Revision of *Dennyus (Collo dennynus)* lice (Phthiraptera: Menoponidae) from swiftlets, with descriptions of new taxa and a comparison of host–parasite relationships

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Abstract. Lice of the subgenus *Dennyus (Collo dennynus)* are host specific, permanent parasites of swiftlets (Aves: Apodidae). As a prelude to a test of the hypothesis that these lice have cospeciated with their hosts, we revise the taxonomy of the subgenus, redescribing the seven previously recognized species, and adding thirteen new species and three new subspecies. All twenty-three of these louse taxa are found on swiftlets (Apodiformes: Apodidae), with four from hosts of the genus *Collocalia*, eighteen from *Aerodramus*, and one from *Hydrochous*. Successful identification is associated in most cases with females; males are only tenuously separable. A complete host–parasite list for the subgenus *Collo dennynus* is provided, as well as a key for the identification of these taxa. Limited morphological variation within the subgenus has prevented ready extraction of discrete characters for cladistic analysis. In the absence of such characters, a cluster analysis of female and male lice is presented. Comparison of a dendrogram for *Dennyus (Collo dennynus)* with a molecular phylogeny for the swiftlet hosts suggests that the history of the swiftlet–louse association has been complex, including episodes of host switching and independent speciation by the lice.

Introduction

Lice are ‘permanent’ parasites of birds and mammals that complete their entire life cycle on the body of the host (Marshall, 1981; Barker, 1994). On the basis of this close ecological association, it has been suggested that there has been extensive parallel cladogenesis, or ‘cospeciation’, between lice and their hosts (Clay, 1949). Despite rapid advances in avian systematics, however (Sibley & Ahlquist, 1990; Sheldon & Biedesc, 1993), there have been very few attempts to test hypotheses of cospeciation between particular groups of birds and lice (Eveleigh & Amano, 1977; Paterson et al., 1993, 1995). More often than not, cospeciation has simply been assumed to occur on the basis of broad concordance of host and parasite classifications (Mauersberger & Mey, 1993).

Page et al. (1996) stipulated five requirements for a more rigorous test of cospeciation: (i) adequate alpha-taxonomy of hosts and parasites; (ii) exhaustive sampling of louse clades; (iii) accurate host and parasite phylogenies, preferably based on homologous DNA sequences; (iv) quantitative comparison of host and parasite phylogenies, and (v) transfer experiments to test the feasibility of lice switching to foreign host taxa.

Lice of the subgenus *Collo dennynus* (genus *Dennyus*) are parasites of swiftlets (Apodiformes: Apodidae) – small insectivorous birds distributed from the Indian Ocean, through South East Asia and North Australia, to the Pacific. The two dozen species of swiftlets and their lice show great promise as a model system for testing all five of the above requirements. Molecular phylogenetic work on swiftlets (Lee et al., 1996), in conjunction with published host records for *Collo dennynus* (Ledger, 1970), suggest that these lice may have cospeciated with swiftlets. Transmission of *Dennyus* lice between individual hosts is known to be strictly vertical (Lee & Clayton, 1995), suggesting that opportunities for colonizing new host taxa are quite limited. Survival of host-specific *Collo dennynus* is severely
reduced when they are transferred to closely related foreign host species, including the sister species of the normal host (D. M. Tompkins and D. H. Clayton, unpublished data). By contrast, survival of less specific Collodennus species transferred among different ‘normal’ host species is not impaired. Experiments of this kind may shed light on parameters governing the extent of copeciation vs. host-switching.

A prerequisite for testing the copeciation hypothesis and for interpreting ecological experiments is a sound taxonomy of swiftlet lice, coupled with a firm knowledge of their host distribution. Through extensive collecting from swiftlets over the past several years, we have obtained twenty-three taxa of Collodennus representing both described and new taxa. In this paper we describe and illustrate all of these taxa and provide a key for their identification and a host-parasite list. We then make a preliminary attempt to infer relationships among the lice based on morphometric data, and we compare these relationships to a recently published molecular phylogeny for the swiftlets (Lee et al., 1996). This comparison suggests that the history of the swiftlet–louse association is a complex one. Teasing apart the relative contributions of copeciation and host switching will require further data, such as a molecularly based phylogeny for the lice.

Materials and methods

Freshly collected lice were preserved in 70% ethanol and later slide-mounted for study. Supplementary lice were borrowed from the National Museum of Natural History (Washington DC), the Natural History Museum (London), the K.C. Emerson Museum at Oklahoma State University (Stillwater), the Essig Museum at the University of California (Berkeley), and the Utah State Museum at the University of Utah (Salt Lake City). Qualitative and quantitative data were gathered from the lice, enabling redescription of the seven species previously recognized by Ledger (1970) and the description of thirteen new species and three new subspecies. Host species names follow Chantler & Driesens (1995), but we recognize Brooke’s (1972) division of Collocaulid into Collocaulid sensu stricto, Aerodromius, and Hydrocrus.

Measurements were made with an ocular micrometer and are given in millimetres. Abdominal tergal setal counts encompass all marginal setae, including the very long lateral setae on each segment; abdominal sternal setae are given as either marginal or anterior, but exclude the two very short lateroanterior setae on each side of sternite II and the setae in brushes on sternites V-VI. The anterior setae on the female subgenital plate include only those between sternite VII and the posterior margin of the plate. As much as possible, our terminology for louse morphology is consistent with that used by Ledger (1970). The disposition of the holotype is given for each new louse taxon; paratypes, in so far as material allows, are distributed among the Natural History Museum (BMNH), the National Museum of Natural History (USNM), Oklahoma State University (OSU), the University of Minnesota (St Paul) (UM), and the Bernice P. Bishop Museum (Honolulu) (BBM).

The recognition of different taxa of Collodennus has proved to be frustrating, as the best separating features usually involve only the female. Males are tenuously separable at best. Useful characters are primarily restricted to abdominal chaetotaxy and dimensions; the structures of the head and thorax appear uniform throughout each species-group. Because of this, descriptions for each species and subspecies emphasize abdomen features and appropriate dimensions. In an attempt to help resolve some difficult taxa, we employed principal component analysis (PCA) of qualitative characters, measurements and setal counts (Table 1). Characters that PCA suggested could be used to discriminate between pairs of taxa were then compared using t-tests (in each comparison reported below the mean ± standard error are given for each variable). All statistical analyses were performed using MINTAB® Release 10.51.

While we generally do not endorse the naming of subspecies within the Phthiraptera, we encountered several situations within the distinctus species-group in which it seemed appropriate to designate subspecies. Our approach is to recognize as species those series that have a clear separation from other taxa by at least one character for one sex. In cases where there are an adequate series of lice and good quantitative indication of differences, but an overlap in ranges that precludes clear differentiation, we have opted for subspecies designation. This approach is further supported by differences in host association and geographical distribution. In these cases, the value in parentheses following a measurement range is the mean, which is to help document a separation between subspecies. The sample size is approximated by the number of specimens in the material examined section.

Cladistic analysis of Dennys (Collodennus) taxa is hampered by their high degree of morphological similarity, making it difficult to extract discrete characters. This is reflected by high correlations among many of the morphometric characters (Table 1). For this reason, we have not performed a cladistic analysis. Instead, we used a principal component analysis of standardized average taxon values (Table 1; females and males treated separately) to identify components with eigenvalues greater than one (Manly, 1994: 82). These components are independent, by definition, and have a variance greater than or equal to any individual character in the original data set. Pairwise Euclidean distances were computed between the component scores for each taxon, and these distances were clustered using average linkage. Two representatives of the subgenus Dennys (Dennys) were included in the analysis: Dennys hirundinus (from Apus apus) and D. cyprianus (from Cypsiurus balasienissus) (Ledger, 1971).

Descriptions

Subgenus Collodennus Ledger


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### Table 1. Qualitative, measurement, and count variables for *Dennyus* lice.

<table>
<thead>
<tr>
<th>Character code</th>
<th>Description</th>
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<tbody>
<tr>
<td>Both sexes</td>
<td></td>
</tr>
<tr>
<td>POW</td>
<td>Proocular width (mm)</td>
</tr>
<tr>
<td>TW</td>
<td>Temple width (mm)</td>
</tr>
<tr>
<td>HL</td>
<td>Head length at midline (mm)</td>
</tr>
<tr>
<td>Preant Mg</td>
<td>Preantennal margin: (1) straight, (2) moderately concave, (3) deeply concave</td>
</tr>
<tr>
<td>dtn 5</td>
<td>Dorsal head seta 5: (1) slender, (2) stout</td>
</tr>
<tr>
<td>MW</td>
<td>Metathorax width (mm)</td>
</tr>
<tr>
<td>AbW</td>
<td>Abdomen width at segment IV (mm)</td>
</tr>
<tr>
<td>AL</td>
<td>Abdomen length at midline (mm)</td>
</tr>
<tr>
<td>MxStn</td>
<td>Number of mesosternal setae</td>
</tr>
<tr>
<td>Ant Mts</td>
<td>Median anterior metanotal setae (1) anterior to or (2) transversely aligned with respect to anterior lateral setae on at least one, usually both sides</td>
</tr>
<tr>
<td>Tgl-TgVIII</td>
<td>Number of marginal setae on tergites I–VIII</td>
</tr>
<tr>
<td>Rel Lgh Tg IV</td>
<td>Relative lengths of median six setae on tergite IV: (1) 5–6 long, (2) at least 2 much shorter than others</td>
</tr>
<tr>
<td>Lght Tg IV</td>
<td>Length of longest median six setae on tergite IV (mm)</td>
</tr>
<tr>
<td>MgStn II-VI</td>
<td>Number of marginal setae on sternites II–VI</td>
</tr>
<tr>
<td>AsStn VI</td>
<td>Number of anterior setae on sternites II–VI</td>
</tr>
<tr>
<td>BrV</td>
<td>Number of setae in brush on sternite V (left and right)</td>
</tr>
<tr>
<td>BrVI</td>
<td>Number of setae in brush on sternite VI (left and right)</td>
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<tr>
<td>BrVI st</td>
<td>Posterior setae in brush on sternite VI (1) similar to or (2) thinner than anterior setae in brush</td>
</tr>
<tr>
<td>Med Term Tg Num</td>
<td>Number of fine terminal setae between long terminal setae</td>
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<tr>
<td>Med Term Tg Lght</td>
<td>Length of longest median terminal seta (mm)</td>
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<tr>
<td>Females</td>
<td></td>
</tr>
<tr>
<td>AnW</td>
<td>Anus width (mm)</td>
</tr>
<tr>
<td>Sh Pts Ant</td>
<td>Number of anterior setae on subgenital plate</td>
</tr>
<tr>
<td>Sh Pts Mg num</td>
<td>Number of marginal setae on subgenital plate</td>
</tr>
<tr>
<td>Sh Pts Mg row</td>
<td>Row of marginal setae (1) irregular or (2) regular</td>
</tr>
<tr>
<td>Sh Pts Mg kind</td>
<td>Marginal setae (1) thinner than or (2) similar to anterior setae</td>
</tr>
<tr>
<td>Lat Mg Lght</td>
<td>Length of longest 1–2 lateral marginal setae on subgenital plate (mm)</td>
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<tr>
<td>Med Mg Lght</td>
<td>Length of longest 1–2 median marginal setae on subgenital plate (mm)</td>
</tr>
<tr>
<td>V An Fr</td>
<td>Number of setae in ventral anal fringe</td>
</tr>
<tr>
<td>Set An Fr</td>
<td>Number of setae anterior to ventral anal fringe</td>
</tr>
<tr>
<td>Males</td>
<td></td>
</tr>
<tr>
<td>GL</td>
<td>Genitalia length (mm)</td>
</tr>
<tr>
<td>GPl</td>
<td>Genital paramere length (mm)</td>
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### Diagnosis

Mesoponid chewing lice with anterior head margin flattened, never smoothly rounded (Fig. 1); prosternal plate with never more than total of 4 setae (Fig. 3); first tarsi without claws (Fig. 1); sternite I reduced, usually with only 2 setae (Figs 1, 2). Female sternite VII fused with following sternites to form subgenital plate (Figs 2, 11, 12, 17, 20); setae of VII typically 2 × 4 × 2; each lateroposterior portion of subgenital plate with 4 medium to long submarginal setae. Male genitalia near Fig. 5, with poorly defined small sclerites associated with lightly spinose sac.

*distinctus species-group*

**Diagnosis**

Head (Fig. 1) with lateral preantennal margin relatively straight; dorsal seta 5 (Fig. 1: arrow) slender, short; other chaetotaxy as shown. Thorax (Fig. 1) with mesosternum having 4 setae (rarely 3 or 5); metasternum with 7–15 setae; metanotum usually with 8–10 marginal setae (less often 7 or 11), and each side with 3 anterior setae, these arranged with median seta anterior to anteriormost lateral seta on at least 1, usually both, sides. Each side of terminal tergite with 2 very long setae, with 1 short, fine seta inserted between them and usually another seta immediately medially to these.

*distinctus species-subgroup*

**Diagnosis**

The four taxa of this subgroup are separated from all others of the group in having the ventral fringe of the female anus without any setae displaced anteriorly from it (Figs 4, 8, 9).
Dennys (Colleodennys) distinctus Ferris (Figs 1–5)

**Female** (Fig. 2). Tergal setae: I, 13–20; II–IV, 18–22; V, 16–21; VI, 14–19; VII, 12–17; VIII, 11–12; median setae of tergite IV with short among long. Marginal sternal setae: II, 9–14; III–IV, 11–17; V, 5–8; VI, 4–6. Anterior sternal setae: II, 3–9; III, 4–12; IV, 9–19; V, 1–7; VI, 0–7; VII, 0–2. Setae in each brush on sternite V, 24–36; VI, 13–25, with posterior setae usually similar in thickness to others in brush. Subgenital plate (Fig. 4) with 13–18 anterior setae, 10–16 marginal setae as thin as anterior setae and arranged in regular row. Anal ventral fringe of 51–64 setae, dorsal of 40–54. Dimensions: sternal width (TW), 0.52–0.57; head length (HL), 0.43–0.46; prothorax width (PW), 0.31–0.35; metathorax width (MW), 0.52–0.67; abdomen width at segment IV (AbW), 0.68–0.8; abdomen length (AL), 1.33–1.49; total length (TL), 2.20–2.44; anus width (AnW), 0.23–0.28.

**Male** (Fig. 1). Tergal setae: I, 10–16; II, 12–19; III–VI, 13–20; VII, 12–17; VIII, 11–14; median setae of tergite IV usually long, occasionally with short among long. Marginal sternal setae: II, 8–11; III–IV, 8–13; V–VI, 3–6; VII, 7–9; VIII, 6–7. Anterior sternal setae: II–III, 3–10; IV, 3–12; V, 0–6; VI, 0–3; VII, 0–1; VIII, 0. Setae in each brush on sternite V, 23–37; VI, 15–24; with posterior setae usually similar in thickness to others in brush. Dimensions: TW, 0.48–0.55; HL, 0.41–0.45; PW, 0.29–0.34; MW, 0.47–0.56; AbW, 0.55–0.70; AL, 1.08–1.30; TL, 1.96–2.17; genitalia length (GL), 0.59–0.68.

**Remarks**

This species is separated from the other two species of the subgroup by the female having a larger number of tergal setae on IV–V and a narrower anus; the male is separated from that of *D.medwayi* Ledger by slightly head dimensions and more tergal setae at least on IV–V.

*Dennys (Colleodennys) distinctus distinctus* Ferris


**Female**. Anterior sternal setae on V, 1–7 (4.6). Setae in each brush on sternite V, 24–33 (28.9); VI, 13–23 (17.3). Dimensions: TW, 0.52–0.56 (0.537); HL, 0.43–0.45 (0.438); MW, 0.52–0.59 (0.555); AbW, 0.68–0.81 (0.738); AL, 1.33–1.49 (1.395); TL, 2.20–2.44 (2.293); AnW, 0.23–0.28 (0.248).

**Male**. Dimensions: TW, 0.48–0.54 (0.517); MW, 0.47–0.53 (0.502); AbW, 0.55–0.66 (0.609); AL, 1.08–1.22 (1.152); TL, 1.96–2.12 (2.027); GL, 0.59–0.66 (0.622).

**Material examined**

Lectotype ♂ and 1 ♀, 1 ♂ paratypes of *D.distinctus*, ex *C.linchi*, JAVA (Eoisig Museum of Entomology, University of California Berkeley); 9 ♀, 4 ♂, same data. 38 ♀, 114 ♂, ex *C.esculenta cyanopitila* Oberholser, MALAYSIA: Sandakan; 12 ♀, 11 ♂, ex *C.esculenta* (Linnaeus), NEW GUINEA. See ‘Remarks’ below regarding males.

**Remarks**

While the females of *D.distinctus* are readily separable from those of *D.somadikartai* sp.n. (see below) co-occurring on the same host, the males of these two species have proven to be inseparable, even using multivariate techniques. Thus, the 130 males listed in the ‘Material examined’ section above undoubtedly include both of these species. From the preponderance of females of *D.somadikartai* (115 compared with sixty-one listed above), and assuming a 1 : 1 sex ratio, the majority of these males probably belong to the other species, but we have no way of being sure.

*Dennys (Colleodennys) distinctus timjonesi* sp.n. (Figs 1–5)

**Type host**: *Collocalia esculenta cyanopitila* Oberholser.

**Female**. Anterior sternal setae on V, 1–5 (2.9). Setae in each brush on sternite V, 28–36 (32.6); VI, 15–22 (19.2). Dimensions: TW, 0.54–0.57 (0.552); HL, 0.43–0.46 (0.449); MW, 0.53–0.60 (0.573); AbW, 0.70–0.82 (0.784); AL, 1.35–1.47 (1.434); TL, 2.26–2.39 (2.350); AnW, 0.25–0.28 (0.265).

**Male**. Dimensions: TW, 0.52–0.55 (0.537); MW, 0.50–0.56 (0.519); AbW, 0.59–0.70 (0.643); AL, 1.14–1.30 (1.209); TL, 2.04–2.17 (2.109); GL, 0.65–0.68 (0.664).

**Type material**

Holotype, ♂, ex *C.esculenta cyanopitila*, MALAYSIA: Kuala Lumpur, Ampang Reservoir, i.1994, (Tomkins) (BMNH).

Paratypes, 3 ♀, 9 ♂, same as holotype (BMNH; USNM; UM); 5 ♀, 5 ♂, same, ex *C.esculenta*, 19.viii.1964 (McCline) (OSU); 1 ♀, 1 ♂, same, except *C.esculenta*, 1967; no collector (BMNH).

**Remarks**

The recognition of these two subspecies is based primarily on the difference in length of the male genitalia; of ninety-eight males measured for the nominate subspecies (including those of the co-occurring *D.somadikartai*), the mean genital length was 0.622. Only eight genitalia were 0.65 long and only three were 0.66 long. Of the sixteen males measured for *D.timjonesi*, none measured less than 0.65, and the mean value was 0.664. Principal component analysis clearly separates females of the two subspecies (Fig. 6). Compared to *D.distinctus, D.timjonesi females* are wider, (e.g. TW: 0.552 ± 0.003 vs. 0.537 ± 0.002, P = 0.003), have fewer
Fig. 6. Principal component analysis of females of the two subspecies of *Dennus distinctus* lace. The first and second principal components (PC 1 and PC 2) account for 18.9 and 16.1% of the variation, respectively.

anterior sternal setae on sternite V (ASTnV: 2.9 ± 0.4 vs. 4.6 ± 0.4, \( P = 0.008 \)) and more setae in the brush on sternite V (BSnV: 32.6 ± 0.8 vs. 28.9 ± 0.6, \( P = 0.001 \)).

**Etymology**

This subspecies is named for Tim Jones, University of Oxford, who was instrumental in the collection of lice described in this paper.

**Dennus (Collodennus) theresaee sp.n. (Fig. 8)**

*Type host:* Collocalia esculenta desiderata Mayr.

**Female.** Tergal setae: 1; 14; II, 18; III, missing; IV-V, 14–15; VI-VII, 12; VIII, 13; median setae of tergite IV long. Marginal sternal setae: II, 9; III–IV, 12–13; V–VI, 6. Anterior sternal setae: II, 4; III, 7; IV, 10; V, 2; VI, 1; VII, 0. Setae in each brush on sternite V, 25–30; VI, 14–15, with posterior setae similar in thickness to others in brush. Subgenital plate (Fig. 8) with 14 anterior setae, 14 marginal setae as thin as anterior setae and arranged in regular row with longer setae laterally. Anal ventral fringe of 58 setae, dorsal of 52. Dimensions: much as for *D. distinctus*, except TW, 0.53; AnW, 0.29.

**Male.** Unknown.

**Type material**

Holotype, ♂, ex *C. esculenta desiderata*, RENNEL IS.: Lavanggu, 15.x.1951 (BMNH).

**Remarks**

Although *D. theresaee* is based only on a single female, the differences between it and those of the other species of this subgroup are sufficient to distinguish it. The wider anus, the small number of tergal setae on IV–VI, the presence of only long median setae on tergite IV, and the subgenital plate with marginal setae longer laterally are all distinct.

**Etymology**

This species is named in honour of the late Theresa Clay in recognition of her many valuable contributions to chewing louse taxonomy.

**Dennus (Collodennus) medwayi** Ledger (Fig. 9)

*Type host:* Hydrochoerus gigas (Hartiert & Butler).

**Female.** Tergal setae: I, 10; II, 12; III, 13; IV–V, 14; VI, 14; VII, 13; VIII, 12. Marginal sternal setae: II, 8; III–IV, 13–14; V, 5; VI, 4. Anterior sternal setae: II, 3; III, 4; IV, 10; V–VII, 0. Setae in each brush on sternite V, 28–38; VI, 20–24, with posterior setae thinner than others in brush. Subgenital plate (Fig. 9) with only 8 anterior setae, completely lacking any medioanterior setae, and with 12 marginal setae as thin as anterior setae and arranged in regular row. Anal ventral fringe of 55 setae, dorsal of 46. Dimensions: TW, 0.59; Hl, 0.50; PW, 0.35; MW, 0.62; AW, 0.84; AL, 1.63; TL, 2.64; AnW, 0.30.

**Male.** Tergal setae: I–II, 10; III–IV, 12; V–VI, 14; VII, 12; VIII, 10; median setae of tergite IV long. Marginal sternal setae: II, 6; III–IV, 10; V–VI, 5–6; VII, 9; VIII, 6. Anterior sternal setae: II–IV, 4; V–VIII, 0. Setae in each brush on sternite V, 28–37; VI, 17–20, with posterior setae similar to others in brush. Dimensions: TW, 0.56; Hl, 0.48; PW, 0.33; MW, 0.54; AW, 0.63; AL, 1.16; TL, 2.12; GL, 0.64.

**Material examined**

1 ♂, 1 ♀ paratypes of *D. medwayi*, ex *H. gigas*, MALAYA.

**Remarks**

The female of *D. medwayi* is easily distinguished from those of the other three taxa of the species-subgroup by the absence of any medioanterior setae on the subgenital plate in conjunction

with the slightly larger dimensions and the small number of tergal setae. The male is separable as discussed under the remarks for *D. distinctus*.

**elliotti species-subgroup**

**Diagnosis**

The six taxa of this subgroup are separated from all others of the *distinctus* species-group in having the female with a few setae dispersed anteriorly from the ventral anal fringe margin (Figs 10–12) in combination with the majority of abdominal tergites II–VI each having ≤ 14 setae. While males also tend to have few tergal setae, the separation is not as distinct as for the females.

**Dennyus (Colloedronymus) elliotti** Ledger (Figs 10, 11)

*Dennyus (Colloedonymus) elliotti* Ledger, 1970: 247. Type host: *Aerodramus whiteheadi* (Ogilvie-Grant).

**Female** (Fig. 11). Tergal setae: I, 8–11; II–III, 11–13; IV–VII, 12–14; VIII, 10–12; median setae of tergite IV long. Marginal sternal setae: II, 7–12; III–IV, 10–14; V, 5–6; VI, 3–4. Anterior sternal setae: II, 4–6; III, 3–5; IV, 4–7; V, 0–1; VI–VII, 0. Setae in each brush on sternite V, 27–40; VI, 9–15, with posterior setae thinner and longer than others in brush (Fig. 11). Total number of setae on sternite VI, 22–34. Subgenital plate (Fig. 10) with 9–10 anterior setae, 12–17 marginal setae thicker than anterior setae and arranged in regular to slightly irregular row. Anal ventral fringe of 46–52 setae, dorsal of 76–46; total of 4–5 setae anterior to ventral fringe. Dimensions: TW, 0.53–0.55; HL, 0.45–0.50; PW, 0.32–0.34; MW, 0.55–0.56; ABW, 0.70–0.73; AL, 1.61–1.71; TL, 2.53–2.70; AnW, 0.24–0.25.

**Male**. Tergal setae: I, 8–11; II, 11–12; III, 12–15; IV–VII, 12–14; VIII, 12–13; median setae of tergite IV long. Marginal sternal setae: II–IV, 9–12; V–VI, 3–6; VII, 8–9; VIII, 6. Anterior sternal setae: II, 5–8; III, 4–5; IV, 3–8; V–VIII, 0. Setae in each brush on sternite V, 23–35; VI, 7–16, with posterior setae thinner than others in brush. Dimensions: TW, 0.48–0.51; HL, 0.43–0.47; PW, 0.29–0.31; MW, 0.47–0.49; ABW, 0.57–0.58; AL, 1.17–1.25; TL, 2.00–2.14; GL, 0.57–0.61.

**Material examined**

1 ♂, 2 ♀ 2 ♀ paratypes of *D. elliotti*, ex *A. whiteheadi*, PHILIPPINE IS.; 2 ♀, 2 ♀, same data.

**Remarks**

The features separating the female of *D. elliotti* from those of the other three species of this subgroup are an arm width > 0.24, sternite V with only 6–10 medioanterior setae, sternite VI without such setae giving this sternite a total of ≤ 34 setae, and the smaller abdomen width and length. The male is recognized by its short genitalia and the thin setae at the posterior margin of brush VI.

**Dennyus (Colloedonymus) hahnae** sp.n.

Type host: *Aerodramus hirundinaceus* (Stresemann).

Close to *D. elliotti*, except as follows.

**Female**. Marginal sternal setae: II, 9–13; III–IV, 11–18; VI, 3–6. Anterior sternal setae: II–III, 3–8; IV, 11–17; V–VII, 0. Setae in each brush on sternite V, 35–45. Total number of setae on sternite VI, 22–30. Subgenital plate with 10–12 anterior setae, 14–19 marginal setae thicker than anterior setae and arranged in irregular row. Anal ventral fringe of 49–56 setae, dorsal of 43–46. Dimensions: ABW, 0.77–0.83; AL, 1.74–1.85; TL, 2.68–2.80; AnW, 0.24–0.27.

**Male**. Marginal sternal setae: II, 7–9. Anterior sternal setae: II, 3–6; III, 2–4; IV, 6–12. Setae in each brush on sternite V, 29–38. Dimensions: ABW, 0.58–0.64; AL, 1.33–1.40; TL, 2.19–2.30; GL, 0.62–0.66.

**Type material**

Holotype, ♀, ex *Collocalia sp.* [most likely ~ *A. hirundinaceus*], NEW GUINEA: West Sepik, Okapomin, 1600 m, 23.iii.1971 (Mirza) (BBM).

Paratypes, 4 ♀, 4 ♀, same as holotype (BBM; BMNH); 2 ♀, 3 ♀, same, except Chibu, Chuave (Limestone cave), 13.iv.1968 (*Gressitt & Maa*) (BBM; USNM); 1 ♀, 1 ♂, same, except Morobe, Meru Cr., 1 mi. W. Edie Cr., 2040 m, 19.vii.1966 (*Wilson & Valma*) (BBM).

**Remarks**

This species is closest morphologically to *D. elliotti*, but may be separated from the latter by both sexes with larger abdomen width and length, females with more anterior sternal setae on IV, and males with longer genitalia.

**Etymology**

This species is named for Caldwell Hahn, Patuxent Wildlife Research Centre, in recognition of her deep interest in the ecology of brood parasites and their lice.

**Dennyus (Colloedonymus) boothi** sp.n.

Type host: *Aerodramus terraearenae* terraearenae (Ramsay).

Much as for *D. elliotti*, except as follows.

**Female**. Anterior sternal setae: II, 4–6; III, 5–8; IV, 10–17;

**Male.** Marginal sternal setae: II, 6–7; III, 8–10; IV, 7–9. Anterior sternal setae: II, 4; III, 3–4. Setae in each brush on sternite V, 24–31; VI, 10–18, with posterior setae similar in thickness to others in brush. Dimensions: GL, 0.62–0.63.

**Type material**

Holotype, ♀, ex *A. terraereginae*, AUSTRALIA: N. Queensland, Tully Gorge, 50 km from Tully, 26.iii.1994 (Clayton) (BMNH).

Paratypes, 1 ♀, 3 ♂, same as holotype (BMNH; USNM; OSU).

**Remarks**

The female of *D. boothi* is distinguished by its narrow anus. The male differs from those of *D. eliotti* and *D. babanae* in having posterior setae of the brushes on sternite VI that are similar to the other brush setae.

**Etymology**

This species is named for David Booth, University of Queensland, in recognition of long-term collaborative work with D.H.C. on host–parasite ecology, including some rather harrowing field work for this paper.

**Dennyus (Collodennyus) carljonesi** sp. n. (Fig. 12)

**Type host:** *Aerodramus fuscipugius* (Thunberg).

**Female.** Tergal setae: I, 10–13; II, 11–13; III–VI, 12–15; VII, 11–14; VIII, 9–12; median setae of tergite IV long. Marginal sternal setae: II, 7–12; III, 11–14; IV, 11–18; V–VI, 4–9. Anterior sternal setae: II, 5–10; III, 7–14; IV, 9–30; V, 0–10; VI, 1–8; VII, 0–3. Setae in each brush on sternite V, 33–54; VI, 12–27, with posterior setae thinner than others in brush. Total number of setae on sternite VI, 36–60. Subgenital plate (Fig. 12) with 9–12 anterior setae; 12–21 marginal setae relatively short, thick, and arranged in regular to irregular row. Anal ventral fringe of 49–64 setae, dorsal of 38–56; total of 2–10 anterior setae to ventral fringe. Dimensions: TW, 0.55–0.60; HL, 0.46–0.51; PW, 0.33–0.37; MW, 0.57–0.65; AbW, 0.72–0.88; AL, 1.54–1.83; TL, 2.48–2.86; AnW, 0.25–0.30.

**Male.** Tergal setae: I, 9–12; II, 11–13; III, 12–14; IV–VI, 12–15; VII, 12–14; VIII, 11–13; median setae of tergite IV long. Marginal sternal setae: I, 2–5; II, 6–12; III–IV, 8–15; V, 4–9; VI, 3–8; VII, 8–10; VIII, 6–8. Anterior sternal setae: II, 3–8; III, 5–12; IV, 4–19; V, 0–7; VI, 0–6; VII–VIII, 0–2. Total setae on sternite IV, 15–30. Setae in each brush on sternite V, 28–50; VI, 13–26, with posterior setae either thinner than others in brush or of similar thickness. Dimensions: TW, 0.52–0.58; HL, 0.44–0.48; PW, 0.31–0.35; MW, 0.50–0.57; AbW, 0.58–0.73; AL, 1.21–1.39; TL, 2.09–2.35; GL, 0.63–0.73.

**Remarks**

The female of *D. carljonesi* is distinguished from females of the other three species of the subgroup by its wide anus, its larger number of total setae on sternite VI, and its larger number of anterior setae on sternites V–VI. The large male genitalia are closest to those of *D. babanae*. Males are also distinguished by a temple width of at least 0.52 and often the presence of anterior setae on sternites V–VI.

Principal component analysis of both the females and males of this species revealed discrete clusters corresponding to geographic locality (Fig. 7). The subgenital plate of female *D. carljonesi* from the Seychelles and Mauritius has more marginal setae (Sb Pt Mg num: 17.7 ± 0.4 vs. 14.1 ± 0.2, P < 0.0001) and shorter lateral marginal setae (Lat Mg Lgh: 0.036 ± 0.001 vs. 0.041 ± 0.001, P < 0.0007) than lice from Malaysian birds. Female lice from the Seychelles (hosted by *Aerodramus elaphra*) and Mauritius (hosted by *A. francicus*) can also be distinguished from each other and from Malaysian *D. carljonesi* lice from the Seychelles have more mesosternal setae (4–6 vs. 4); lice from Mauritius have shorter abdomens (AL, 1.60 ± 0.06 vs. 1.71 ± 0.06, P = 0.0003). PCA of male *D. carljonesi* revealed a similar separation between Indian Ocean and Malaysian lice, primarily due to the wider head and thorax of the former (e.g. TW: 0.555 ± 0.002 vs. 0.543 ± 0.002, P < 0.0001). Based on these differences, we recognize three subspecies of *D. carljonesi*, as described below.

**Etymology**

This species is named in honour of Carl Jones, Mauritius Wildlife Fund, in recognition of his important contributions.
to the conservation of biodiversity in Mauritius; may the work prosper!

**Dennys (Colldennys) carltoni* carltoni**
Clayton, Price & Page (Fig. 12)

**Type host:** Aerodramus jaciphagus (Thunberg).

**Female.** With 2 setae on sternite I. Anterior sternal setae: III, 7–14 (10.0); IV, 9–30 (16.3); V, 2–10 (5.8); VI, 2–8 (4.1); VII, 0–1 (0.3). Setae in each brush on sternite V, 34–54 (43.4). Subgenital plate with 12–16 (14.1) marginal setae. Anal ventral fringe of 49–61 (55.5) setae, dorsal of 46–56 (50.3); total of 4–10 (6.3) setae anterior to ventral fringe. Dimensions: TW, 0.55–0.60 (0.575); HL, 0.46–0.51 (0.494); MW, 0.57–0.65 (0.609); ABW, 0.72–0.88 (0.788); AL, 1.63–1.83 (1.721); TL, 2.59–2.86 (2.720); AnW, 0.25–0.30 (0.277).

**Male.** With 2 setae on sternite I. Total setae on sternite IV usually 16–26, much less often up to 30. With 32–50 (39.0) setae in each brush on sternite V. Dimensions: TW, 0.52–0.56 (0.542); HL, 0.45–0.48 (0.470); MW, 0.50–0.56 (0.529); AW, 0.58–0.68 (0.632); GL, 0.66–0.73 (0.700).

**Type material**

Paratypes, 6 ♀, 15 ♂, same as holotype (BMNH; USNM; OSU; UM); 1 ♀, 1 ♂, same, except 20.vi.1973 (Cheke) (BMNH); 1 ♀, 1 ♂, same, except Vacoas, 26.i.1974 (Cheke) (BMNH).

**Remarks**

The separation of *D.c.roseteri* from the other two subspecies is based on the female having only 2 setae on sternite I, usually no anterior setae on sternite VII, the subgenital plate with at least 16 marginal setae, often fewer than 6 setae anterior to the ventral anal fringe, and a shorter abdomen. The male can be tentatively recognized by its smaller genitalia and certain other dimensional differences.

**Etymology**

This species is named in honour of Donald Forrester, University of Florida, in recognition of his interest in Florida birds and their parasites, including chewing lice.

**Dennys (Colldennys) carltoni* fosteri** ssp.n.

**Type host:** Aerodramus elaphrus (Oberholser).

Much as for *D.c.carltoni*, except as follows.

**Female.** Sternite I with 2–4 (3.0) setae. Anterior sternal setae on III, 7–11 (8.6); VII, 1–3 (1.9). Subgenital plate with 16–21 (18.7) marginal setae. Anal ventral fringe of 58–64 (61.3) setae. Dimensions: TW, 0.59–0.60 (0.595); AW, 0.76–
0.85 (0.826); AnW, 0.27–0.30 (0.291).

**Male.** Sternite I with 2–3 (2.5) setae. With all but 1 specimen having posterior setae in brush on sternite V thick, much like others in brush. Dimensions: TW, 0.53–0.57 (0.556); HL, 0.46–0.48 (0.478); MW, 0.52–0.57 (0.547); AW, 0.64–0.73 (0.675); GL, 0.66–0.70 (0.678).
Type material

Paratypes, 6♀, 14 ♂, same as holotype (BMNH; USNM; OSU; UM); 1 ♂, 1 ♂, ex A. elaphrus, SEYCHELLES: Praslin, Mt. Cabrils, 2.viii.1977 (Macdonald) (BMNH).

Remarks

The female of D. fosteri is separable from those of the other two subspecies in having more setae on sternite V, more anterior setae on sternite VII, and a larger temporal width. The male is often separable by its genitalia length and head dimensions.

Etymology

This species is named for Garry Foster, University of Florida, in appreciation of his interest in the birds of Florida and their parasites.

emersoni species-subgroup

Diagnosis

The five species of this subgroup are separable from all others in the group in having females with some setae displaced anteriorly from the ventral anal fringe margin (Figs 13, 14) and each of abdominal tergites II–VI with >15 setae. Males do not show a separation as distinct as for the females.

Dennyus (Colloddenyus) emersoni Ledger

Dennyus (Colloddenyus) emersoni Ledger, 1970: 249. Type host: Aerodramus brevirostris (Horsfield).

Female. Tergal setae: I, 19; II–III, 20–21; IV–VI, 17–22; VII, 15–17; VIII, 12; median setae of tergite IV either long or with short among long. Marginal sternal setae: II, 9–13; III–IV, 16–18; V, 6–7; VI, 4–5. Anterior sternal setae: II, 8; III, 14–15; IV, 23; V, 2–3; VI, 1; VII, 0. Setae in each brush on sternite V, 33–36; VI, 13–16, with posterior setae thinner than others in brush. Total number of setae on sternite VI, 32–37. Subgenital plate with 10 anterior setae, 13–14 marginal setae similar in thickness to anterior setae and arranged in regular row. Anal ventral fringe of 44–52 setae, dorsal of 46–50; total of I–3 setae anterior to ventral fringe. Dimensions: TW, 0.56–0.57; HL, 0.46–0.47; PW, 0.34–0.35; MW, 0.58–0.60; AbW, 0.80; AL, 1.61–1.68; TL, 2.57–2.62; AnW, 0.24–0.27.

Male. Tergal setae: I, 9; II–VII, 13–14; VIII, 12; median setae of tergite IV long. Marginal sternal setae: II, 8; III–IV, 12; V–VI, 4; VII, 8; VIII, 6. Anterior sternal setae: II–IV, 6–7; V, 1; VI–VIII, 0. Setae in each brush on sternite V, 31–33; VI, 16–17, with posterior setae similar in thickness to others in brush. Dimensions: TW, 0.52; HL, 0.43; PW, 0.31; MW, 0.50; AbW, 0.60; AL, 1.19; TL, 2.05; Gl, 0.60.

Material examined

2 ♂, 1 ♂, paratypes of D. emersoni, ex A. brevirostris, THAILAND.

Remarks

This species, along with the following two, are distinguished by the female having a relatively narrow anus <0.28 wide. Dennyus emersoni is separated from the two other narrow-anus species by having the female with a total of ≤ 37 setae on sternite VI and with <4 anterior setae on sternite V. The male of D. emersoni is close to that of D. carljonasi, but with shorter genitalia.

Dennyus (Colloddenyus) kriniae sp.n.

Type host: Aerodramus spodiopyggius spodiopyggius (Peale).

As for D. emersoni, except as follows.

Female. Tergal setae: I, 17–18; II, 17–19; III–VII, 15–17; median setae of tergite IV long. Marginal sternal setae: III, 13–14; IV, 14–16; V, 6–9; VI, 5–8. Anterior sternal setae: II, 6–11; III, 8–17; IV, 17–28; V, 7–10; VI, 5–9; VII, 0–2. Setae in each brush on sternite V, 41–50; VI, 19–24. Total number of setae on sternite VI, 54–58. Subgenital plate with 12–16 anterior setae, 13–18 marginal setae thinner than anterior setae and arranged in irregular row. Anal ventral fringe of 53–57 setae, dorsal of 43–52; total of 6–9 setae anterior to ventral fringe. Dimensions: TW, 0.58–0.60; HL, 0.49–0.50; PW, 0.35–0.36; MW, 0.60–0.61; AbW, 0.76–0.80; TL, 2.60–2.69; AnW, 0.26–0.28.

Male. Tergal setae: I, 11–13; II, 12–15; III, 13–16; IV–VII, 14–16; VIII, 12–14. Marginal sternal setae: II, 7–10; III–IV, 9–15; V–VI, 5–8; VII, 8–9; VIII, 6–9. Anterior sternal setae: II, 4–8; III, 7–13; IV, 16–27; V, 2–9; VI, 2–6. Total setae on sternite IV, 27–39. Setae in each brush on sternite V, 36–45; VI, 16–22. Dimensions: TW, 0.56–0.58; HL, 0.47–0.49; PW, 0.34–0.35; MW, 0.54–0.57; AbW, 0.63–0.70; AL, 1.32–1.36; TL, 2.30–2.33; Gl, 0.70–0.76.

Type material

Holotype, ♂, ex A. spodiopyggius, WESTERN SAMOA: Upolu, Ole Papu-Pue National Park, Peapea Cave, 31.iii.1994 (Clayton) (BMNH).
Paratypes, 2 ♂, 8♀, same as holotype (BMNH; USNM; OSU).

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Remarks

The female of *D. krisitae* is distinguished from other females of the subgroup by its narrow anus, the larger number of sternal setae on V-VI, the smaller number of setae on most tergites, and the number and thickness of the setae on the subgenital plate. The male, with its long genitalia and numerous setae on sternite IV, allies itself morphologically with *D. ferrisi* Ledger; it may be separated from that species by the larger number of anterior sternal setae on V-VI and fewer tergal setae on I-II.

Etymology

This species is named for Kristin Clayton in recognition of many years of encouragement and support for her husband’s esoteric excursions into the mysteries of host-parasite coevolution.

*Dennysus (Collopendyus) singhi* sp. n. (Fig. 13)

*Type host:* *Aerodramus spodiopygius assimilis* (Stresemann).

As for *D. emersoni*, except as follows.

**Female.** Tergal setae: IV-VI, 16-19; VIII, 13-14; median setae of tergite IV with short among long. Marginal sternal setae: III, 13-14; IV, 14-17; V-VI, 6-8. Anterior sternal setae: III, 8-11; IV, 20; V, 6-10; VI, 5-7; VII, 1-2. Setae in each brush on sternite V, 39-43; VI, 18-23. Total number of setae on sternite VI, 52-56. Subgenital plate (Fig. 13) with 11-13 anterior setae, 19-21 marginal setae thicker than anterior setae and arranged in irregular row. Anal ventral fringe of 50-59 setae; total of 4-7 setae anterior to ventral fringe. Dimensions: HL, 0.48-0.49; AL, 1.58-1.61; AnW, 0.28.

**Male.** Tergal setae: I, 10-15; II, 13-16; III-VII, 14-18; VIII, 12-14. Marginal sternal setae: II, 8-12; III-IV, 11-14; V-VI, 5-7; VII, 8-10; VIII, 6-8. Anterior sternal setae: II, 5-7; III, 6-9; IV, 9-17; V, 1-6; VI, 0-5. Setae in each brush on sternite V, 30-42; VI, 15-23. Dimensions: TW, 0.54-0.56; HL, 0.45-0.47; PW, 0.32-0.34; MW, 0.51-0.55; AbW, 0.60-0.65; AL, 1.25-1.29; TL, 2.16-2.24; GL, 0.65-0.68.

Type material


Paratypes, 1 ♀, 8 ♂, same as holotype (BMNH; USNM; OSU; UM); 1 ♀, same, except Lao Group, Vavau Balavu, Hot Springs Cave, 1 km north of Namalata Channel, 20.xii.1993 (Wragg) (USNM).


*Dennysus (Collopendyus) lice from swiftlets* 189

Remarks

The female of *D. singhi* is morphologically closest to that of *D. krisitae*, but the former has more abdominal tergal setae on most segments and more marginal subgenital plate setae. The male of *D. singhi* has shorter genitalia and a tendency to smaller dimensions and fewer anterior sternal setae than *D. krisitae*.

Etymology

This species is named for Biranda Singh, National Trust for Fiji, for making the collection of these lice possible.

*Dennysus (Collopendyus) ferrisi* Ledger


**Female.** Tergal setae: I, 21; II, 24; III, 20; IV, 22; V, 19; VI-VII, 18; VIII, 14; median setae of tergite IV with short among long. Marginal sternal setae: II, 15; III, 16; IV, 19; V, 8; VI, 5. Anterior sternal setae: II, 7; III, 18; IV, 35; V, 7; VI, 3; VII, 0. Setae in each brush on sternite V, 54-58; VI, 25-28, with posterior setae similar in thickness to others in brush. Total number of setae on sternite VI, 61. Subgenital plate with 10 anterior setae, 13 marginal setae similar in thickness to anterior setae and arranged in regular row. Anal ventral fringe of 53 setae, dorsal of 56; total of 8 setae anterior to ventral fringe. Dimensions: TW, 0.62; HL, 0.51; PW, 0.38; MW, 0.65; AbW, 0.92; AL, 1.77; TL, 2.86; AnW, 0.33.

**Male.** Tergal setae: I, 18; II-III, 17; IV, 19; V, 18; VI-VII, 17; VIII, 14; median setae of tergite IV missing. Marginal sternal setae: II, 11; III-IV, 13; V, 6; VI, 4; VII, 9; VIII, 6. Anterior sternal setae: II, 5; III, 10; IV, 24; V-VI, 0; VII, 1; VIII, 0. Setae in each brush on sternite V, 44; VI, 21-23, with posterior setae similar in thickness to others in brush. Dimensions: TW, 0.58; HL, 0.48; PW, 0.34; MW, 0.56; AbW, 0.72; AL, 1.34; TL, 2.32; GL, 0.69.

Material examined

Holotype ♂, 1 ♀ paratype of *D. ferrisi*, ex *A. occita*, MARQUESAS (Emiss Museum of Entomology, University of California Berkeley).

Remarks

This species represents the first of two in this subgroup with a wide female anus measuring ≥0.33. The consistently large dimensions, larger number of setae on abdominal sternites III–IV, and differences in the number of brush setae on sternite VII separate *D. ferrisi* from the other wide-anus species (described below). Dimensions of male *D. ferrisi* either exceed, or are in
the upper range, those of the probable mixture of males of D.d.distinctus and the second wide-anus species (see ‘Remarks’ for D.d.distinctus). Males of D.ferrisi also have more anterior sternal setae on IV and more setae in the brushes on sternite V.

Dennys (Colloddenys) somadikartai sp.n. (Fig. 14)

Type host: Collocalia linchi linchi Horsfield & Moore.

Much as for D.ferrisi, except as follows.

Female. Tergal setae: I, 14–19; II, 16–22; III-IV, 17–22; V-VI, 15–23; VII, 13–17; VIII, 11–12. Marginal sternal setae: II, 10–14; III, 11–15; IV, 12–17; V, 5–6. Anterior sternal setae: II, 5–11; III, 7–15; IV, 7–32; V, 2–9; VI, 1–5. Setae in each brush on sternite V, 30–45; VI, 16–25, with posterior setae thinner than others for 10 specimens, similar to others in brush for 4. Total number of setae on sternite VI, 43–57. Subgenital plate (Fig. 14) with 10–14 anterior setae, 10–16 marginal setae. Anal ventral fringe of 55–68 setae, dorsal of 50–62; total of 4–10 setae anterior to ventral fringe. Dimensions: TW, 0.54–0.57; HL, 0.45–0.47; PW, 0.34–0.35; MW, 0.57–0.63; AbW, 0.74–0.89; AL, 1.54–1.63; TL, 2.45–2.58; AnW, 0.33–0.36.

Male. Discussed under D.d.distinctus.

Type material


Paratypes, 5 ♂, same as holotype (BMNH; USNM; OSU); 2 ♂, same, except only JAVA, 13.vi.1968 (OSU).

Other material

107 ♂, ex C.excludens cyanoptila, MALAYSIA: Sandakan.

Remarks

The means of separating the female of D.somadikartai from that of D.ferrisi were discussed earlier under D.ferrisi and will not be repeated here. We are unable to distinguish males of D.somadikartai from those of D.d.distinctus (see remarks for D.d.distinctus).

Etymology

This species is named in honour of Soekarja Somadikarta, in recognition of his important contributions to swiftlet systematics and for making the fieldwork in Java possible.

Thompsoni species-group

Diagnosis

Head (Figs 13, 18) with lateral preantennal margin concave; dorsal seta 5 (Fig. 15: arrow) short, heavy, other chaetotaxy as shown. Thorax (Fig. 15) usually with 8 marginal metanotal setae (less often 7 or 9), and each side with 3 anterior setae, these arranged with median seta longest and on line with anteriormost lateral seta. Median setae of tergite IV long, without much shorter setae in row. Each side of terminal tergite with 2 very long setae, with 1 short, fine seta inserted between them and variable number of short setae mediad of them.

Thompsoni species-subgroup

Diagnosis

The four taxa of this subgroup are separated from all others of the group by having both sexes with the preantennal lateral head margin only moderately concave, the mesosternum with 4–7 setae, the metasternum with 8–16 setae, and the index of abdomen length divided by abdomen width ranging from 1.7–2.2; the female with an anus width >0.32 and with a total of 1–7 setae distinctly anterior to ventral anal fringe (Fig. 17); and the male genitalia (Fig. 16) large, with only irregular small sclerites associated with spinose sac.

Dennys (Colloddenys) Thompsoni Ledger (Figs 15–17)

Dennys (Colloddenys) thompsoni Ledger, 1970: 255. Type host: Aerodramus maximus bowi Sharpe.

Female (Fig. 17). Tergal setae: I, 9–11; II-IV, 12–15; V, 12–17; VI-VII, 14–18; VIII, 14–15. Marginal sternal setae: II, 5–8; III, 7–13; IV, 10–15; V, 5–6; VI, 4–8. Anterior sternal setae: II, 6–10; III, 9–16; IV, 12–27; V, 10–12; VI, 4–8; VII, 0. Setae in each brush on sternite V, 32–44; VI, 21–27, with posterior setae usually similar in thickness to others in brush, occasionally thinner; total setae in brushes on VI, 45–51. Subgenital plate (Fig. 17) with 8–11 anterior setae, 18–22 marginal setae as thin as anterior setae and arranged in regular to slightly irregular row. Anal ventral fringe of 70–80 setae, dorsal of 48–56. Dimensions: TW, 0.56–0.58; HL, 0.46–0.48; PW, 0.32–0.35; MW, 0.56–0.61; AbW, 0.78–0.89; AL, 1.57–1.67; TL, 2.55–2.62; AnW, 0.38–0.42.

Male (Fig. 15). Tergal setae: I, 8–10; II, 11–13; III-IV, 12–14; V-VI, 14–16; VII, 14–18; VIII, 15–22. Marginal sternal setae: II, 4–5; III-IV, 5–9; V-VI, 3–4; VII, 8; VIII, 6. Anterior sternal setae: II-III, 4–7; IV, 4–12; V, 2–6; VI, 0–3; VII, 0–1; VIII, 0. Setae in each brush on sternite V, 24–34; VI, 16–24, with posterior setae similar in thickness to others in brush; total setae in brushes on VI, 34–45. Dimensions: TW, 0.52–0.56; HL, 0.44–0.46; PW, 0.30–0.32; MW, 0.49–0.54; AbW, 0.58–0.68; AL, 1.09–1.20; TL, 1.95–2.12; GL, 0.64–0.70.

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Fig. 12. Dennyus carlsoni carlsoni Clayton, Price & Page, female ventral terminal abdomen.

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Material examined

1 ♂, 1 ♀ paratypes of D. thompsoni, ex A. m. lowi, SARAWAK; 6 ♂, 6 ♀, ex A. maximus (Hume), MALAYSIA: Balembangen Is. & Gomantong Caves; 1 ♂, ex A. fuciphagus (Thunberg), MALAYSIA: Gomantong Caves.

Remarks

This species is separated from the other three species of the subgroup by the female having a wide anus, a short abdomen and total length, and a larger number of total setae in the brushes on sternite VI and subgenital plate margin. The male
of *D. thomsoni* is inseparable from one of the other species and tenaciously separable from the remaining two (see below) only by a larger total setae in the brushes on sternite VI, a smaller number of marginal setae on sternite IV, and smaller genitalia.

**Dennysus (Coliodennysus) wellsi** sp.n.

*Type host: Aerodramus salanganus* (Streobel).

As for *D. thomsoni*, except as follows.

**Female.** Tergal setae: I, 8–12; VI–VIII, 13–16. Marginal sternal setae: II, 4–7; III, 6–12; IV, 7–14; V, 4–7; VI, 3–6. Anterior sternal setae: II, 5–11; III, 7–14; IV, 7–21; V, 4–14; VI, 2–7. Setae in each brush on sternite V, 25–39; VI, 15–23; total setae in brushes on VI, 32–42. Subgenital plate with 13–18 marginal setae. Anal ventral fringe of 63–78 setae, dorsal of 46–52. Dimensions: TW, 0.55–0.58; HL, 0.45–0.48; PW, 0.31–0.34; MW, 0.55–0.69; ABW, 0.74–0.90; AL, 1.53–1.67; TL, 2.47–2.64; AaW, 0.37–0.43.

**Male.** Tergal setae: I, 8; II, 10–12; V–VI, 12–16; VIII, 13–17. Anterior sternal setae: II–IV, 3–8; V, 1–6; VI, 1–2. Setae in each brush on sternite V, 23–29; VI, 14–20; total setae in brushes on VI, 29–39. Dimensions: TW, 0.50–0.54; PW, 0.29–0.31; MW, 0.48–0.52; ABW, 0.57–0.63; GL, 0.63–0.65.

**Type material**

Holotype, ♀, ex *A. salanganus*, MALAYSIA: Sabah, Gomantong Caves, i.1994 (Clayton) (BMNH).

Paratypes, 11 ♂, 2 ♀, same as holotype (BMNH; USNM); 1 ♀, 2 ♂, same, except 21.vii.1994 (UM); 5 ♂, 4 ♀, same, except 22.vii.1994 (BBM); 1 ♂, same, except 7.vi.1994 (Tomkins) (UM); 1 ♀, same, except 18.vi.1994 (Tomkins) (UM); 2 ♂, same, except 5.vii.1994 (Tomkins) (BMNH); 3 ♂, 2 ♀, same, except 4.vii.1994 (Tomkins) (OSU); 1 ♀, same, except 16.viii.1994 (Tomkins) (UM); 1 ♂, 1 ♀, same, except 18.viii.1994 (Tomkins) (OSU); 3 ♀, 2 ♂, same, except 16.viii.1994 (Tomkins) (UM); 1 ♂, 1 ♀, same, except 18.viii.1994 (Tomkins) (BMNH); 3 ♀, 2 ♂, same, except 16.viii.1994 (Tomkins) (BMNH); 3 ♀, 2 ♂, same, except 16.viii.1994 (Tomkins) (BMNH); 3 ♀, 2 ♂, same, except 16.viii.1994 (Tomkins) (BMNH).

**Remarks**

The female of *D. wellsi*, with the wide anus, short abdomen and short total length, is similar to that of *D. thomsoni* and thereby different from the other two species of this subgroup; it is separable from *D. thomsoni* in having fewer total setae in the brushes on sternite VI and fewer marginal setae on the subgenital plate. The male is quite close to those of the other subgroup taxa, but it tends to have shorter genitalia and fewer total setae in the brushes on sternite VI than *D. thomsoni*.


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**Dennysus (Coliodennysus) collinsi** sp.n.

*Type host: Aerodramus brevirostris vulcanorum* (Stresemann).

Close to *D. thomsoni*, except as follows.

**Female.** Tergal setae: I, 8–12; IV, 14–17; V–VIII, 13–16; VIII, 13–14. Marginal sternal setae: II, 6–9; III–IV, 10–17; V, 6–8; VI, 4–7. Anterior sternal setae: II, 6–12; III, 11–17; IV, 13–32; V, 6–16; VI, 4–10; VII, 0–2. Setae in each brush on sternite V, 34–45; VI, 21–30; total setae in brushes on VI, 42–58. Subgenital plate with 9–12 anterior setae, 15–23 marginal setae. Anal ventral fringe of 72–85 setae. Dimensions: MW, 0.58–0.63; AL, 1.73–1.79; TL, 2.68–2.76; AaW, 0.40–0.45.

**Male.** Tergal setae: IV, 14–16; V, 14–17; VI, 16–17; VII, 16–20. Marginal sternal setae: II, 4–6; III, 8–9; IV, 9–12. Dimensions: HL, 0.43–0.47; ABW, 0.65–0.69; AL, 1.12–1.22; TL, 1.97–2.15; GL, 0.68–0.70.

**Type material**


Paratypes, 7 ♀, 5 ♂, same as holotype (BMNH; USNM; OSU; UM; BBM).

**Remarks**

The female of *D. collinsi*, with its wide anus, is allied with the previous two species, but differs from them in having a consistently longer abdomen and total length. The male, with ≥10 marginal setae on sternite IV and a genitalia length ≥0.68, is distinguished from most males of the other three species of this subgroup.

**Etymology**

This species is named in honour of Charles Collins, California State University, in recognition of his many contributions to swift biology and his critical assistance to this project.

---

**Dennysus (Coliodennysus) adamsae** sp.n.

*Type host: Aerodramus terraereginae terraereginae* (Ramsay).

**Female.** Tergal setae: I, 8–12; II, 12–15; III–VIII, 13–17.
Marginal sternal setae: II, 4–6; III, 7–12; IV, 9–13; V–VI, 3–6. Anterior sternal setae: II, 5–10; III, 10–13; IV, 11–21; V, 7–11; VI, 1–8; VII, 0–1. Setae in each brush on sternite V, 29–39; VI, 16–25, with posterior setae similar in thickness to others in brush; total setae in brushes on VI, 35–49. Subgenital plate with 9–12 anterior setae, 16–20 marginal setae as thin as anterior setae and arranged in regular row. Anal ventral fringe of 60–76 setae, dorsal of 29–54. Dimensions: TW, 0.54–0.56; HL, 0.43–0.46; PW, 0.31–0.33; MW, 0.56–0.62; AbW, 0.73–0.85; AL, 1.48–1.64; TL, 2.38–2.56; AnW, 0.33–0.35.

Male. Tergal setae: I, 8–10; II, 11–14; III–IV, 12–15; V–VI, 13–17; VII–VIII, 17–20. Marginal sternal setae: II, 3–4; III–IV, 7–10; V–VI, 3–4; VII, 8–9; VIII, 6–7. Anterior sternal setae: II, 4–7; III, 4–13; IV, 5–14; V, 2–7; VI, 0–5; VII–VIII, 0. Setae in each brush on sternite V, 21–31; VI, 15–23, with posterior setae similar in thickness to others in brush; total setae in brushes on VI, 32–45. Dimensions: TW, 0.50–0.53; HL, 0.42–0.44; PW, 0.28–0.31; MW, 0.47–0.53; AbW, 0.58–0.68; AL, 1.06–1.19; TL, 1.88–2.04; GL, 0.63–0.67.

Type material
Holotype, ♀, ex A. terraearingae, AUSTRALIA: N. Queensland, Tully Gorge, 50 km from Tully, 26.III.1994 (Clayton) (BMNH).
Paratypes, 3 ♀, 3 ♂, same as holotype (BMNH, USNM; OSU).

Other material
2 ♀, 3 ♂, ex A. terraearingae chillagoensis Pecotich, AUSTRALIA.

Remarks
The female of D. adamsiae is easily distinguished from those of the other three taxa of this subgroup by its narrower anus. The male is separable principally on the basis of its host and their isolated locality in North Queensland, Australia.

Etymology
This species is named for Nancy Adams, National Museum of Natural History, in recognition of her labours in organizing the chewing lice in that collection and her generosity in responding to my many loan requests.

francicus species-subgroup

Diagnosis
The four taxa of this subgroup are separated from all others of the group by having both sexes with the preantenal lateral head margin deeply concave, the mesosternum with only 4 setae, the metasternum with only 7–12 setae, and the index of abdomen length divided by abdomen width ranging from 1.3–1.7 for females, 1.3–1.5 for males; the female with an anus <0.30 and with a very irregular ventral anal fringe laterally (Fig. 20); and the male genitalia smaller, with well defined small sclerites associated with spinose sac (Fig. 19).

Dennysus (ColloDennysus) francicus Thompson

Dennysus (ColloDennysus) francicus Thompson, 1941; 530. Type host: Aerodramus spodiopygius reichenowi (Stresemann).

Female. Much as in Fig. 20. Tergal setae: I, 11; II, 15; III–VII, 16–18; VIII, 14. Terminal tergite with total of 4 setae medioventral of very long setae. Marginal sternal setae: II, 11; III, 13; IV, 16; V, 8; VI, 6. Anterior sternal setae: II–III, 5; IV, 10; V–VI, 2; VII, 1. Setae in each brush on sternite V, 30–33; VI, 20, with posterior setae similar in thickness to others in brush; subgenital plate with 15 anterior setae, 13 marginal setae similar in thickness to anterior setae and arranged in regular row. Anal ventral fringe of 52 setae, dorsal of 48. Dimensions: TW, 0.53; HL, 0.44; PW, 0.30; MW, 0.54; AbW, 0.87; AL, 1.12; TL, 2.03; AnW, 0.23.

Male. Much as in Fig. 18. Tergal setae: I, 8; II, 13; III–IV, 16–17; V, 19; VI–VII, 17; VIII, 15. Terminal tergite with total of 4 setae medioventral of very long setae. Marginal sternal setae: II, 6; III, 9; IV, 11; V–VI, 5–6; VII, 9; VIII, 6. Anterior sternal setae: II–IV, 5–6; V–VII, 1–2; VIII, 0. Setae in each brush on sternite V, 19–26; VI, 16, with posterior setae similar to others in brush. Dimensions: TW, 0.51; HL, 0.42; PW, 0.29; MW, 0.48; AbW, 0.67; AL, 0.89; TL, 1.71; GL, 0.54.

Material examined
Allotype ♂, 1 ♀ paratype of D. francicus, ex A. s. reichenowi, BRITISH SOLOMON IS.

Remarks
The features separating the female of D. francicus from those of the other three species of this subgroup are the terminal tergite with a total of 4 setae medioventral of the very long setae, in combination with the smaller temple width, anus width, and total length. The male is distinguished by also having a total of 4 setae medioventral of the very long setae on the terminal tergite, in combination with >18 setae on tergite V.

Dennysus (ColloDennysus) simberloffii sp.n. (Figs 18–20)

Type host: Aerodramus maximus (Hume).

Much as for D. francicus, except as follows.

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**Dimensions:** TW, 0.54–0.57; HL, 0.44–0.46; PW, 0.30–0.32; MW, 0.54–0.60; AbW, 0.81–0.97; AL, 1.26–1.47; TL, 2.17–2.37; AnW, 0.24–0.29.


Setae in each brush on sternite V, 21–33; VI, 18–24. Dimensions: TW, 0.50–0.53; HL, 0.39–0.43; PW, 0.28–0.31; MW, 0.46–0.50; AbW, 0.60–0.69; AL, 0.87–0.98; TL, 1.71–1.82; GL, 0.52–0.58.

**Type material**

Holotype, ♀, ex *A. maximus*, MALAYSIA: Sabah, Bomontong Caves, 2.viii.1994 (Tomkins) (BMNH).
Paratypes, 3 ♀, 1♂, same as holotype (BMNH; USNM); 4 ♀, 2♂, same, except 4.vii.1994 (OSU; UM); 1♂, same, except 14.viii.1994 (USNM); 1♀, same, except 1.9.1994 (Clayton) (OSU); 3♀, 2♂, ex *A. maximus*, MALAYSIA: N. Sabah, Dalembang Is., 18.iii.1994 (Clayton) (USNM; BBM).

**Other material**

1♂, ex *A. fuscogriseus*, MALAYSIA: Sabah, Bomontong Caves.

**Remarks**

The female of *D. simberloff* is allied with *D. francicus* in having a total of at least 4 setae between the very long setae on the last tergite; it is separated from this species in having a wider temple, wider anus, and longer abdomen and total length. The male of *D. simberloff* is similarly grouped with *D. francicus* on the basis of the chaetotaxy of the terminal tergite; it may tenuously be separated by the smaller number of setae on tergite V and by a total ≥5 setae between the very long setae on the terminal tergite.

**Etymology**

This species is named in honour of Daniel Simberloff, Florida State University, in recognition of his important and wide-ranging studies of ecology and airline silverware.

**Dennyus (Collodennyus) wraggi** sp.n.

**Type host**: Aerodrampus spodiopygius assimilis (Stresemann).

**Female**. Tergal setae: I, 10–15; II–VI, 15–19; VII, 14–18; VIII, 12–14. Terminal tergite usually with total of only 2, less often 3, setae medially of very long setae. Marginal sternal setae: II, 9–10; III, 11–13; IV, 12–15; V, 5–8; VI, 4–7. Anterior sternal setae: II, 4–6; III–IV, 6–13; V–VI, 1–7; VII, 0–3. Setae in each brush on sternite V, 24–32; VI, 19–25, with posterior setae similar in thickness to others in brush. Subgenital plate with 13–15 anterior setae, 14–17 marginal setae in thickness to anterior setae and arranged in regular row. Anal ventral fringe of 52–61 setae, dorsal of 46–52. Dimensions: TW, 0.51–0.53; HL, 0.41–0.42; PW, 0.29–0.31; MW, 0.51–0.53; AbW, 0.74–0.80; AL, 1.06–1.20; TL, 1.88–2.05; AnW, 0.22–0.23.

**Male**. Tergal setae: I, 8–9; II, 12–14; III, 14–16; IV–VI, 16–18; VII, 15–17; VIII, 13–15. Terminal tergite with total of only 2 setae medially of very long setae. Marginal sternal setae: II, 5–7; III, 8–9; IV, 8–12; V–VI, 4; VII, 8–9; VIII, 6. Anterior sternal setae: II, 4–7; III, 3–5; IV, 2–3; V–VI, 0–1; VII–VIII, 0. Setae in each brush on sternite V, 18–23; VI, 13–18, with posterior setae similar in thickness to others in brush. Dimensions: TW, 0.48–0.51; HL, 0.39–0.40; PW, 0.27–0.29; MW, 0.44–0.47; AbW, 0.54–0.66; AL, 0.80–0.85; TL, 1.56–1.62; GL, 0.48–0.51.

**Type material**

Paratypes, 5 ♀, 5♂, same as holotype (BMNH; USNM; OSU; UM; BBM); 1♀, 1♂, ex *A. assimilis*, FIJI: Lau Group, Vanua Balavu, Hot Springs Cave, 1 km north of Namalata Channel, 20.xii.1993 (Wragg) (USNM).

**Remarks**

The female of *D. wraggi* is distinguished from those of the first two species of this subgroup by having a total of 2, less often 3, setae between the very long setae on the terminal tergite. The reduced number of setae on tergite V and sternite III separate it from the female of the fourth species of this subgroup. The male of *D. wraggi* also differs from the first two species by having a total of only 2 setae between the very long setae on the terminal tergite. Its reduced number of setae on tergites VII–VIII and tendency for reduced chaetotaxy and smaller dimensions also distinguish it from the fourth species of this subgroup.

**Etymology**

This species is named for Graham Wragg, University of Oxford, in appreciation for his assistance and advice on this project.

**Dennyus (Collodennyus) tarbutoni** sp.n.

**Type host**: Aerodrampus spodiopygius spodiopygius (Peale).

Much as for *D. wraggi*, except as follows.


of 52–54 setae, dorsal of 48–54. Dimensions: MW, 0.53–0.54; AnW, 0.24–0.25.

Male. Tergal setae: II, 14–15; III, 17; IV–VI, 16–19; VII, 18–20; VIII, 18–21. Marginal sternal setae: II, 6–9; VII, 8–10. Anterior sternal setae: II, 3–4; IV, 2–4. Setae in each brush on sternite V, 21–25; VI, 18–20. Dimensions: HL, 0.38–0.40; MW, 0.46–0.48; AL, 0.82–0.89; TL, 1.63–1.68; GL, 0.50–0.52.

Type material

Holotype, ♀, ex A.s. spodiopygus, WESTERN SAMOA: Upolu, Ole Pupu-Pue National Park, Pepea Cave, 31.i.1994 (Clayton) (BMNH).
Paratypes, 1 ♀, 3 ♂, same as holotype (BMNH; USNM; OSU).

Remarks

The distinguishing features for both sexes of D.tarbutoni have been discussed under the remarks for the preceding species.

Etymology

This species is named in honour of Michael Tarbuton, Adventist College, Apia, in recognition of his important research on swiftlet biology and his critical assistance to this project.

Discussion

Host associations

Table 2 lists the hosts for the twenty-three known taxa of Dennys (Colloddenys). Within the Dennys distinctus species-group, three of the four taxa in the distinctus species-subgroup are restricted to hosts of the genus Collucalia. These three taxa are found on C.esculentum in diverse geographical localities, and one of them, D.distinctus, also occurs on C.linchi. The fourth member of this subgroup, D.medwayi, occurs only on the monotypic genus Hydrochus. What is unusual is that D.somadikartai, the sole member of the other two species-subgroups not from Aerodramus hosts, co-occurs on the two species of host that also have D.distinctus. This represents the only case of sympatric species of lice from the distinctus species-group. The females of these two species are quite distinct from one another, but the males have proven inseparable.

The remaining eight species in the distinctus species-group are all found on species of the genus Aerodramus, with most being specific to a single host species or subspecies. Only D.carlojones has been collected from more than a single host taxon. D.carlojones has been collected from three species of hosts occurring within Gomantong Caves of Sabah, Malaysia.

A second subspecies (D.c.fosteri) is restricted to A.elaphrus in the Seychelles and a third subspecies (D.c.forrestieri) is restricted to A.franicus in Mauritius.

The eight species of the thompsoni species-group are all found on species of genus Aerodramus. The most intriguing pattern involving these lice is the co-occurrence on A.maximus of D.thompsoni, a member of the thompsoni species-subgroup, D.simberloffi, a member of the francicus species-subgroup, and D.carrjonesi, a member of the distinctus species-group. Specimens of all three of these louse taxa have been collected from individual birds nesting in Gomantong Caves, Sabah, Malaysia. Were it not for the fact that these lice are so morphologically distinct, we might well have overlooked the presence of this many taxa on a single host.

Phenetic relationships

Figures 21 and 22 show principal component ordinations for individuals of twelve species of the distinctus group. In the ordination of male lice (Fig. 21), the three subgroups recognized here are nonoverlapping, with the notable exception of D.medwayi (ex Hydrochus gigas) from the distinctus subgroup which nestles among the elliottii subgroup (all ex Aerodramus). The ordination for male lice (Fig. 22) resembles that for females, and again D.medwayi groups with elliottii lice. Males of D.distinctus and D.somadikartai are indistinguishable; interestingly, females of these two taxa are adjacent in the principal components ordination (Fig. 21). Male D.emersoni appear close to D.distinctus and D.somadikartai males. Female and male D.ferrisi occupy an isolated position in both ordinations, paralleling the geographic isolation of the host, Aerodramus octist, which is restricted to the Marquesas Islands.

Principal components analysis of female thompsoni group lice confirms the distinctiveness of the thompsoni and francicus subgroups (Fig. 23). Within the francicus subgroup, the lice hosted by subspecies of Aerodramus spodiopygus form one cluster distinct from D.simberloffi (hosted by A.maximus and A.fuciphaque). Ordinations of both females (Fig. 23) and males (not shown) failed to cleanly separate taxa in the thompsoni subgroup.

Figures 24 and 25 show the results of the cluster analysis for female and male lice computed from scores for the first five principal components. In both dendrograms Dennys (Colloddenys) and D. (Dennys) taxa group together. The trees for both sexes display the division into the distinctus and thompsoni species-groups, and both trees support the division of the thompsoni species-group into the thompsoni and francicus subgroups. The two sexes disagree over relationships of some taxa within the distinctus species-group; however, both suggest that D.medwayi is not related to other members of the distinctus subgroup.

Cladistic analysis of relationships among Dennys (Colloddenys) will require adequate numbers of discrete characters. Because of the paucity of morphological variation within this subgenus, morphology is likely to provide few discrete characters. The morphometric characters used in this
### Table 2. Host list for all known species of Dennyua (Colloidennysa).

<table>
<thead>
<tr>
<th>Host taxon</th>
<th>Colloidennysa species-group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>distinctus</td>
</tr>
<tr>
<td>Collocalia esculenta e. cyanoptila</td>
<td>*d. distinctus</td>
</tr>
<tr>
<td>e. desiderata</td>
<td>#somadikartai sp.n.</td>
</tr>
<tr>
<td>Collocalia linchi</td>
<td>*d. distinctus</td>
</tr>
<tr>
<td>Hydrochous gigas</td>
<td>*medwayi</td>
</tr>
<tr>
<td>Aerodramus whiteheadi</td>
<td>*eliotii</td>
</tr>
<tr>
<td>Aerodramus hirundinaceus</td>
<td>*haliaeae sp.n.</td>
</tr>
<tr>
<td>Aerodramus terraereginae 1. terraereginae</td>
<td>*boothi sp.n.</td>
</tr>
<tr>
<td>1. chilagoensis</td>
<td>*carljensei sp.n.</td>
</tr>
<tr>
<td>Aerodramus faciphus</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus salanganus</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus vonkorensis</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus maximus</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus francicus</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus elaphus</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus brevirastris</td>
<td>*francicus</td>
</tr>
<tr>
<td>Aerodramus spodiopygium 1. spodiopygium</td>
<td>#kristiani sp.n.</td>
</tr>
<tr>
<td>1. assimilis</td>
<td>#ranghi sp.n.</td>
</tr>
<tr>
<td>1. reichenowi</td>
<td></td>
</tr>
<tr>
<td>Aerodramus ocista</td>
<td></td>
</tr>
</tbody>
</table>

* distinctus species-subgroup.
# emersoni species-subgroup.
$ eliotii species-subgroup.
§ thomposoni species-subgroup.
¶ francicus species-subgroup.

The louse trees shown in Figs 24 and 25 are phenetic, and are best viewed as hypotheses of relationships to be tested by future phylogenetic analysis of characters showing more informative variation. However, with this caveat firmly in mind, it is worth comparing the phenetic trees to the host phylogeny as a preliminary test of host-parasite cooccupation. Figure 26 shows a phylogeny for swiftlets and their relatives obtained from cytochrome b mitochondrial DNA sequences (Lee et al., 1996) and a consensus of the dendrograms shown in Figs 24 and 25 for the subset of lice collected from swiftlets included in the host phylogeny. While there are some elements common to the bird and louse trees, such as the close phenetic relationship among lice from Collocalia, the occurrence of a pair of similar lice (thomposoni and collinsi) on the sister taxa Aerodramus maximus and A. vulcanorum, and the proximity of most carljensei subspecies hosts, the immediate visual impression is one of incongruence between the two trees.

One explanation for such incongruence is past episodes of host switching between unrelated swiftlet taxa. Indeed, incongruence between host and parasite phylogenies is almost always cited as evidence for host switching (Barker, 1994). However, incongruence can arise for other reasons (Lyal, 1986; Page et al., 1996). A second possibility is presence on the ancestral host of more than one parasite lineage, followed by cospeciation of each parasite lineage, as well as considerable extinction, resulting in a phylogenetically patchy distribution (Clay, 1949; Page et al., 1996).

Host-switching by Colloidennysa is suggested by the presence of some species on phylogenetically unrelated hosts, notably the occurrence of D.c.carljensei on Aerodramus faciphus (type host), A.maximus, and A.salanganus. All three of these hosts nest in Gomantong Caves, Malaysia, suggesting that physical proximity may have facilitated host switching, as appears to be the case for owl lice (Clayton, 1990). In contrast, multiple lineages are suggested by the presence of two pairs...
Fig. 21. Principal components ordination of female *Dennyus distinctus* group lice. The first and second principal components (PC 1 and PC 2) account for 31.6% and 19.8% of the variation, respectively.

Fig. 22. Principal components ordination of male *Dennyus distinctus* group lice. Males of *D. d. distinctus* and *D. somakaiturai* are indistinguishable and hence *D. distinctus* and *D. somakaiturai* are represented by the same symbol. The first and second principal components (PC 1 and PC 2) account for 31.1% and 18.9% of the variation, respectively.

of closely related lice (*tarburtoni* and *wragei; kristinae* and *singhi*) on *A.s.spodiopygus* and *A.s.sassilis*, respectively. This pattern suggests that distinct lineages of lice (members of the *distinctus* and *thompsoni* species-groups) have been tracking the same set of hosts.

Teasing apart the relative contributions of speciation, host switching, and multiple lineages will be challenging and may well be facilitated by molecular data. The host switching and multiple lineages explanations make different predictions about the relative ages of bird and louse clades (Page et al., 1996). Host switching predicts that louse taxa will tend to have evolved more recently than their hosts, whereas multiple lineages predicts that at least some louse clades will be older than their hosts. If rates of DNA sequence divergence in birds and lice are relatively constant (molecular clocks ticking at similar rates), then molecular data can be used to compare the relative ages of the two groups. Such a comparison could help to distinguish between competing explanations for the apparent incongruence of swiftlet–louse relationships. This work is currently in progress.

**Key to the species of *Dennyus* (Collocomynus)**

**Females**

1. Lateral preantennal margin essentially straight; dorsal head seta 5 (Fig. 1: arrow) short, slender (*distinctus* species-group)………………………………………………………2

2. Lateral preantennal margin concave; dorsal head seta 5 (Fig. 15: arrow) stout, peg-like (*thompsoni* species-group)………………………………………………………3

3. With setae anterior to ventral anal fringe (Figs 4, 8, 9) (*distinctus* species-subgroup)………………………………………………………3

4. Without setae anterior to ventral anal fringe (Figs 10–14) 6

3. At least 16 setae on each tergite IV–V (Fig. 2); anus width <0.28 (*D.distinctus* Ferriss)…………………………………………………4

4. Not over 15 setae on each tergite IV–V (Fig. 11); anus width >0.29……………………………………………………………………………5

5. Usually temple width ≤0.54, abdomen width ≤0.75, and ≤31 setae in each brush on sternite V. Ex *Collocalia linchi* (Java), *C.esculenta* (New Guinea; Malaysia [Sandakan])……………………………*D. distinctus* distinctus Ferriss

6. Temple width >0.54, abdomen width usually ≥0.78, and often ≥31 setae in each brush on sternite V. Ex *Collocalia esculenta* (Malaysia [Ampang Reservoir])……………………………………………………………………………*D. distinctus* limonest ssp.n.
5. Subgenital plate with 6 medioanterior setae (Fig. 8); temple width < 0.55, D. thersae sp.n.  
   Subgenital plate without medioanterior setae (Fig. 9); temple width > 0.57, D. medwayi Ledger

6. Most of tergites II–VI with < 15 setae (Fig. 11) emersoni species-subgroup)
   Each tergite II–VI with > 15 setae (emersoni species-subgroup) ........................................ 12

7. Anus ≈0.22 wide .................................................. D. boothi sp.n.
   Anus > 0.24 wide .................................................. 8

8. Over 35 total setae on sternite VI (Fig. 12); sternite VI with > 1 medioanterior seta, sternite V usually with > 2 such setae (D. carlJonesi sp.n.) ........................................................................ 9

9. Fewer than 35 total setae on sternite VI; sternite VI without medioanterior setae, sternite V with only 0–1 such setae ........................................................................................................ 11

10. Often 3–4 setae on sternite I; 1–3 anterior setae on sternite VII; temple width > 0.59; from Seychelles
   Only 2 setae on sternite I; usually no anterior setae on sternite VII; temple width usually < 0.59; from Mauritius
   Abdomen length > 1.68; from Malaysia ....................................................................................... 10

D. hirundinis

D. csitrus

D. (Dennyus) (CoX)
— Subgenital plate usually with $\geq 16$ marginal setae; often $< 6$ total setae anterior to ventral anal fringe; abdomen length $\leq 1.68$; from Mauritius ....... D. c. forresteri ssp.n.

11. Abdomen width $< 0.75$; abdomen length $< 1.72$; sternite IV with $< 9$ anterior setae (Fig. 11) .... D. elliotti Ledger

— Abdomen width $> 0.75$; abdomen length $> 1.73$; sternite IV with $> 9$ anterior setae.............. D. hahnae sp.n.

12. Anus width $> 0.31$.................................13

— Anus width $< 0.30$................................. 14

13. Temple width $> 0.60$; abdomen length $> 1.72$; $> 17$ anterior setae on sternite III, $> 34$ on sternite IV.............. D. ferrisi Ledger

— Temple width $< 0.59$; abdomen length $< 1.68$; $< 16$ anterior setae on sternite III, $< 33$ on sternite IV.............. D. somadikartai sp.n.

14. Total of $< 42$ setae on sternite VI; $< 4$ anterior setae on sternite V; marginal subgenital plate setae similar in thickness to anterior setae, in regular row........................................ D. emersoni Ledger

— Total of $> 47$ setae on sternite VI; $> 5$ anterior setae on sternite V; marginal subgenital plate setae thicker than anterior setae, in irregular row........................................ 15

15. Tergites II–III each with $< 19$ setae; subgenital plate with $< 18$ marginal setae; from Western Samoa.............. D. kristinae sp.n.

— Tergites II–III each with $> 20$ setae; subgenital plate $> 19$ marginal setae (Fig. 13); from Fiji.............. D. singhi sp.n.

16. Anus $> 0.32$ wide; abdomen generally narrow, elongate, with abdomen length/abdomen width $1.7–2.2$ (Fig. 17) (thompsoni species-subgroup)................................. 17

— Anus $< 0.30$ wide; abdomen generally short, rounded, with abdomen length/abdomen width $1.3–1.7$ (Fig. 20)
Fig. 26. Comparison of molecular phylogeny for swifts and swiftlets with a tree for Denysia lice hosted by those birds. The host phylogeny is based on a maximum likelihood analysis of cytochrome b mitochondrial DNA sequences (Lee et al., 1996). The tree for Denysia is a strict consensus of the dendrograms shown in Figs 24 and 25, after deleting lice from birds for which molecular data are unavailable. Each house is connected to its host(s) by a thin line (see Table 2).

17. Anas <0.35 wide ........................................ D. adamsiae sp.n. 18. Abdomen length >1.72; total length >2.67 ....................... D. collinsi sp.n. — Abdomen length <1.70; total length <2.65 ................. 19. Total of >43 setae in brushes on sternite VI; >18 (mean = 20.0) marginal subgenital plate setae ............... D. thompsoni Ledger — Total of <43 setae in brushes on sternite VI; <18 (mean = 16.2) marginal subgenital plate setae ............... D. wellsi sp.n. 20. Terminal tergite with total of 2 setae between very long setae, less often 1 or 3 .................................................. 21 — Terminal tergite with total of >4 setae between very long setae. ................................................................. 22 21. Tergite V with >20 setae; sternite III with >14 marginal setae .......................................................... D. wraggi sp.n. — Tergite V with <19 setae; sternite III with <14 marginal setae .......................................................... D. thompsoni sp.n. 22. Temple width >0.54; anus width >0.24; total length >2.15 ................................................................. D. franciscus Thompson Males

The male of D. thomasae sp.n. is unknown. As discussed earlier, males are often difficult to separate and characters in the following key may be true for only the majority of specimens.

1. Lateral preantennal margin essentially straight; dorsal head seta 5 (Fig. 1: arrow) short, slender (distinctus species-group) ................................................................. 2 — Lateral preantennal margin concave; dorsal head seta 5 (Fig. 15: arrow) stout, peg-like (thompsoni species-group). ........................................................................ 16
2. Posterior setae of both sternite VI brushes with some to all slender, long, similar to median marginal setae (Figs 11, 12) ................................................................. 3 — Posterior setae of both sternite VI brushes thicker and shorter than median marginal setae (Fig. 1) ................................................................. 6
3. Temple width >0.52; from Malaysia or Mauritius [D. carlsoni sp.n. (in part)] ........................................ 4 — Temple width <0.51; from elsewhere ......................... 5
4. Genitalia length >0.69; from Malaysia [D. carlsoni Clayton, Price & Page (in part)] .......................... 6 — Genitalia length <0.69; from Mauritius ......................... 7

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Dennysus (Colloedennys) lice from swiftlets

II–III ≥9; from Philippine Is. — D.elliottii Ledger
Genitalia length >0.60; total anterior setae on sternites II–III ≤7; from New Guinea — D. bahnae sp.n.
6. Genitalia length ≥0.60 and ≥27 total setae on sternite IV. — D. ferrisi Ledger
8. Total of <14 anterior setae on sternites II–IV; ex H. gigas or A. terraereginae. — D. cristinus sp.n.
9. Total of >15 anterior setae on sternites II–IV; ex other host taxa. — D. medwayi Ledger
10. Temple width >0.50; head length >0.47; metathorax width >0.53; ex Malaysian Hydrochoerus — D. emersoni Ledger
11. Temple width >0.53; head length >0.46; metathorax width >0.52; ex Australian Aerodramus D. boothi sp.n.
12. Head length ≥0.47; sternite I with 2–3 setae; from Seychelles — D. cristinus sp.n.
13. Head length ≥0.47; sternite I with only 2 setae; from Mauritius — D. cristinus sp.n.
14. Ex Aerodramus from Fiji — D. singhi sp.n.
15. Ex Collocalia from elsewhere. — D. singhi sp.n.
16. Genitalia length >0.50; from Malaysia (Sandakan), Java, New Guinea. — D. distinctus Ferris
17. Genitalia length >0.50; from Malaysia (Ampang Reservoir). — D. timonensis Ferris
18. Ex Aerodramus terraereginae from N. Queensand. — D. adamsii sp.n.
19. With total >34 (mean = 39.1) setae in brushes on sternite VI; genitalia >0.64 (mean = 0.661) long; ex A. maximus or A. faciplicatus; D. thompsoni Ledger
20. Terminal tergite with total of only 2 setae aligned between very long setae. — D. thompsoni Ledger
21. With >18 setae on each of tergites VII–VIII. — D. thompsoni Ledger
22. Terminal tergite with total of only 4 setae between very long setae; tergite V with >18 setae; ex A. spodioprygius — D. franciscus Thompson
23. Terminal tergite with total of ≥5 setae between very long setae; tergite V with <18 setae; ex A. maximus. — D. simberloffi sp.n.

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References


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