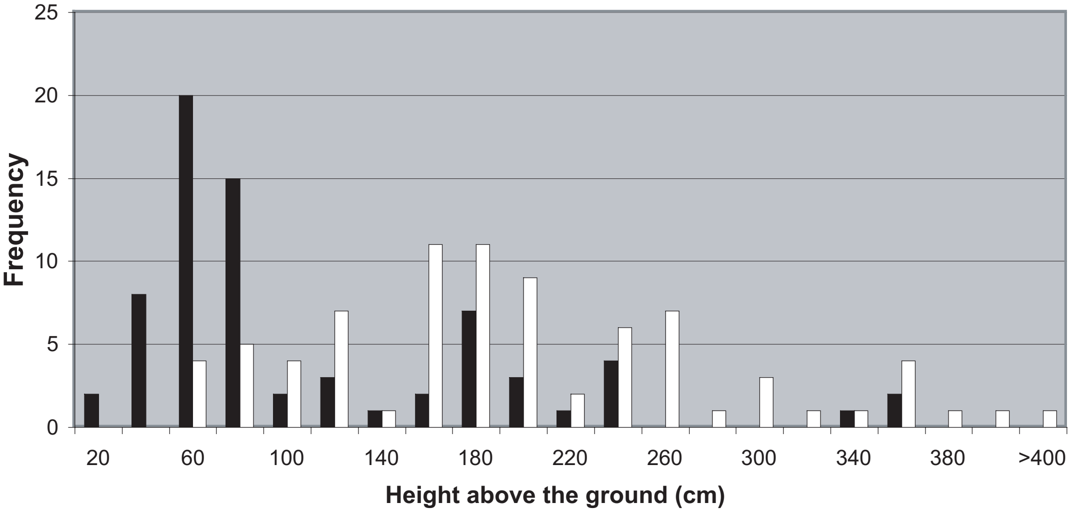

Fig. 1. Frequency of web heights of 71 female *Leucauge* sp. (black bars) and 80 female *Gasteracantha cancriformis* (white bars) in open areas near Gingerland, Nevis. The height of the hub is estimated to the nearest 20 cm.

are comparable in size, form and apparently in strength, and it is fair to assume that they are suited to capture similar arrays of prey, although those of *G. cancriformis* appear on average to be oriented closer to the vertical. This gives rise to the question of the ecological niche separation between them where they co-occur.

Under these circumstances, we might expect separation through the simple parameter of web height. In farmland in the Gingerland area, we estimated to the nearest 20 cm web heights of apparent mature and subadult females of both species as we found them, mostly along the edges of secondary forest.

As seen in Fig. 1, there is a substantial overlap between them. However, the mean web height of *G. cancriformis* (198 cm) is significantly greater than that of *Leucauge* sp. (111 cm; Mann-Whitney U test, $p<0.01$). This result is consistent with the hypothesis that web height by itself leads to differences in the array of prey captured.

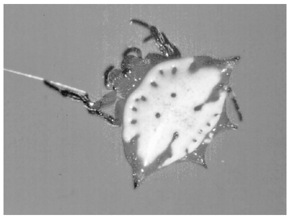
Fig. 2

G. cancriformis is quite variable in colouration, even at a single locality, so that it was long thought to comprise a number of distinct species (Levi 1996). Part of this variation is seen in the usually very large central pale area on the top of the female abdomen (Fig. 2). At least in the Lesser Antilles, this can be either white or bright yellow, not intermediate in our experience, and is strongly reduced in some individuals. In the Gingerland area we recorded 47 white and 30 yellow females, as well as three in which the abdomen was mostly black above. The adaptive significance, if any, of this polychromism is unknown.

Specimens of both species collected and identified by the authors on Nevis and deposited in the Land Arthropod Collection at the University of the West Indies will serve as vouchers. Support for this project came from the University of the West Indies and the Nevis office of the Ministry of Agriculture. Thanks also to Quentin Henderson and Pam Barry for local facilitation, Bruce Cutler for comments on the species, and John Agard for statistical advice.

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On the Food Plant of the Large Southern White Butterfly, G*anyra phaloe lamonti* (Kaye) (Pieridae)

Kaye (1919) described *lamonti* as a subspecies of *Pieris phaloe* Godart from specimens captured by Sir Norman Lamont at Morne Diable, 9.iv.1917. Barcant (1970) treats it as *Ascia buniae lamonti* and coined the common name "Large Southern White". Lamas (2004), in the recent checklist of Neotropical butterflies, places *phaloe* (with *buniae* as a synonym) in the genus *Ganyra* (previously treated as a subgenus of *Ascia*), and lists more than ten other subspecies from other parts of South America.

Ganyra phaloe lamonti appears to be a subspecies endemic to Trinidad. Barcant (1940) considers it to be a forest species restricted to the South of Trinidad, particularly the south-western peninsula and south central Trinidad (e.g. Morne Diable, Inniss Field, Quinam). More recent records also support this assessment.

Kaye (1921) includes the surprising statement "Larva on *bidens*" – surprising, because Pieridae are not recorded to feed as caterpillars on Asteraceae. Barcant (1970) does not include this information, perhaps because he considered it suspect. In view of our observations below, I believe that Kaye's food plant record is a transcription error for a reference to adults nectaring on *Bidens*.

On 17 May, 1999, Scott Alston-Smith and I observed a female *G. phaloe lamonti* at Inniss Field. The female was fluttering around a low growing plant in dappled sunlight within the light forest cover that prevails in that area. She showed typical ovipositing behaviour – alighting, taking off, fluttering, alighting again nearby, and appeared to oviposit once before flying away. On the leaves where we thought we had seen the female oviposit, we found two typical spindle-shaped pierid eggs. One, which we assume had just been laid, was yellow, but the other was orange and probably was some days older. The eggs were both laid in the middle of the leaf lamina on the upper surface of the leaf. We did not attempt to rear from these eggs. Closer examination showed that the plant was sprawling across the forest floor, and my herbarium specimen (No 259) was subsequently identified by Winston Johnson of the National Herbarium as *Steriphoma elliptica* Spreng. (Capparaceae).

Williams (1929) treated the Capparaceae (as Capparidaceae) in the Flora of Trinidad and Tobago: *Steriphoma elliptica* is a shrub or small tree, reported from Gasparee, Chacachacare, Philippine, near San Fernando. More recent records from the 1980s are from Cedros, Quinam Rd., Southern Range, and San Fernando Hill (Y. Baksh-Comeau pers. comm. 2006). The correlation with the distribution of *G. phaloe lamonti* in southern Trinidad suggests that a restricted distribution for its main or only food plant is a major explanatory factor for the distribution of this butterfly in Trinidad.

Cock (1984) reported the food plant of the congeneric *G. josephina janeta* (Dixey) (as *Ascia menciae janeta*) to be *Capparis odoratissima* (Capparaceae). Other records for this species across its range include other *Capparis* spp., and *Forchhammeria* spp. (Capparaceae) (DeVries 1987; Smith *et al*. 1994; Janzen and Hallwachs 2006). *Ganyra howarthi* (Dixey) feeds on *Atamisquea* (Capparaceae) in the Sonoran desert of California (Bailowitz 1988). Thus, Capparaceae are the only food plants recorded for the three recognised species of the genus *Ganyra*.

Now that a food plant is known, it would be of interest to record the full life history of *G. phaloe lamonti*, for possible comparison with other subspecies.

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BOOK REVIEWS

The Remarkable Life of William Beebe: Explorer and Naturalist

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C. William Beebe (1877-1962) stood out for many years as the most famous naturalist in North America, perhaps in the world, not just a respected public figure but a true celebrity. He was a formative influence on a great many young naturalists of the early 20th century. This fame continues today in durable, if muted form. One can even log onto "The Official William Beebe Web Site" – what can "official" possibly mean in this case? – at *http://members.aol.com/chines6930/mw1.beebe1.htm* for a fan's-eye view of his life and writings.

Like almost all serious naturalists, Beebe turned to natural history at an early age. He attended Columbia University, but did not graduate, preferring instead to join the newly established Bronx Zoo of the New York Zoological Society (NYZS) as assistant curator of birds. He early turned to tropical exploration and first visited Trinidad in 1908 and Guyana in 1909. Under Beebe's prodding and guidance, the NYZS established Simla as a research station in Trinidad's Arima Valley in 1949 after earlier stations in Guyana and Venezuela had been devalued by surrounding agricultural development and political instability.

Beebe's research had three main thrusts. He began as an ornithologist, doing taxonomic studies with a large biological component (see e.g. *Pheasants: Their Lives and Homes*). Establishment of field research stations, including Simla, was motivated by the belief that the tropical environment and its wildlife were best understood through long-term studies at fixed sites (e.g. *Tropical Wildlife in British Guiana* and *High Jungle*). And he is perhaps best remembered for his undersea exploration, including a series of descents to unprecedented depths in the bathysphere with its designer, Otis Barton (e.g. *Beneath Tropic Seas* and *Half Mile Down*). In these latter, Beebe and Barton were able to observe strange creatures never before seen alive and intact, if at all.

In his writings, Beebe was both engaging and extremely prolific, so that a bibliography occupies an entire book (Berra 1977). Berra lists 23 books and 821 articles by Beebe. Of the latter, about 100 are original research reports. His fame during his lifetime largely rested on an outpouring of popular articles that drew credibility from the fact that he was, after all, a scientist, not just a journalist reporting what others had found. Some of his many books – I am aware of 24 volumes of which he was author or editor – are compilations of these articles. It was an age of grand scientific explorations, complete with sizeable teams and voluminous baggage, just the sort of thing to fire the reading public's imagination. The hazards of tropical and marine field work were greater than they are today, although Beebe's narration of some episodes is sufficiently lurid that one suspects some exaggeration.

This kind of biology was and is relatively expensive, so Beebe had to exercise considerable political skills to gain the necessary funding. In this, he had advantages available to few other naturalists. He had the backing of the New York Zoological Society and of some very influential friends. Among these latter were former president Theodore Roosevelt and several millionaires with an interest in natural history. And the public popularity of his writings certainly strengthened his hand.

The scientific value of the deep-sea explorations and of much of Beebe's land-based work remains controversial. While the general public enthused, many contemporary biologists saw them more as adventures than research, and it must be admitted that Beebe is very little cited today as a source of new data. As an example, I have seen his paper on the ecology of the Arima Valley (1952) rarely cited even by biologists in Trinidad.

At the same time, Beebe was certainly a major contributor to new results in a different, indirect way. In promoting field stations to be utilized over time by a variety of researchers, he pioneered a new approach to the understanding of tropical plants and animals, one that relied on a deep entry into their environment. Similarly, his early studies of pheasants in the wild, for example, added greatly to the understanding of a group that was mostly known only from dead museum specimens. And his papers detailing the organisms to be found in four square feet (1916) and later of one-quarter square mile (1925) of forest leaf-litter in Guyana presented a radically new way to look at a microhabitat.

Unlike many other leading naturalists of his time, Beebe wrote no autobiography and strenuously objected to any suggestion that anyone else should undertake his biography. His personal papers went to Princeton University, where they remained sealed for many years. His reasons are not obscure. Beebe was very protective of his image, and as far as he was concerned, the abundant details of his life and activities in his books was all the public needed to know.

This wish that no one else should write his life has not been respected, and rightfully so. Robert Welker's (1975) intellectual/literary biography of Beebe is a strong, valuable book within its limitations. Welker could not see Beebe's personal papers and did not interview the many people alive who had known and worked with him, so that his sources extended very little beyond Beebe's published writings. In particular, there is next to nothing on family background and early years. Still, Welker took care not to reach beyond the evidence in interpreting Beebe's thoughts and character, and he was well qualified to assess Beebe's scientific legacy.

Now comes a second book-length biography that satisfyingly transcends these limitations. Carol Gould had access to the personal papers and the full co-operation of Jocelyn Crane, Beebe's closest scientific associate and successor as Director of Simla. Her treatment also benefits from interviews with Crane and others and various auxiliary unpublished documents. In addition, she presents a much more complete treatment of Beebe in the context of his many associates and the NYZS. This, then, is the definitive Beebe biography.

Even so, there are various types of biography, and this one makes no attempt to be all in one. In contrast to Welker's book, Gould's is only slightly a literary and hardly at all a critical biography. Rather, it is a straightforward, sympathetic, thoughtful and thorough account of Beebe's life and person. It is very close to the autobiography Beebe might have written if he had chosen to do so. In fact, this is very much an authorized biography, as Gould was chosen by Crane, who held the keys to the rich mass of unpublished material and the co-operation of Beebe's living associates.

Many of Welker's remarks about Beebe's personality and science were deeply resented by the latter's friends and admirers. While Gould – very much a Beebe admirer –presents a picture at variance with Welker's, she makes no attempt to directly dispute any of the criticisms. Gould's assessment of Beebe as a researcher is neatly summarized in the following passage (page 408):

"The effects William Beebe had on science, particularly deep ocean biology and neotropical ecology, are enormous and lasting. He made an effective transition between Victorian natural historian, content to collect and classify the natural world, and the modern experimental biologist, alive to the effects of its natural habitat and mode of living on every aspect of an animal's life."

In fact, I found no mention of Welker at all outside of the bibliography at the end of the book. When I asked about this, Gould told me that she had seen Welker's book as so very different in nature from her own that it was better to simply disregard it. Maybe, although many readers will likely find it surpassingly odd that she did not at least mention this earlier biography in her preface, if only to set it aside. And it would have been relevant to say more pointedly why the above quoted assessment is accurate and Welker's much less laudatory view is mistaken.

The book is physically very attractive, richly illustrated with photos, well organized and written in a clear, engaging style. In the early pages Gould indulges in some bits of purple prose – as, when treating the dangers of field exploration in the early 20th century, she writes of "paddling up plague-ridden rivers in Malaysia, and bushwhacking through malarial jungles in Borneo" [since when do rivers carry plague?] – but then settles down to a consistent narrative sobriety. The account of the worldwide 1910-11 expedition to study pheasants is especially gripping. The 37 chapters are grouped into four sections with focus on a) formative years, b) studies of birds, c) studies of marine life, and d) tropical ecology. The chapters on Simla will be of special interest to readers in Trinidad and Tobago.

In short, *The Remarkable Life of William Beebe* fills a long-standing need. At the same time, those with a serious interest in understanding Beebe's place in ecology and natural history will want to treat Welker's book as a valuable supplement.

As a final note, let me mention that it would be worthwhile if someone did a comparative treatment of Beebe and Raymond L. Ditmars (1876-1942), the herpetologist who joined the Bronx Zoo staff at the same time as Beebe and whose life and prolific writings show many parallels. (Disclosure: As a boy, I was much more a Ditmars than a Beebe fan.) Just a thought.

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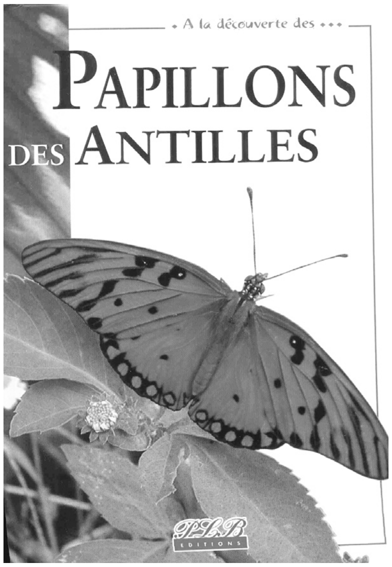

This little book presents (in French) the butterflies of Guadeloupe, Martinique and associated islands, with occasional reference to St. Bartholomew in the Virgin Islands. It covers 57 species: 13 Nymphalidae, 12 Lycaenidae, 12 Pieridae, 1 Papilionidae and 19 Hesperiidae, of which 11, 5, 12, 1 and 14 respectively also occur in Trinidad, although in several cases as different subspecies. Each species gets a one page summary, including comments on preferred habitat and observed food plants, and pictures of a pinned adult and a living adult. No less than 47 species have been reared and the early stages of these are also illustrated. At the back are two further pages illustrating pinned adults – new to Guadeloupe, or endemic subspecies. The illustrations are in full colour throughout.

It is of particular interest to see the early stages of the two species of *Junonia* side by side. *Junonia evarete* is the donkey's eye, one of Trinidad's commonest garden butterflies. The brown, patterned caterpillars feed on *Stachytarpheta*. In contrast, *Junonia genoveva* is restricted to mangrove swamps and adjacent areas, as the black caterpillars feed on black mangrove, *Avicennia germinans*. Although both species were described long ago, they have been treated as synonyms, and only recently confirmed as distinct. *Junonia genoveva* has not been formally reported from Trinidad, although it is present, and S. Alston-Smith (pers. comm. 2004) has found larvae.

I was particularly interested and appreciative that colour illustrations of the early stages are included. Comparisons of the food plants and early stages in Trinidad, particularly of species treated as distinct subspecies will be of interest. For example, I note that the caterpillar of the grass-feeding skipper butterfly, *Nyctelius nyctelius agari*, matches the one that I illustrated from Nevis (Cock 2001), but differs from that of ssp. *nyctelius* from Trinidad (Cock 2001, 2003); it seems likely that the larvae are consistently different for the two subspecies. Similarly, based on the picture of the caterpillar of *Astraptes talus* on *Mucuna urens*, I now believe that I have found, but not reared, larvae of this rather uncommon skipper butterfly on *M. rostrata* in Trinidad.

This book is a useful introduction to the butterflies of Guadaloupe and Martinique. It is not technical, and includes no references, but rather it is written for the amateur naturalist. It is very informative, yet leaves plenty of unanswered questions to encourage those interested to go out and fill the gaps. I obtained my copy on the internet from the amazon.fr website for 11 Euro plus postage.

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CONTENTS