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Subscriptions: Year 2021 (Volume 61): 450 €
http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php
Previous volumes (2010-2020): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France
ISSN 0044-586X (print), ISSN 2107-7207 (electronic)

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under
the reference ID 1500-024 through the « Investissements d’avenir » programme
(Labex Agro: ANR-10-LABX-0001-01)

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THREE NEW SPECIES OF TICKS (IXODIDA : ARGASIDAE : CARIOS) FROM FRUIT BATS (CHIROPTERA : PTEROPODIDAE) IN THE AUSTRALASIAN REGION, WITH NOTES ON HOST ASSOCIATIONS.

BY J. S. H. KLOMPEN *, J. E. KEIRANS ** and L. A. DURDEN **

ABSTRACT: The tick fauna on Australasian fruit bats (Chiroptera : Pteropodidae) is reexamined. In addition to the previously described species Carios batuensis (Hirst, 1929), C. solomonis (Dumbleton, 1958) and C. rennellensis (Clifford & Sonenshine, 1962), three new species are recognized: C. papuensis n. sp. described from the larva and adults, and C. multisetosus n. sp. and C. hadiae n. sp. described from larvae only. Carios steini (Schulze, 1935) is synonymized with C. batuensis. All species examined are associated with cave inhabiting bats in the genera Dobsonia, Rousettus and Eonycteris. Most tick species have a relatively narrow host range, but this may be a secondary effect of high specificity for off-host habitat, rather than the result of coadaptation to specific hosts.

INTRODUCTION

The tick fauna associated with Old World fruit bats (suborder Megachiroptera, family Pteropodidae) consists almost exclusively of representatives of a single lineage of argasid ticks, the batuensis group of the genus Carios. Formerly classified as Ornithodoros, subgenus Reticulinasus, this lineage has been included in an expanded genus Carios (KLOMPEN & OLIVER, 1993), following the results of a phylogenetic analysis of relationships within the Argasidae. In the revised concept Carios contains among others nearly all bat-associated argasids, including the previously recognized genera Antricola and Nothoaspis, and subgenera Argas (Carios), A. (Chiropertargas), Ornithodoros (Alectorobius), O. (Subparmatus) and O. (Reticulinasus).

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Associations of old world fruit bats with ticks in other taxa have been reported, but appear to be largely accidental. So far four species have been reported from the Australasian faunal region, *Carios batuensis* (Hirst, 1929), *C. steini* (Schulze, 1935), *C. solomonis* (Dumbleton, 1958) and *C. rennellensis* (Clifford & Sonenshine, 1962). New records of ticks from fruit bats collected on the Indonesian islands of Halmahera (Peterson et al., 1990) and Seram (Durden et al., 1990), combined with previously unreported collections from the lesser Sundas and New Guinea (U.S. National Tick Collection), suggest a considerably richer tick fauna for that region. In this study three new species are described, with notes on host association patterns and geographical ranges.

**MATERIALS AND METHODS**

Larvae were cleared in lactophenol and mounted in Hoyer's medium. Available postlarval stages were examined under a dissecting microscope (70X). The capitulum, dorsal and ventral cuticle and legs of dissected males of *C. papuensis* n. sp. were slide mounted. Preparation of these stages for examination by scanning electron microscopy was precluded due to the poor condition of the specimens. Only one female and one male were in good condition, all other specimens were damaged, very brittle, and almost uniformly lacking legs. Unless stated otherwise, all material examined is deposited in the U.S. National Tick Collection, Georgia Southern University, Statesboro.

Terminology for ventral body setation of the larva follows Kohls et al. (1965), that of leg setation Edwards (1975) with some modifications (Klompen, 1992). Hypotheses of homology for individual setae could not be established for the majority of dorsal body setae of the larva due to extensive variability in both number and position. The relatively fixed arrangement of both dorsal and ventral lyrifissures (= sensilla auriforme sensu Schulze (1942)) allowed establishment of such hypotheses for these structures. They are identified by a strictly arbitrary numbering system, illustrated in Fig. 1. Pairs 1-11 occur on the dorsum proper, pairs 12-15 are posteromarginal (apparently associated with the marginal setae) and pairs 16-20 are posteroventral. None are present in the sternal region. The establishment of homologies for lyrifissures also provided reference points in identifying added or lost setae.

Where possible, at least 10 larvae of each species were measured and examined for all qualitative characteristics discussed. If available, this included specimens from a variety of populations to incorporate the effects of possible geographical variability. Measurements are presented as averages with a standard deviation (SD) and are summarized in Table 1. Unfortunately, their value in species determinations is limited due to their large relative variability. This variability was expressed between populations, within populations and, occasionally, even between homologous structures on the left and right side of a single specimen. Coefficients of variation (SD/average X 100 %) averaged between 8-14 % and, especially for setal lengths, often exceeded 15-20 %. In contrast the coefficient of variation for the number of dorsal setae was below 5 % for most species examined (8 % for *C. multisetosus* n. sp.).

**Carios papuensis** n. sp. (Figs. 1-5)

Diagnosis. The presence of an average of 17 pairs of dorsal setae in the larva is unique within the *batuensis* species group. The combination of low density of dorsal mammillae, absence of a raised rim on the discs and numerous and relatively long setae on the mammillae of the anterior and lateral periphery differentiate the adults from all other species in the group.

Larva (Figs. 1, 2). Average length of unengorged specimens 630 μm (N = 11, SD = 146), average width 570 μm (SD = 110). Dorsal shield poorly sclerotized, triangular to rounded, width slightly exceeding the length (average length 99 μm, width 137 μm). Setal complement including 15-19 pairs of dorsal and dorsolateral setae (average 16.9, SD = 0.3), substantially richer than the 14 pairs in *Carios*
*batuensis*, *C. solomonis* and all the African and Southern Asian species in the *batuensis* group. Relative to the complement in *C. batuensis*, the added setae are inserted anterolaterally between, respectively, lyrifissures 1 and 3 and lyrifissures 3 and 4, and posterolaterally between lyrifissures 7 and 8/9. Ventral setation standard for the species group, including 3 pairs of circumanal (CA), 1 pair of postcoxal (PC), 1 pair of anal (A) and 3 pairs of sternal setae. Lyrifissure complement usually complete for the species group with a total of 20 pairs (Fig. 1). One (33 %) or both (24 %) of the lyrifissures in the 8/9 position occasionally absent. Coxae poorly developed, with 2 setae each. Small slit-like openings, inferred to be part of the respiratory system (Klompen, 1992), present between coxal fields I-II and II-III. Similar, but very poorly developed openings, are present posterior to coxal field III in some specimens. Hypostome: blunt, arising from a poorly developed median extension, not directly from the basis capituli. Dentition 4/4 in the anterior portion, 2/2 posteriorly. Number of denticles per file, respectively, 8 (occasionally 7), 7, 3 (2) and 2 (1). Posthypostomal setal pairs PH1 and PH2 subequal in length (average, respectively, 15 and 19 μm). Distance between setae PH2 almost 4 times that between setae PH1. Palpal trochanter and femur at least partially fused (unusual within the Argasidae). Palpal femur with 4 (al, ad, pd1, pl), palpal genu with 5 (al, ad1, ad2, pd, pl) and palpal tibiotarsus with 9 setae (2 basal (ad, v) and 7 in the distal tuft). Legs (Fig. 2): The setal pattern in *C. papuensis* corresponds to the ancestral pattern for the *batuensis* group (Klompen, 1992): trochanter I: 0 1/1 0/1 1, trochanter II: 1 1/1 0/1 1, trochanter III: 1 1/1 0/1 0; femur I: 0 2/2 2/1 1, femur II: 1 2/2.
**Fig. 2:** Carios papuensis n. sp., larva. Dorsal view of legs I (A), II (B) and III (C).

$^{2/1}_1$ 1, femur III : $^{3/2}_2$ $^{2/1}_1$ 0; genua I-III : $^{1/1}_1$ $^{1/0}_0$ 1; tibiae I-III : $^{1/1}_1$ $^{1/1}_1$ 1; tarsus I (excluding Haller's organ and dm setae) : $^{2/3}_3$ $^{3/3}_3$ 2; tarsi II-III : $^{2/3}_2$ $^{1/0}_1$ $^{3/2}_2$ 2. Comparative measurements in Table 1.

**Postlarval Stages:** A total of 3 nymphs, 4 females and 14 males is tentatively associated with the larvae described above. They were collected at the same locality and at the same time as some of the larvae included in *C. papuensis* — collections which did not include larvae of any other species. Nonetheless, these associations need to be confirmed by rearing.

**Nymphs:** Two early instar nymphs (length, respectively, 1250 and 1330 μm, width 550 and 660 μm) and one late instar nymph (length 2170 μm, width 1250 μm) were available for measurements.

**Male** (Figs. 3, 4): Average body length 3590 μm (range 3030-3950 μm, N = 11), average width 2050 μm (range 1590-2360 μm). Cuticle mammillate. Individual mammillae relatively flat, quite variable in size, never adjoining, and widely spaced with wrinkled cuticle in between (Fig. 3A). Ventral mammillae generally less well-developed. Peripheral mammillae slightly higher, more uniform in size and more rounded (Fig. 3B, inset). Spacing more dense, occasionally adjoining. With the exception of the smallest, all mammillae bear at least one seta and some peripheral ventral mammillae bear two. Most dorsal setae very small (15-25 μm), those on the periphery longer (25-35 μm). Discs distinct, showing considerable size variation. Arranged in roughly parallel rows on the anterior dorsum and more or less radial on the posterior half of the dorsum and on the venter. Preanal groove well
Coxa I separated from coxa II, coxae II-IV adjoined (Fig. 4A). Anal valves with 4 setae each.

Table 1. Comparative measurements for the larvae of some Australasian species of Carios (in μm).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>body length</th>
<th>SD</th>
<th>width</th>
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<td>570 110</td>
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<td>661 33</td>
<td>721 88</td>
<td>510 69</td>
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<tr>
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<td>9 7</td>
<td>2 6</td>
<td>116 18 95</td>
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<td>6</td>
<td>137 10 104</td>
<td>9 7</td>
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<td>116 18 95</td>
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<tr>
<td>batuensis</td>
<td>25</td>
<td>137 10 104</td>
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<td>116 18 95</td>
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*Hypostome* tapering to a slightly notched, relatively blunt tip; dentition extending to half the length of the shaft; corona well developed, with approximately nine rows of minute denticles arranged in a 4/4 lateral and 9-10 very small (20-35 μm) dorsal setae. Setae PH1 (posthypostomal setae) long (about 260 μm), extending to the palpal genu, setae PH2 (postpalpal setae) shorter (about 145 μm), extending to the basal margin of the palpal femur.
to 7/7 pattern. Hypostomal dentition below the corona, 4/4 to 5/5, reduced to 2/2 for the basal rows; file 1 with approximately 8 well-developed but somewhat rounded denticles, file 2 with 7-8 smaller denticles. Palps exceeding the length of the hypostome by the length of the distal portion of the genu plus the tibiotarsus. Palpal trochanter slightly wider than the remaining segments, subequal in length to the femur, distinctly longer than the genu and tibiotarsus. Palpal setation rich compared to other adult Argasidae (CARIASO, 1967). Setal numbers for the trochanter, femur, genu and tibiotarsus, respectively, 15-16 (11 ventral and lateral), 21 (8 ventral and lateral), 16 (6-7 ventral and lateral) and 13-16 (8-11 in the distal tuft). Legs: Tarsus I with a distinct elevation near Haller's organ, but without
FIG. 4: *Carios papuensis* n. sp., male. Genital area (A), Capitulum, ventral view (B) and an anterior view of tarsus I (C) and tarsus IV (D).
additional tarsal humps (Fig. 4C). Anterior pit of Haller’s organ with 10 setae, including 2 serrate, 3 porose, 2 grooved and 3 setae of an undetermined type (probably conical and fine). Both serrate type setae are inserted slightly distal of the remaining setae. Tarsi II-IV without distinct humps (Fig. 4D). Setal complement on all leg segments rich (> 20 setae/segment). Leg cuticle, especially the anterdorsal face of all segments, with micromammillae, resembling the leg structure of many South American Caryos species.

**FEMALE** (Fig. 5): Average body length 4450 µm (range 4090-4910 µm, N=4), average width 2390 µm (range 2100-2990 µm). Structure of the mammillae, coxae, hypostome, palps and legs similar to that in the male. Body margin rounded, lateral suture absent. Genital area as figured (Fig. 5B).

**Hosts and distribution**: Holotype larva and 15 paratype larvae on *Dobsonia viridis* (Heude, 1896) from INDONESIA, Halmahera Is., Jailolo distr., Kampung Pasir Putih, collectors A. C. Messer & P. M. Taylor, 1.IV.1981, RML 119511. Additional material: same host and locality, 27.IV.1981 to 26.VI.1981, RML 119461, 119463, 119496, 119507-08, 119515 (22 paratype larvae); on *Dobsonia moluccensis* (Quoy & Gaimard, 1830) from PAPUA NEW GUINEA, Central distr., Kairuku, Kukuba Cave, collector R. L. Vanderwal, 1.XI.1972, RML 107654 (5 larvae); same host and locality, collectors D. E. Moorhouse et al., 3.VII.1973, RML 107655 (5 paratype larvae, 2 early instar nymphs); in cave, PAPUA NEW GUINEA, Central distr., Kairuku, Kukuba Cave, “with *Dobsonia* and other fruit bats”, collector R. L. Vanderwal, 18.VII.1970, RML 107653 (1 female, 2 males); same locality, “*Dobsonia* chamber”, collectors D. E. Moorhouse & G. Wolf, 3.VII.1973, RML 61059 (16 paratype larvae, 1 late instar nymph, 3 females, 12 males). One larva each on *Eonycteris spelaea* (Dobson, 1871), RML 119493, and *Nyctimene albiventer* (Gray, 1863), RML 119531, from INDONESIA, Halmahera Is. The latter 2 host records are considered accidental.

The material from Halmahera has been reported previously as *Ornithodoros* (*Reticulinasus*) sp. 1 by Peterson et al. (1990).

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**Carios multisetasos** n. sp. (Fig. 6)

This species is known only from the larva.

**Diagnosis.** The larva shares with *Carios rennelliens* a pyriform to triangular dorsal shield and the unusual characteristic (within *Carios*) of possessing genual and tibial setae ad2 and pd2. It is unique within the *batuensis* species group by its average of 43 pairs of dorsal setae (*C. rennelliens* has only 20-23 pairs, all others have less).

**LARVA** (Fig. 6). Average length of unengorged specimens 715 µm (N= 10, SD= 81), average width 656 µm (SD = 83). Dorsal shield triangular to pyriform, width slightly exceeding the length (average length 104 µm, width 130 µm). Shield resembling that in *C. rennelliens*, but more pointed. Setal complement including 38-49 pairs of dorsal and dorsolateral setae (average 43.2, SD = 3.6). Relative to the complement in larval *C. papuensis* and *C. batuensis*, all added setae inserted anterolaterally and laterally in the region between lyriﬀissures 1 and 8/9. Median dorsal, posterolateral and ventral setal complements as in *C. papuensis*. One lyriﬀisure in the 8/9 pair (homology unclear) absent in most specimens (84 %), both absent in some (20 %). Hypostome arising from a weak median extension, not directly from the basis capituli. Dentition 4/4 in the anterior portion (occasionally almost 5/5) and 2/2 posteriorly. Number of denticles per file, respectively, 8 (occasionally 7), 6 (7) and 1-3. Post hypostomal setae PH1 and PH2 subequal in length (both average length 18 µm); distance between setae PH2 almost 4 times that between setae PH1. Palpal morphology and setation as in *C. papuensis*. The leg setation differs from that in *C. papuensis* by the presence of genual and tibial setae ad2 and pd2, and the presence in most specimens of an additional anterior dorsal seta on trochanter II (Fig. 6A). The latter condition has not been reported previously for larval Argasidae. Comparative measurements in Table 1.

**Hosts and distribution**: Holotype larva and 4 paratypes on *Dobsonia moluccensis* from PAPUA NEW GUINEA, Madang distr., 15 km north Madang, collector E. R. Easton, 15.XII.1988,
Carios rennellensis (Clifford & Sonenshine, 1962)

Ornithodoros (Reticulinasus) rennellensis Clifford & Sonenshine, 1962 : 25.

This species is known only from the larva.

Remarks. The larva shares with Carios multisetosus a pyriform to triangular dorsal shield and the presence of genual and tibial setae ad2 and pd2. It is unique within the batuensis species group by its complement of 20-23 pairs of dorsal setae (average 20.5, SD = 0.7). The added setae, relative to the complement in larval C. papuensis, are inserted posterolaterally between lyrifissures 4 and 7 (1, occasionally 2 added setae), between lyrifissures 8/9 and 10 and near lyrifissure 13. Occasionally an additional seta is inserted anterolaterally between lyrifissures 1 and 3. The complement of lyrifissures...
is complete for the species group. The hypostome arises from a very weak extension of the basis capituli or directly from the basis capituli. Dentition of the hypostome 4/4, but the internal file is very weakly developed. The number of denticles per file is, respectively, 8, 7 (occasionally 8), 2 (3) and 1. Remaining characteristics as in *C. papuensis*. Comparative measurements in Table 1.

**Hosts and distribution**: on bat (possibly *Dobsonia inermis* Andersen, 1909 (CLIFFORD & SONENSHINE, 1962)) from SOLOMON ISLANDS, Rennell Is., 2 km west Lavanggu, 11.VI.1951, collectors Galathea Exp., RML 60988 (1 paratype larva); on *Dobsonia* sp. from PAPUA NEW GUINEA, East Sepik distr., Maprik, 2.II.1960, RML 37751 (2 larvae); same locality, collector K. KEITH, 14.V.1965, RML 102296 (5); Morobe distr., 12 mi NE of Lae, collector A.B. MIRZA, 18.IV.1970, RML 45990 (2).

**Additional records**: on *Dobsonia* sp. from PAPUA NEW GUINEA, Manus distr., Manus (Admiralty Is.), RML 37777 (SONENSHINE et al., 1966).

**Carios hadiae** n. sp. (Fig. 7)

This species is known only from the larva. **Diagnosis.** The larva shares with larval *C. solomonis* the poor development of the hypostomal dentition and the presence of setae I3 on tarsi I (unusual within *Carios*). It differs from that species by having a much shorter and stockier hypostome (length 184 μm in *C. solomonis* vs. 112 μm in *C. hadiae*), a smaller number of denticles in the outer file (9 to 10 in *C. solomonis* vs. 6 to 7 in *C. hadiae*).
and considerably longer body setae (average length of the circumanals 30-49 µm in C. solomonis vs. 73-125 µm in C. hadiae). This combination of characters warrants recognition as a new species, even though the number of available specimens (6) is small.

**Larva (Fig. 7).** Average length of unengorged or partially engorged specimens 917 µm (N = 6, SD = 200), average width 721 µm (SD = 88). Dorsal shield subtriangular to oval, width distinctly exceeding the length (average length 66 µm, width 118 µm). Setal complement including 14-15 pairs of dorsal and dorsolateral setae (average 14.4, SD = 0.5). All setae and leg segments unusually long (Table 1). Lyrifissure and ventral setal complement as in C. papuensis. Hypostome arising from a weak median extension of the basis capituli. Dentition 3/3 to 4/4 in the anterior portion and 2/2 or 1/1 posteriorly. Number of denticles per file, respectively, 7, 5, 1 and 0-1. Post hypostomal setae PH1 much shorter than PH2 (average length, respectively, 16 and 30 µm); distance between setae PH2 almost 3 times that between setae PH1. Palpal morphology and setation patterns of the palps and legs largely as in Carios papuensis but setae 13 on tarsi I present. Leg segments longer than in all other species measured (Table 1).

**Hosts and distribution:** Holotype larva and 4 paratypes on Rousettus amplexicaudatus from INDONESIA, Halmahera Is., Jailolo distr., Kampung Pasir Pitu, collectors A. C. MESSER & P. M. TAYLOR, 11.V.1981, RML 119470. Additional material: same host species from INDONESIA, Lombok Is., Bilekedit, 17.V.1978, RML 45989 (1 paratype); on Dobsonia viridis from INDONESIA, Halmahera Is., Jailolo distr., Kampung Pasir Pitu,

Additional records: on Rousettus amplexicaudatus and Cynopterus brachyotis (Muller, 1838) from INDONESIA, Java. The larvae listed as “Ornithodoros (Reticulinasus) sp.”, are most probably of this species (Wiroreno et al., 1979). The descriptions of the hypostome length and structure, palpal genu and femur shape, tarsus I length and body and tarsus I setation all fit C. hadiae.

Etymology: The species is named in honor of the late Dr. Tuti R. Hadi, for her contributions to medical entomology in Indonesia.

Carios solomonis (Dumbleton, 1958)

Ornithodoros (Reticulinasus) solomonis Dumbleton, 1958: 306.

This species is known only from the larva.

Remarks (based in part on Dumbleton (1958) and Sonenshine et al. (1966)). Dorsal setal complement as in C. batuensis and C. hadiae (14 pairs). The larva shares with C. hadiae the poor development of the denticles of the hypostome and the presence of setae B on tarsi I. The differences with C. hadiae have been listed above. The shield shape and the complement of lyrifissures could not be studied in the 2 specimens available.

Hosts and distribution: on “small flying fox”: SOLOMON ISLANDS, Vella Lavella, Joroveto, RML 30587 (2 specimens). The specific identity of the host is most likely Dobsonia inermis or Rousettus amplexicaudatus (Geoffroy, 1810). These are the only 2 species of cave-roosting fruit bats occurring in this area (Wilson and Reeder, 1993).

Carios batuensis (Hirst, 1929)

Ornithodoros batuensis Hirst, 1929: 365.
Argas steini Schulze, 1935: 34.
Reticulinasus steini (Schulze, 1935), Schulze, 1941: 546.

Remarks: Dorsal shield of the larvae slightly wider than long, subtriangular with a blunted anterior tip. Larvae usually with 14 pairs of dorsal setae (average 14.2, SD = 0.6, N = 25) and 20 pairs of lyrifissures on the body. The hypostome arises directly from the basis capituli, not from a median extension. Hypostomal dentition is 3/3 to 4/4 in the anterior portion, 2/2 posterior, with, respectively, 7, 5-7, 2(1) and 0-1 denticles per file. The capsule of Haller’s organ is often pyriform (this characteristic cannot be evaluated properly if tarsus I is oriented in a lateral position, a very common occurrence in slide-mounted specimens). Leg setation as in C. papuensis. Comparative measurements in Table 1.

Given the considerable geographical (Fig. 8) and host range (see below) of this species we conducted a preliminary investigation of geographical variation and/or indicators of the possible formation of host races. Comparisons of measurements of tick larvae collected from different geographical regions (mainland S.E. Asia (7 specimens measured), Java and the Lesser Sundas (10), and the papuan region (6)) and from different hosts (Eonycteris spelaea (6 specimens measured), Rousettus amplexicaudatus (11) and R. leschenaulti (4)) showed no consistent differences between either the regions or the hosts. This suggests that geographical variability or differentiation of host races is either absent or small relative to the level of within-population variability.

Argas steini was described based on larvae collected from a flying fox from Timor, Lesser Sunda islands (Schulze, 1935). Subsequently Schulze (1941) chose this species as the type of Reticulinasus, a new genus within the Argasidae. He also presented a new record of this species based on larvae collected from Nycteris javanica Geoffroy, 1813 (Nycteridae) in W. Java (Schulze, 1941). Unfortunately the description of this species is inadequate by modern standards. The type material could not be examined because the holotype, which was to be deposited in the Zoological Museum of Berlin (Schulze, 1935), is not listed in the current holdings of that institution (Moritz & Fischer, 1981). Reexamination of larval Carios in the U.S. National Tick Collection from fruit bats in the lesser Sunda islands produced only specimens that could be identified as Carios batuensis. This result is notable, because these collections include specimens from most of the genera of cave-roosting fruit bats (Rousettus, Eonycteris, Dobsonia) in this area (spe-
Fig. 8: Geographical range of the Australasian representatives of the *batuensis* group associated with fruit bats. Abbreviations: b, *C. batuensis*; h, *C. hadiae*; m, *C. multisetusus*; p, *C. papuensis*; r, *C. rennellensis*; s, *C. solomonis*.

cimens from *Cynopterus*, which occasionally roosts in caves and buildings, were not available). It strongly suggests that *C. steini* (Schulze, 1935) is a synonym of *C. batuensis* Hirst, 1929. The scant data on *C. steini* that can be extracted from the description do not contradict such a hypothesis. With respect to the record of *C. steini* on *Nycteris javanica*, the presently available evidence on host distribution patterns supports earlier suggestions (Dumbleton, 1958) that these specimens might well belong to a different species.


The Philippine material is deposited in the collection of the University of Michigan Museum of Zoology, Ann Arbor, Michigan. The material from Halimahera and Java has been reported previously as, respectively, Ornithodoros (Reticulinasus) sp. by PETTERSON et al. (1990) and Ornithodoros sp. by HADI et al. (1983).

Additional records: on Eonycteris spelaea from MALAYSIA, Selangor, Batu Caves (HIRST, 1929; SONENSHINE et al., 1966) (type host and locality); on Rousettus amplexicaudatus from the PHILIPPINES, Mindanao (KOHLS, 1950). We also include in this species specimens from Rousettus amplexicaudatus and Eonycteris spelaea from INDONESIA, Sumatra, reported by WIRORENO et al. (1979) as Ornithodoros sp. These specimens are unusual in that setae I3 on tarsus I are reported to be present (WIRORENO et al., 1979).

**DISCUSSION**

**Affinities.**

Although the available data are insufficient to resolve relationships within the species group, the present study does allow a few notable observations on shared character states. *Carios rennellensis* and *C. multisetosus* share the very unusual character state (within *Carios*) of the presence of genual and tibial setae ad2 and pd2, while *C. solomonis* and *C. hadiae* share the presence on tarsus I of setae I3. The larvae of the 3 species associated with *Dobsonia* spp., *C. papuensis*, *C. rennellensis* and *C. multisetosus*, share a dorsal setal complement exceeding 14 pairs and the presence of a more or less triangular dorsal shield (both unusual within the species group). The triangular shape is also found in many New World bat-associated taxa, while the dorsal shield is more rounded in the remaining members of the *batuensis* group and the remaining Argasidae. The significance of these observations cannot be evaluated properly until further investigations of phylogenetic relationships within the genus *Carios* are conducted.

**Host associations and biogeography.**

The host association pattern of ticks in the *batuensis* group shows some specificity in addition to the relatively trivial observation that all species occur solely on bats. Most species examined are restricted to one or two genera of hosts. For example, *Carios papuensis*, *C. rennellensis* and *C. multisetosus* are almost exclusively associated with *Dobsonia* species, and *C. batuensis* is largely restricted to *Rousettus* and *Eonycteris* species. Host associations for the remaining species are less clear. The host of the type series of *C. solomonis* may have been a *Rousettus* or a *Dobsonia* species, while *C. hadize* was collected from hosts in the genera *Rousettus* (Halmahera, Lombok and possibly Java), *Dobsonia* (Halmahera) and perhaps *Cynopterus* (Java). Additional collections should help clarify host associations of the latter 2 species. This genus...
level specificity is not perfect. *Dobsonia peroni* from Timor, at the western margin of the range of the genus *Dobsonia*, is not parasitized by any of the specific *Dobsonia* associates, none of which occur in the lesser Sundas, but by *C. batuensis*. It is unclear whether this association is accidental and, if it is not, why *C. batuensis* is so uncommon on *Dobsonia* spp. in areas where specific *Dobsonia* associates occur.

The moderate level of specificity at the genus level is not reflected at the species level. All tick species for which 5 or more collections were available appear to use a number of different host species. For example, *Carios papuensis* and *C. multisetosus* are reliably associated with *Dobsonia viridis* and *D. moluccensis* and *C. batuensis* with *Rousettus amplexicaudatus*, *R. leschenaulti*, *R. celebensis* and *Eonycteris spelaea*. The association of *C. multisetosus* with *Dobsonia* sp. from Biak and Owi Islands (northwest New Guinea) could refer to *D. moluccensis*, *D. beauforti* and/or *D. emersa*, all of which occur on these islands (Wilson and Reeder, 1993). Similarly, the records of *C. rennellensis* from bats in the genus *Dobsonia* from the Solomon Is., the Admiralty Is., and northeast New Guinea, could refer to *D. inermis* (only the Solomon Is.), *D. praedatrix* (only the Bismarck Is.), *D. minor* (only western and central New Guinea) and/or *D. moluccensis*. The observations of multiple host species for each tick species and a broad overlap in host ranges between tick species suggest that strict parasite host coadaptation alone is insufficient to explain the observed host association patterns.

Overall, the host association patterns are more consistent with ecological specificity: the ticks are specific for a given type of off-host habitat. Under this hypothesis there should be an overlap in habitat use of all recorded hosts of a given tick species and a difference in habitat choice between tick species. Thus the frequency of infestation of a given host species by a given tick species should be correlated with the frequency of that host visiting the specific off-host habitat of that tick species. Presently, these predictions cannot be tested because the available data are not sufficiently detailed. Ecological specificity might result in the observed pattern of host specificity if the different host genera use different sites within caves (or different caves) and the roosting habits of different species within a host genus overlap. There is some evidence for these predictions. *Dobsonia* species tend to roost in the twilight area, while *Rousettus* species, which possess a crude echo location system, prefer darker sites (Hill & Smith, 1985). *Eonycteris* species have been reported to roost in sites similar to those of *Rousettus* species. Ecological specificity is also indicated for the host association patterns of the *batuensis* group as a whole. These patterns appear to correlate better with the hosts roosting habitat (caves) and roosting behavior (large colonies) than with host phylogeny.

The macrogeographic distribution patterns of the species studied indicate broad sympatry (Fig. 8). For example, *C. papuensis*, *C. multisetosus*, *C. hadiae* and *C. batuensis* co-occur on Halmahera, and *C. rennellensis*, *C. multisetosus* and *C. batuensis* co-occur in northeast New Guinea. However, at a more refined level there appears to be segregation as predicted in the ecological specificity hypothesis. Although different tick species may use the same host species in a given area they rarely co-occur on the same host individual. Only two cases were observed: the first on a *Dobsonia viridis* from Halmahera with *Carios papuensis* and *C. hadiae* (RML 119507) and the second on a *Rousettus amplexicaudatus* from the same locality with *Carios batuensis* and *C. hadiae* (RML 119470). The ecological specificity hypothesis predicts that co-occurrence of different species on one host individual can take place only if the host visits different caves or cave sections. Because most bat species are very site loyal, this situation is assumed to be uncommon.

In summary, although the evidence is incomplete it appears that ecological specificity is the most important factor in determining the host association patterns of ticks in the *batuensis* group. Observed host specificity can be explained as a secondary result of ecological specificity.

**Acknowledgements**

We thank Dr. M. Moritz, Museum für Naturkunde, Humboldt University, Berlin, for confi-
ming the absence of any material of Carios steini in that collection. This research was supported by National Institute of Allergy and Infectious Diseases Grant no. AI 30026.

REFERENCES

CARIASO (B. L.), 1967. — Developmental chaetotaxy and morphology of the gnathosoma of some argasid and ixodid ticks. — Ph.D. dissertation, University of California, Riverside.


HILL (J. E.) and SMITH (J. D.), 1985. — Bats, a natural history. — British Museum (Natural History), London : 1-243.


Paru en Janvier 1995.