

# Revision of *Dennyus* (*Collodennyus*) 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* (*Collodennyus*) 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 *Collodennyus* 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* (*Collodennyus*) 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 & Bledsoe, 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 *Collodennyus* (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 *Collodennyus* (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 *Collodennyus* is severely

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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 *Collodennyus* species transferred among different 'normal' host species is not impaired. Experiments of this kind may shed light on parameters governing the extent of cospeciation vs. host-switching.

A prerequisite for testing the cospeciation 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 *Collodennyus* 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-lice association is a complex one. Teasing apart the relative contributions of cospeciation 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 & Driessens (1995), but we recognize Brooke's (1972) division of *Collocalia* into *Collocalia sensu stricto*, *Aerodramus* and *Hydrochous*.

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 *Collodennyus* 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  $\pm$  standard error are given for each variable). All statistical analyses were performed using MINITAB® 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 *Dennyus* (*Collodennyus*) 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 *Dennyus* (*Dennyus*) were included in the analysis: *Dennyus hirundinus* (from *Apus apus*) and *D. cypsiurus* (from *Cypsiurus balasiensis*) (Ledger, 1971).

## Descriptions

### Subgenus *Collodennyus* Ledger

*Collodennyus* Ledger, 1970: 240. Type species: *Dennyus distinctus* Ferris.

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

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

**Diagnosis**

Menoponid 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 mediad 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).

***Dennyus (Collodennyus) 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, 13–23, 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: temple width (TW), 0.52–0.57; head length (HL), 0.43–0.46; prothorax width (PW), 0.31–0.35; metathorax width (MW), 0.52–0.60; abdomen width at segment IV (AbW), 0.68–0.82; 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, 3–15; V, 0–6; VI, 0–3; VII, 0–1; VIII, 0. Setae in each brush on sternite V, 23–37; VI, 13–24, 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 smaller head dimensions and more tergal setae at least on II–IV.

***Dennyus (Collodennyus) distinctus distinctus Ferris***

*Dennyus distinctus* Ferris, 1916: 310. Type host: *Collocalia* sp. = *Collocalia linchi linchi* Horsfield & Moore.

*Dennyus orientalis* Büttiker, 1954: 160. Type host: *Collocalia esculenta stresemanni* Rothschild & Hartert.

**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 ♂ paralectotypes of *D. distinctus*, ex *C. l. linchi*, JAVA (Essig Museum of Entomology, University

of California Berkeley); 9 ♀, 4 ♂, same data. 38 ♀, 114 ♂, ex *C. esculenta cyanoptila* Oberholser, MALAYSIA: Sandakan; 12 ♀, 11 ♂, ex *C. esculenta* (Linnaeus), NEW GUINEA. See 'Remarks' below regarding males.

**Remarks**

While the females of *D. 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.

***Dennyus (Collodennyus) distinctus timjonesi ssp.n. (Figs 1–5)***

**Type host:** *Collocalia esculenta cyanoptila* 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).

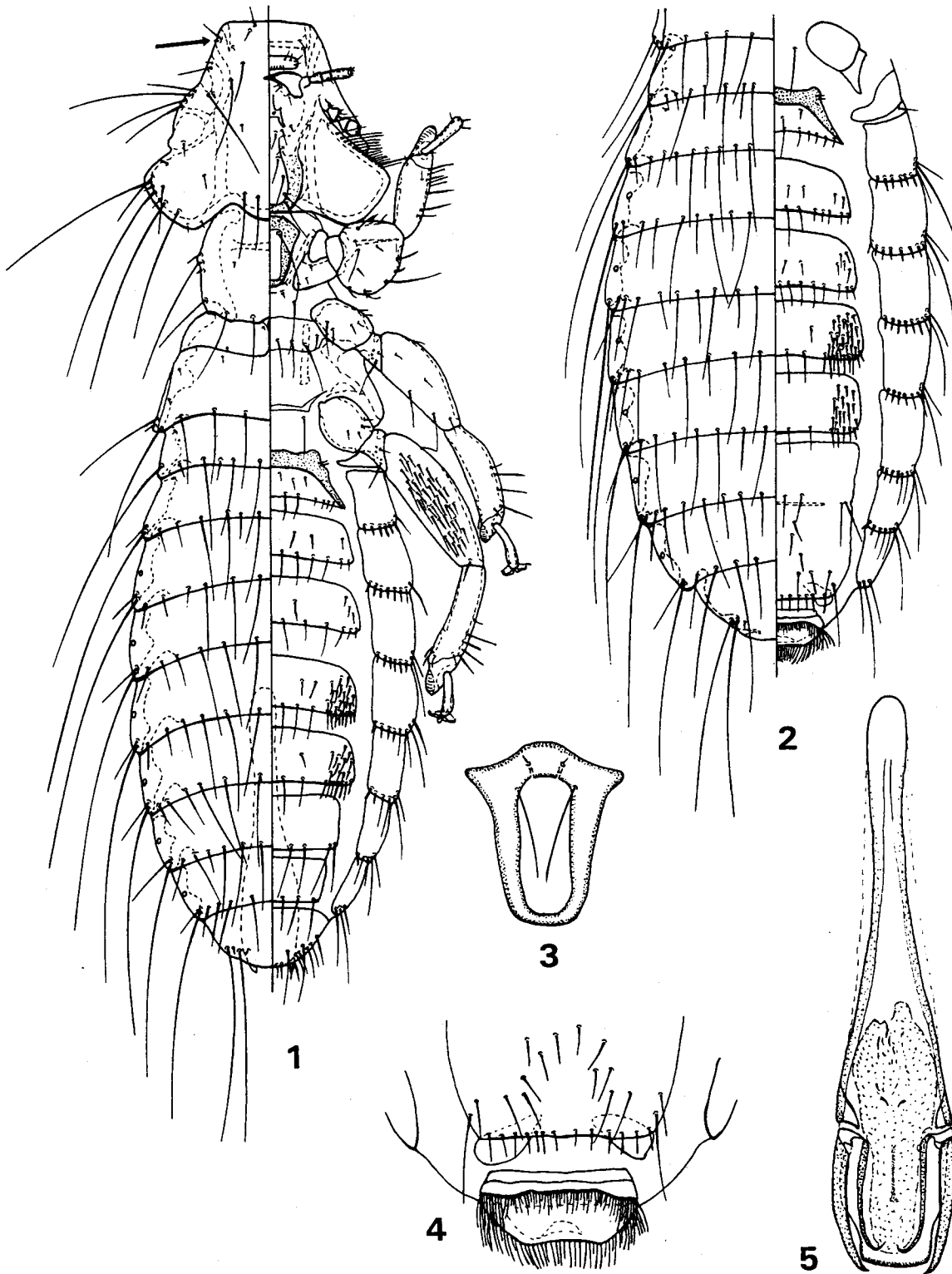
**Type material**

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

Paratypes, 3 ♀, 9 ♂, same as holotype (BMNH; USNM; UM); 5 ♀, 5 ♂, same, except ex *C. esculenta*, 19.viii.1964 (McClure) (OSU); 1 ♀, 1 ♂, same, except ex *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 genitalic 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. 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. d. distinctus*, *D. d. timjonesi* females are wider, (e.g. TW:  $0.552 \pm 0.003$  vs.  $0.537 \pm 0.002$ ,  $P = 0.003$ ), have fewer



**Figs 1–5.** *Dennyus distinctus timjonesi* ssp.n. 1. Male. 2. Female abdomen. 3. Female prosternal plate. 4. Female ventral terminalia. 5. Male genitalia.

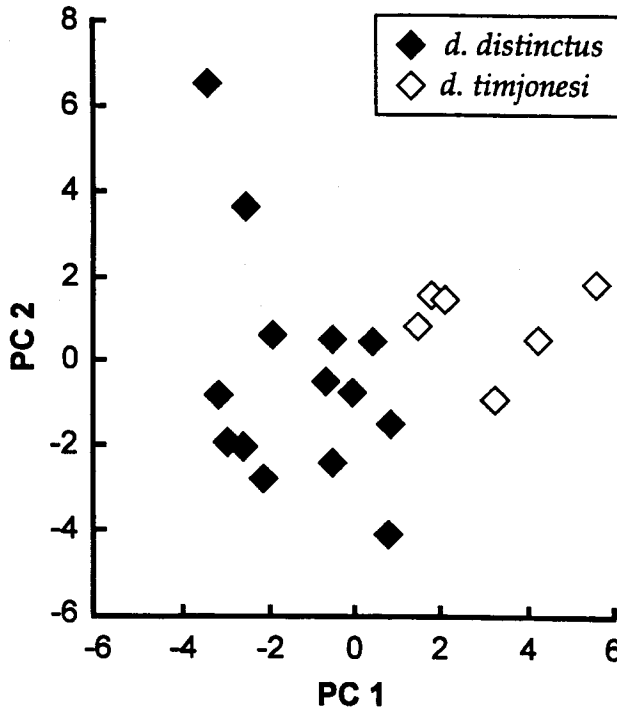


Fig. 6. Principal component analysis of females of the two subspecies of *Dennyus distinctus* lice. The first and second principal components (PC 1 and PC 2) account for 18.9 and 16.1% of the variation, respectively.

anterior sternal setae on sternite V (AS<sub>tn</sub>V:  $2.9 \pm 0.4$  vs.  $4.6 \pm 0.4$ ,  $P = 0.008$ ) and more setae in the brush on sternite V (BrV:  $32.6 \pm 0.8$  vs.  $28.9 \pm 0.6$ ,  $P = 0.001$ ).

#### Etymology

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

#### *Dennyus (Collodennyus) theresae* sp.n. (Fig. 8)

*Type host:* *Collocalia esculenta desiderata* Mayr.

*Female.* Tergal setae: I, 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, 26–30; 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. theresae* 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.

#### *Dennyus (Collodennyus) medwayi* Ledger (Fig. 9)

*Dennyus (Collodennyus) medwayi* Ledger, 1970: 245. *Type host:* *Hydrochous gigas* (Hartert & Butler).

*Female.* Tergal setae: I, 10; II, 12; III, 13; IV, 14; V, 12; 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; AbW, 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; AbW, 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 displaced anteriorly from the ventral anal fringe margin (Figs 10–12) in combination with the majority of abdominal tergites II–VI each having  $\leq 14$  setae. While males also tend to have few tergal setae, the separation is not as distinct as for the females.

### *Dennyus (Collodennyus) elliotti* Ledger (Figs 10, 11)

*Dennyus (Collodennyus) 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 37–46; 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 ♂ 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 anus width  $\geq 0.24$ , sternite V with only 0–1 medioanterior setae, sternite

VI without such setae giving this sternite a total of  $\leq 34$  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 (Collodennyus) 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, 2–6; 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, Okaspmin, 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 & Valima*) (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 (Collodennyus) boothi* sp.n.

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

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

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

V, 2–3. Total number of setae on sternite VI, 30–36. Marginal setae of subgenital plate in irregular row. Dimensions: AnW, 0.22.

**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.t.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.elliotti* and *D.hahnae* in having posterior setae of the brushes on sternite VI that are similar to the other brush setae.

#### Etymology

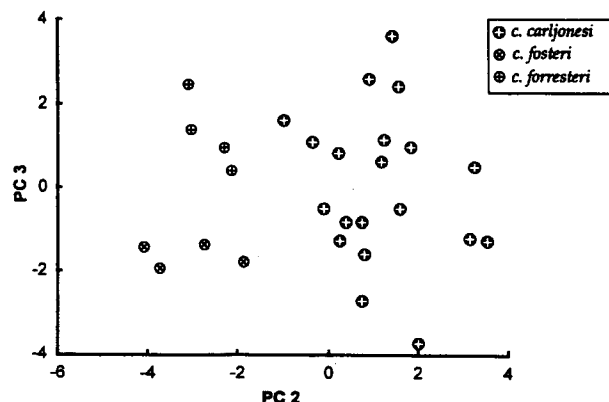
This species is named for David Booth, University of Queensland, in recognition of long-term collaborative work with D.H.C. on host-parasite ecology, including some rather harrowing field work for this paper.

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

**Type host:** *Aerodramus fuciphagus* (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 setae anterior 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, 2–3; 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



**Fig. 7.** Principal component analysis of female *Dennyus carljonesi* lice from Malaysia (*D.c.carljonesi*), Seychelles (*D. c. fosteri*) and Mauritius (*D.c.forresteri*). The second and third principal components (PC 2 and PC 3) account for 12.2 and 7.4% of the variation, respectively. Nearly all variables have positive scores for PC 1, which is interpreted as representing overall size.

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.hahnae*. 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 Plt Mg num:  $17.7 \pm 0.4$  vs.  $14.1 \pm 0.2$ ,  $P < 0.0001$ ) and shorter lateral marginal setae (Lat Mg Lgth:  $0.036 \pm 0.001$  vs.  $0.041 \pm 0.001$ ,  $P < 0.0007$ ) than lice from Malaysian birds. Female lice from the Seychelles (hosted by *Aerodramus elaphra*) and Mauritius (hosted by *A.franciscus*) 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:  $1.60 \pm 0.06$  vs.  $1.71 \pm 0.06$ ,  $P = 0.0003$ ). 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:  $0.555 \pm 0.002$  vs.  $0.543 \pm 0.002$ ,  $P < 0.0001$ ). 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!

**Dennyus (Collodennyus) carljonesi carljonesi**  
Clayton, Price & Page (Fig. 12)

*Type host:* *Aerodramus fuciphagus* (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*

Holotype, ♀, ex *A.fuciphagus*, MALAYSIA: Sabah, Gomantong Caves, 25.vii.1994 (Clayton) (BMNH).

Paratypes, 7 ♀, 9 ♂, same as holotype (BMNH; USNM); 3 ♀, 3 ♂, same, except i.1994 (OSU; UM); 1 ♀, same, except 21.vii.1994 (OSU); 5 ♀, 6 ♂, same, except 1994 (Tompkins) (BMNH; USNM; OSU); 2 ♀, 2 ♂, ex *A.famechana* (Oberholser), WEST MALAYSIA: Trengganu, Kuala Trengganu, 1.iii.1974 (*Grn. Lawit Expdn.*) (BMNH).

*Other material*

6 ♀, 10 ♂, ex *A.maximus* (Hume), MALAYSIA: Gomantong Caves; 4 ♀, 2 ♂, ex *A.salanganus* (Streubel), MALAYSIA: Gomantong Caves.

*Remarks*

In addition to the differences given above under *D.carljonesi*, the female of *D.c.carljonesi* is separable from those of the other two subspecies by having only 2 setae on sternite I, and usually no anterior setae on sternite VII.

**Dennyus (Collodennyus) carljonesi forresteri ssp.n.**

*Type host:* *Aerodramus francicus* (Gmelin).

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

*Female.* Anterior sternal setae: III, 7–11 (8.9); IV, 9–16

(12.3); V, 0–6 (3.7); VI, 1–5 (2.7). Setae in each brush on sternite V, 33–42 (38.7). Subgenital plate with 15–19 (16.8) marginal setae. Anal dorsal fringe of 38–49 (44.8) setae; total of 2–6 (4.8) setae anterior to ventral fringe. Dimensions: HL, 0.46–0.48 (0.470); AL, 1.54–1.68 (1.596); TL, 2.48–2.65 (2.549).

*Male.* With 28–41 (34.4) setae in each brush on sternite V. TW, 0.52–0.58 (0.554); HL, 0.44–0.47 (0.455); MW, 0.52–0.56 (0.541); AW, 0.62–0.70 (0.664); GL, 0.63–0.69 (0.664).

*Type material*

Holotype, ♀, ex *A.francicus*, MAURITIUS, 4–5.i.1995 (Clayton) (BMNH).

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

*Remarks*

The separation of *D.c.forresteri* 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 tenuously 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.

**Dennyus (Collodennyus) carljonesi fosteri ssp.n.**

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

Much as for *D.c.carljonesi*, 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*

Holotype, ♀, ex *A.elaphrus*, SEYCHELLES: Mahe, 11.i.1995 (Clayton) (BMNH).

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

*Remarks*

The female of *D.c.fosteri* is separable from those of the other two subspecies in having more setae on sternite I, more anterior setae on sternite VII, and a larger temple 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 separated 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  $\geq 15$  setae. Males do not show a separation as distinct as for the females.

***Dennyus (Collodennyus) emersoni* Ledger**

*Dennyus (Collodennyus) 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, 10–14 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 1–3 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  $\leq 0.28$  wide. *Dennyus emersoni* is separated from the two other narrow-anus species by having the female with a total of  $\leq 37$  setae on sternite VI and with  $< 4$  anterior setae on sternite V. The male of *D.emersoni* is close to that of *D.carljonesi*, but with shorter genitalia.

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

*Type host: Aerodramus spodiopygius spodiopygius* (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 thicker 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.s.spodiopygius*, WESTERN SAMOA: Upolu, Ole Pupu-Pue National Park, Peapea Cave, 31.iii.1994 (Clayton) (BMNH).

Paratypes, 2♀, 8♂, same as holotype (BMNH; USNM; OSU).

## Remarks

The female of *D. kristinae* 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.

***Dennyus (Collodennyus) 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*

Holotype, ♀, ex *A. spodiopygius assimilis*, FIJI: 9 mi. from Suva, Wainibuku Rd., Nasinu Cave, 4.iv.1994 (Clayton) (BMNH).

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

## Remarks

The female of *D. singhi* is morphologically closest to that of *D. kristinae*, 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. kristinae*.

## Etymology

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

***Dennyus (Collodennyus) ferrisi* Ledger**

*Dennyus (Collodennyus) ferrisi* Ledger, 1970: 250. *Type host:* *Aerodramus ocista* (Oberholser).

*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. ocista*, MARQUESAS (Essig Museum of Entomology, University of California Berkeley).

## Remarks

This species represents the first of two in this subgroup with a wide female anus measuring  $\geq 0.33$ . The consistently large dimensions, larger number of setae on abdominal sternites III–IV, and differences in the number of brush setae on sternite V 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.

### ***Dennyus (Collodennyus) 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*

Holotype, ♀, ex *C.l.linchi*, INDONESIA: West Java, Bogor, 9.iv.1995 (Clayton) (BMNH).

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

#### *Other material*

107 ♀, ex *C.esculenta 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 15, 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*

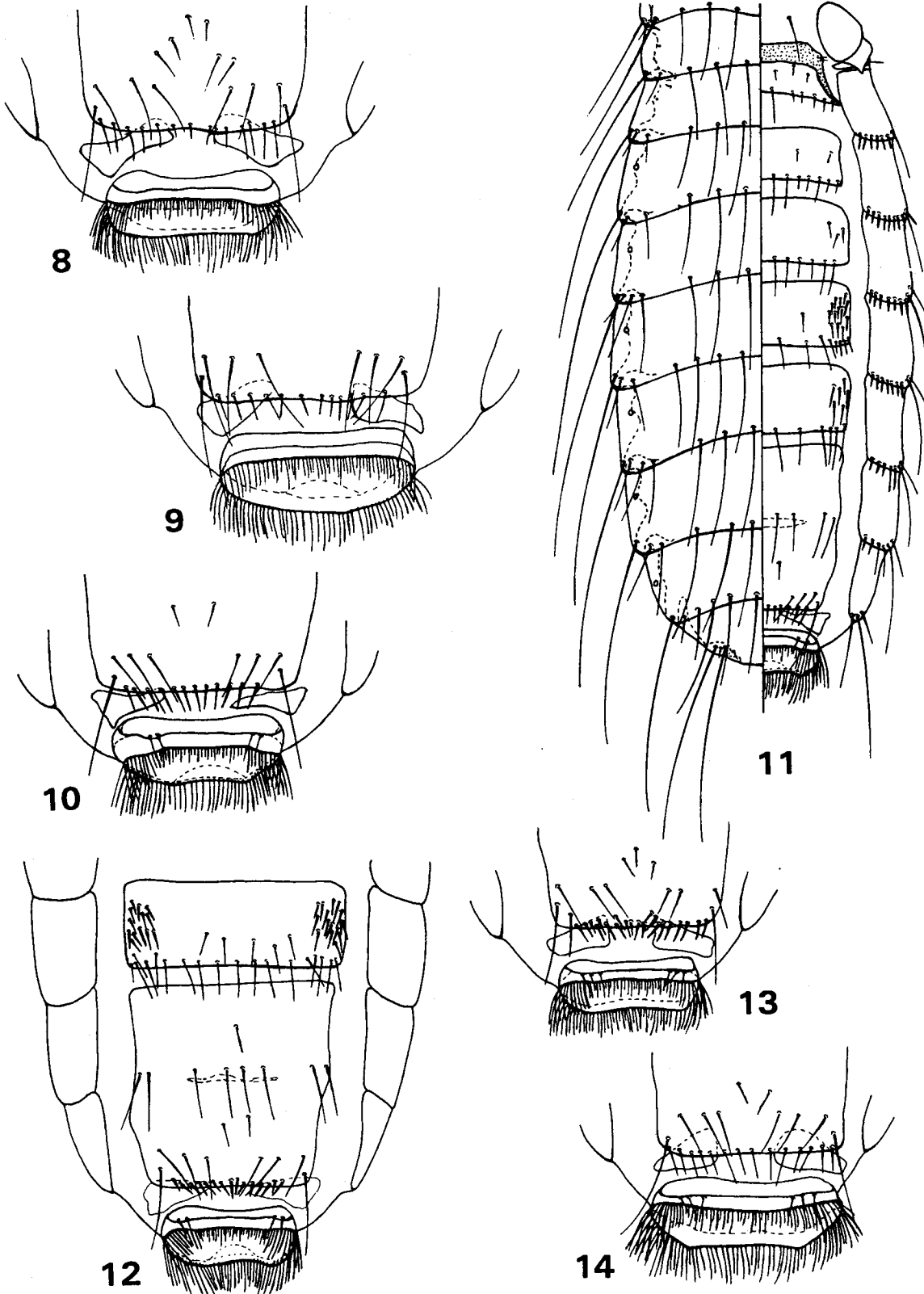
The four taxa of this subgroup are separated from all others of the group by having both sexes with the preantennal lateral head margin only moderately concave, the mesosternum with 4–7 setae, the metasternum with 8–16 setae, and the index of abdomen length divided by abdomen width ranging from 1.7–2.2; the female with an anus width  $\geq 0.32$  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.

### ***Dennyus (Collodennyus) thompsoni* Ledger (Figs 15–17)**

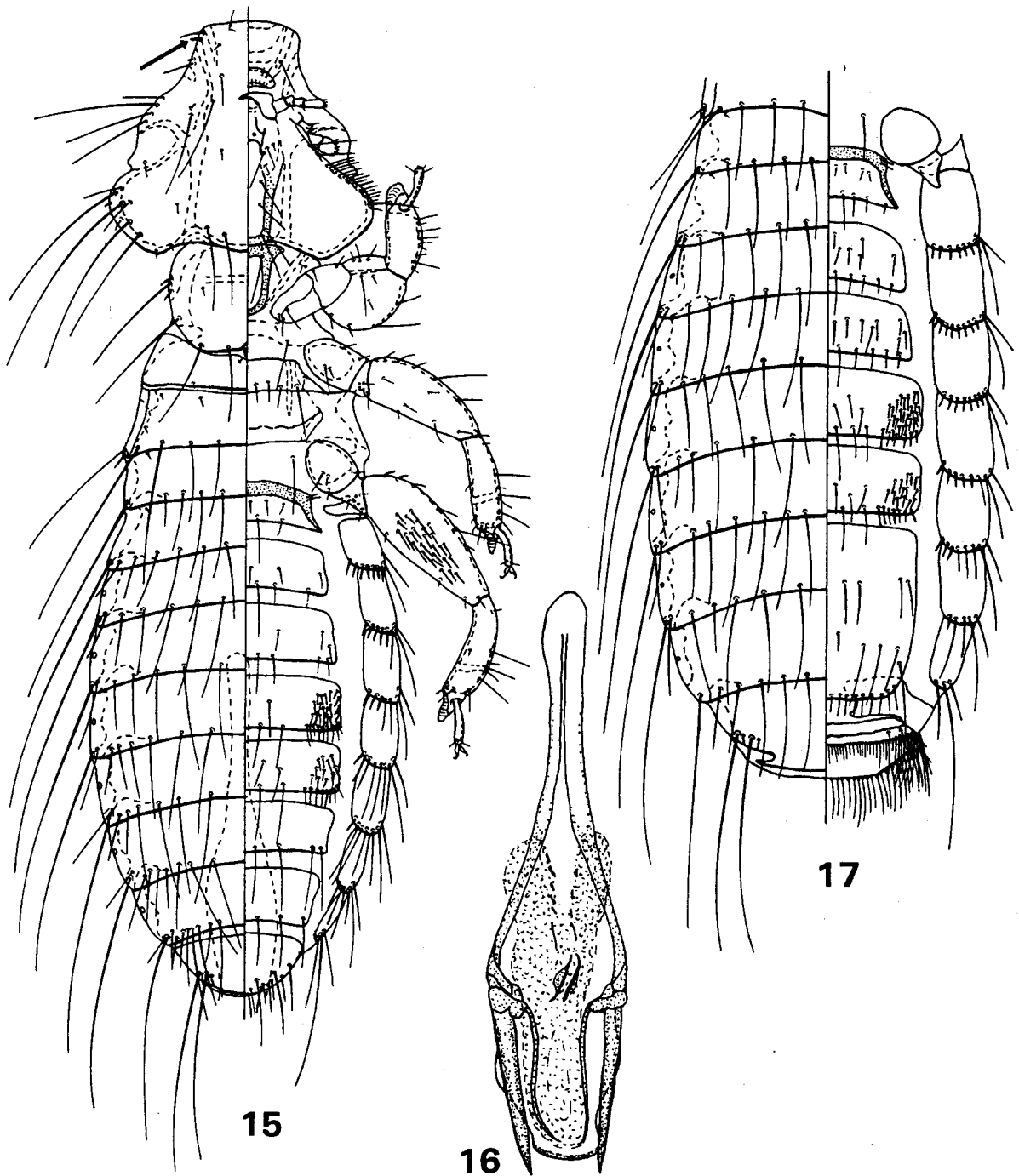
*Dennyus (Collodennyus) thompsoni* Ledger, 1970: 255. *Type host:* *Aerodramus maximus lowi* Sharpe.

*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, 5–8; VI, 4–6. 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.



**Figs 8 and 9.** Female ventral terminalia. 8. *Dennyus theresae* sp.n. 9. *D. medwayi* Ledger.  
**Figs 10 and 11.** *Dennyus elliotti* Ledger, Female. 10. Ventral terminalia. 11. Abdomen.  
**Fig. 12.** *Dennyus carljonesi carljonesi* Clayton, Price & Page, female ventral terminal abdomen.  
**Figs 13 and 14.** Female ventral terminalia. 13. *D. singhi* sp.n. 14. *D. somadikartai* sp.n.



Figs 15–17. *Dennyus thompsoni* Ledger. 15. Male. 16. Male genitalia. 17. Female abdomen.

*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.thompsoni* is inseparable from one of the other species and tenuously separable from the remaining two (see below) only by a larger total number of setae in the brushes on sternite VI, a smaller number of marginal setae on sternite IV, and smaller genitalia.

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

*Type host:* *Aerodramus salanganus* (Streubel).

As for *D.thompsoni*, 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, 0.55–0.60; AbW, 0.74–0.90; AL, 1.53–1.67; TL, 2.47–2.64; AnW, 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 (Tompkins) (UM); 1 ♀, same, except 18.vi.1994 (Tompkins) (UM); 2 ♂, same, except 5.vii.1994 (Tompkins) (BMNH); 3 ♀, 2 ♂, same, except 4.viii.1994 (Tompkins) (OSU); 1 ♀, same, except 16.viii.1994 (Tompkins) (UM); 1 ♀, 1 ♂, same, except Balemangan Is., 18.iii.1994 (USNM); 2 ♀, 1 ♂, ex *A.salanganus*, PAPUA NEW GUINEA: Copper mine shaft near Port Moresby, 5.vii.1988 (Easton & Burrows) (OSU); 2 ♂, ex *A.vanikorensis* (Quoy & Gaimard), NEW HEBRIDES: Erromanga, Ipota, 3.viii.1971 (Marshall) (BMNH).

*Remarks*

The female of *D.wellsii*, with the wide anus, short abdomen and short total length, is similar to that of *D.thompsoni* and thereby different from the other two species of this subgroup; it is separable from *D.thompsoni* 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.thompsoni*.

*Erymology*

This species is named in honour of David Wells, University of Malaysia, for his important contributions to Malaysian ornithology and his assistance with this project.

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

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

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

*Female.* Tergal setae: I, 8–12; IV, 14–17; V–VII, 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; AnW, 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*

Holotype, ♀, ex *A.brevirostris vulcanorum*, INDONESIA: West Java, Tangkuban Prahur, 7.iv.1995 (Clayton) (BMNH).

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  $\geq 10$  marginal setae on sternite IV and a genitalia length  $\geq 0.68$ , is distinguished from most males of the other three species of this subgroup.

*Erymology*

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.

***Dennyus (Collodennyus) 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 39–54. 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.terraereginae*, 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 ♀, 8 ♂, ex *A.terraereginae chillagoensis* Pecotich, AUSTRALIA.

#### Remarks

The female of *D.adamsae* 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 hosts 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 our 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 preantennal 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).

#### *Dennyus (Collodennyus) francicus* Thompson

*Dennyus (Collodennyus) 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 mediad 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 mediad 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

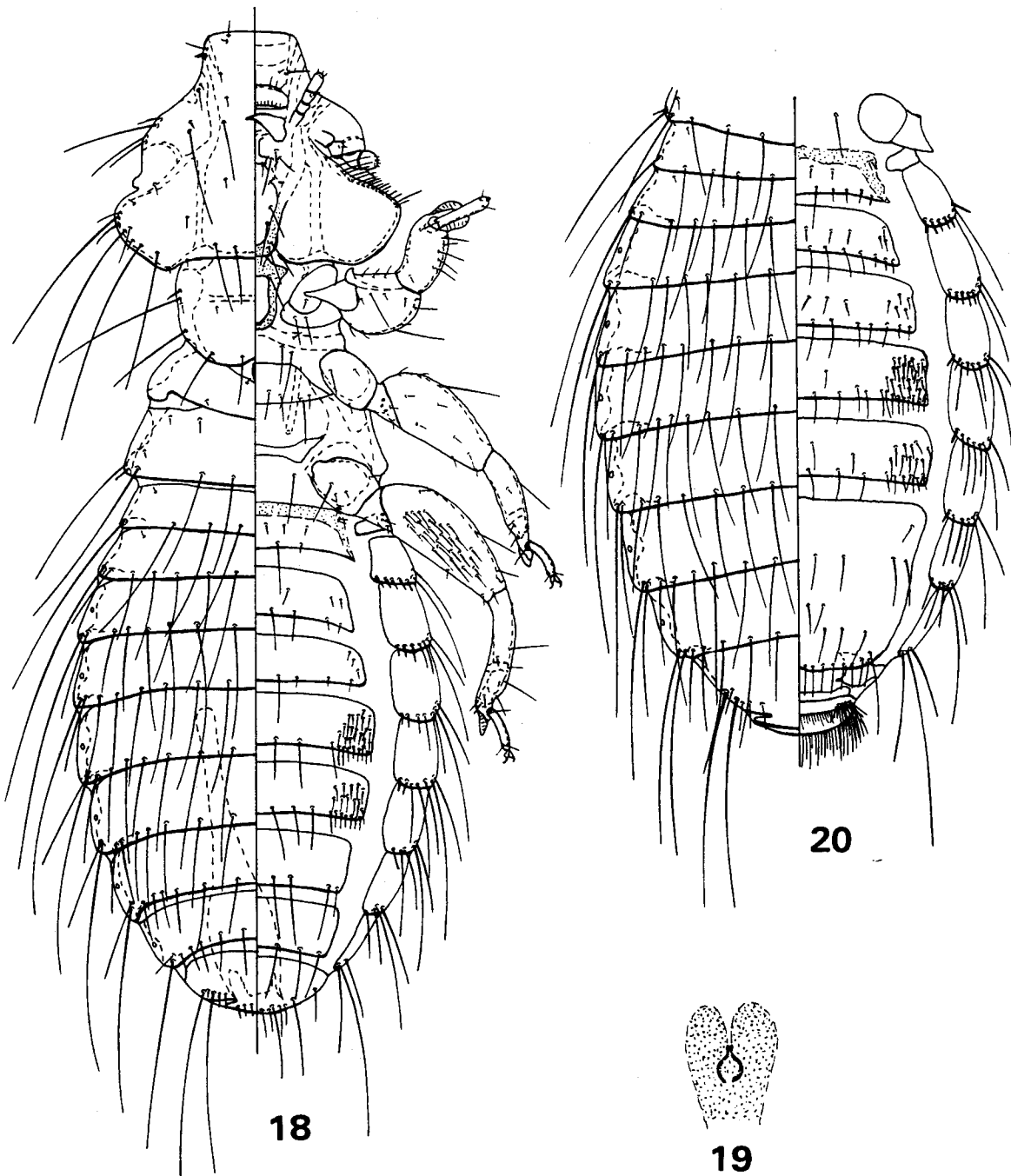
The features separating the female of *D.francicus* from those of the other three species of this subgroup are the terminal tergite with a total of 4 setae mediad of the very long setae, in combination with the smaller temple width, anus width, and total length. The male is distinguished by also having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

#### *Dennyus (Collodennyus) simberloffii* sp.n. (Figs 18–20)

Type host: *Aerodramus maximus* (Hume).

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





**Figs 18–20.** *Dennyus simberloffii* sp.n. 18. Male. 19. Male genital sac sclerite. 20. Female abdomen.

*Female* (Fig. 20). Tergal setae: I, 8–12; II, 13–16; III–IV, 14–18; V, 16–20; VI–VII, 15–18; VIII, 14–15. Terminal tergite with total of 4–7 setae mediad of very long setae. Marginal sternal setae: II, 9–12; III, 9–15; IV, 10–19; V–VI, 5–9. Anterior sternal setae: II, 4–8; III, 6–11; IV, 10–23; V–VI, 2–8; VII, 0–6. Setae in each brush on sternite V, 30–39; VI, 18–28. Subgenital plate with 11–16 anterior setae, 12–20 marginal setae. Anal ventral fringe of 50–58 setae, dorsal of 41–52.

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.

*Male* (Fig. 18). Tergal setae: II, 12–14; III, 13–17; IV–V, 15–17; VI, 15–18; VII, 15–17; VIII, 13–16. Terminal tergite with total of 5–7 setae mediad of very long setae. Marginal sternal setae: II, 5–8; III–IV, 7–10; V–VI, 3–6; VII, 7–8. Anterior sternal setae: II, 2–6; III, 4–8; IV, 4–11; V, 1–4; VI–VII, 0–3.

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, Gomantong Caves, 2.viii.1994 (*Tompkins*) (BMNH).

Paratypes, 3 ♀, 1 ♂, same as holotype (BMNH; USNM); 4 ♀, 2 ♂, same, except 4.viii.1994 (OSU; UM); 1 ♂, same, except 14.viii.1994 (USNM); 1 ♀, same, except i.1994 (*Clayton*) (UM); 1 ♀ same, except 25.vii.1994 (*Clayton*) (OSU); 3 ♀, 2 ♂, ex *A.maximus*, MALAYSIA: N. Sabah, Balembangen Is., 18.iii.1994 (*Clayton*) (USNM; BBM).

*Other material*

1 ♂, ex *A.fuciphagus*, MALAYSIA: Sabah, Gomantong Caves.

*Remarks*

The female of *D.simberloffi* is allied with *D.franciscus* in having a total of at least 4 setae between the very long setae on the last tergite; it is separated from that species in having a wider temple, wider anus, and longer abdomen and total length. The male of *D.simberloffi* is similarly grouped with *D.franciscus* 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  $\geq 5$  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: Aerodramus 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 mediad 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 similar 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 mediad 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*

Holotype, ♀, ex *A.s.assimilis*, FIJI: 9 mi. from Suva, Wainibuku Rd., Nasinu Cave, 4.iv.1994 (*Clayton*) (BMNH).

Paratypes, 5 ♀, 5 ♂, same as holotype (BMNH; USNM; OSU; UM; BBM); 1 ♀, 1 ♂, ex *A.s.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) tarburtoni* sp.n.**

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

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

*Female.* Tergal setae: I, 12–14; II, 18–21; III–IV, 16–18, V, 21–22; VI, 18–20; VII, 16–19. Terminal tergite with total of only 1–2 setae mediad of very long setae. Marginal sternal setae: III, 15–17; IV, 15–16; V, 8–10. Subgenital plate with 12–13 anterior setae, 12–15 marginal setae. Anal ventral fringe

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.spodiopygius*, WESTERN SAMOA: Upolu, Ole Pupu-Pue National Park, Peapea Cave, 31.iii.1994 (Clayton) (BMNH).

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

#### Remarks

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

#### Etymology

This species is named in honour of Michael Tarburton, 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 *Dennyus* (*Collodennyus*). Within the *Dennyus distinctus* species-group, three of the four taxa in the *distinctus* species-subgroup are restricted to hosts of the genus *Collocalia*. These three taxa are found on *C.esculenta* in diverse geographical localities, and one of them, *D.d.distinctus*, also occurs on *C.linchi*. The fourth member of this subgroup, *D.medwayi*, occurs only on the monotypic genus *Hydrochous*. 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.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.carljonesi* has been collected from more than a single host taxon, *D.c.carljonesi* having 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.forresteri*) is restricted to *A.francicus* 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.c.carljonesi*, 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 female lice (Fig. 21), the three subgroups recognized here are nonoverlapping, with the notable exception of *D.medwayi* (ex *Hydrochous gigas*) from the *distinctus* subgroup which nestles among the *elliotti* subgroup (all ex *Aerodramus*). The ordination for male lice (Fig. 22) resembles that for females, and again *D.medwayi* groups with *elliotti* lice. Males of *D.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 ocista*, 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 spodiopygius* form one cluster distinct from *D.simberloffi* (hosted by *A.maximus* and *A.fuciphagus*). 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 *Dennyus* (*Collodennyus*) and *D.* (*Dennyus*) 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.

Clastic analysis of relationships among *Dennyus* (*Collodennyus*) 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 *Dennyus* (*Collodennyus*).

Host taxon	<i>Collodennyus</i> species-group	
	<i>distinctus</i>	<i>thompsoni</i>
<i>Collocalia esculenta</i>		
<i>e. cyanoptila</i>	* <i>d. distinctus</i> * <i>d. timjonesi</i> ssp.n. # <i>somadikartai</i> sp.n.	
<i>e. desiderata</i>	* <i>theresae</i> sp.n.	
<i>Collocalia linchi</i>	* <i>d. distinctus</i> # <i>somadikartai</i> sp.n.	
<i>Hydrochous gigas</i>	* <i>medwayi</i>	
<i>Aerodramus whiteheadi</i>	¶ <i>elliotti</i>	
<i>Aerodramus hirundinaceus</i>	¶ <i>hahnae</i> sp.n.	
<i>Aerodramus terraereginae</i>		
<i>t. terraereginae</i>	¶ <i>boothi</i> sp.n.	§ <i>adamsae</i> sp.n.
<i>t. chillagoensis</i>		§ <i>adamsae</i> sp.n.
<i>Aerodramus fuciphagus</i>	¶ <i>c. carljonesi</i> ssp.n.	§ <i>thompsoni</i> ‡ <i>simberloffii</i> sp.n.
<i>Aerodramus salanganus</i>	¶ <i>c. carljonesi</i> ssp.n.	§ <i>wellsi</i> sp.n.
<i>Aerodramus vanikorensis</i>		§ <i>wellsi</i> sp.n.
<i>Aerodramus maximus</i>	¶ <i>c. carljonesi</i> ssp.n.	§ <i>thompsoni</i> ‡ <i>simberloffii</i> sp.n.
<i>Aerodramus francicus</i>	¶ <i>c. forresteri</i> ssp.n.	
<i>Aerodramus elaphrus</i>	¶ <i>c. fosteri</i> ssp.n.	
<i>Aerodramus brevirostris</i>	# <i>emersoni</i>	
<i>b. vulcanorum</i>		§ <i>collinsi</i> sp.n.
<i>Aerodramus spodiopygius</i>		
<i>s. spodiopygius</i>	# <i>kristinae</i> sp.n.	‡ <i>tarburtoni</i> sp.n.
<i>s. assimilis</i>	# <i>singhi</i> sp.n.	‡ <i>wraggi</i> sp.n.
<i>s. reichenowi</i>		‡ <i>francicus</i>
<i>Aerodramus ocista</i>	# <i>ferrisi</i>	

\* *distinctus* species-subgroup.# *emersoni* species-subgroup.¶ *elliotti* species-subgroup.§ *thompsoni* species-subgroup.‡ *francicus* species-subgroup.

study are highly correlated and most do not lend themselves to being coded as discrete characters. DNA sequences are likely to be a more profitable source of phylogenetic characters.

#### Comparison with swiftlet phylogeny

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 cospeciation. 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 (*thompsoni* and *collinsi*) on the sister taxa

*Aerodramus maximus* and *A. vulcanorum*, and the proximity of most *carljonesi* 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 *Collodennyus* is suggested by the presence of some species on phylogenetically unrelated hosts, notably the occurrence of *D.c.carljonesi* on *Aerodramus fuciphagus* (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

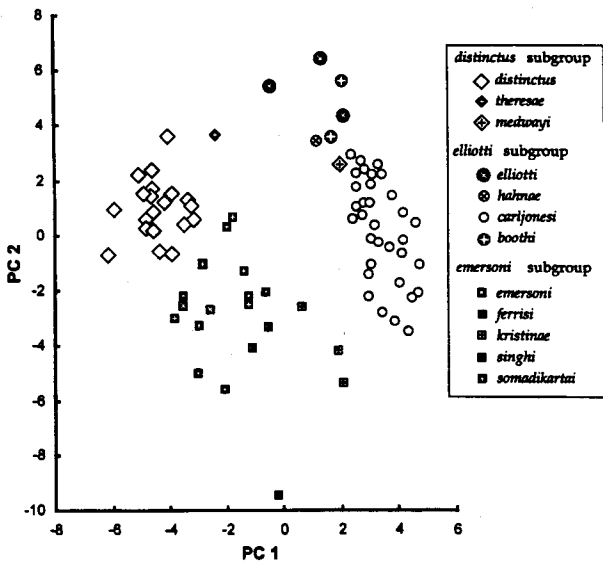


Fig. 21. Principal components ordination of female *Dennyus distinctus* group lice. The first and second principal components (PC 1 and PC 2) account for 31.6 and 19.8% of the variation, respectively.

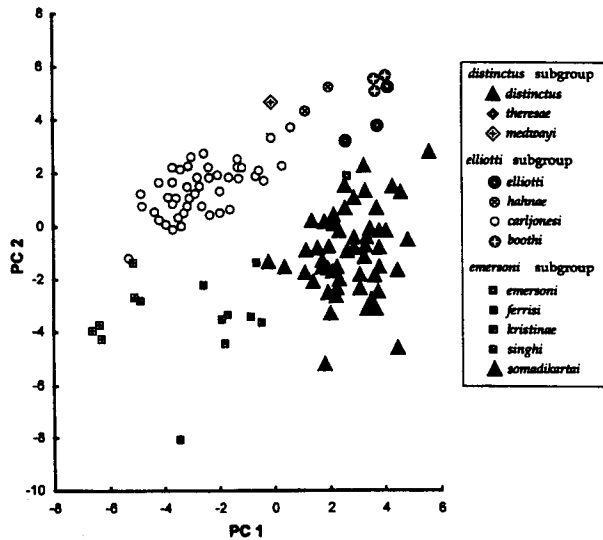


Fig. 22. Principal components ordination of male *Dennyus distinctus* group lice. Males of *D. d. distinctus* and *D. somadikartai* are indistinguishable and hence *D. distinctus* and *D. somadikartai* are represented by the same symbol. The first and second principal components (PC 1 and PC 2) account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

of closely related lice (*tarburtoni* and *wraggi*; *kristinae* and *singhi*) on *A.s.spodiopygius* and *A.s.assimilis*, 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 cospeciation, 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

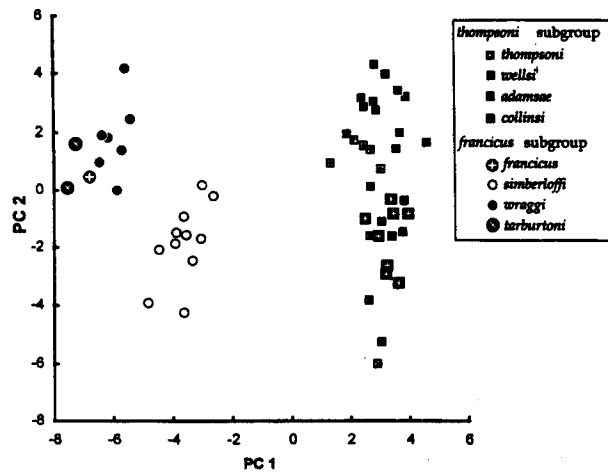


Fig. 23. Principal component analysis of female lice from the *Dennyus thompsoni* group. The first principal component (PC 1) accounts for 42.9% of the variation, the second (PC 2) accounts for 15.8%.

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* (*Collodennyus*)

#### Females

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. Without setae anterior to ventral anal fringe (Figs 4, 8, 9) (*distinctus* species-subgroup) .....3
- With setae anterior to ventral anal fringe (Figs 10–14)6
3. At least 16 setae on each tergite IV–V (Fig. 2); anus width  $\leq 0.28$  (*D. distinctus* Ferris).....4
- Not over 15 setae on each tergite IV–V (Fig. 11); anus width  $\geq 0.29$  .....5
4. Usually temple width  $\leq 0.54$ , abdomen width  $\leq 0.75$ , and  $\leq 31$  setae in each brush on sternite V. Ex *Collocalia linchi* (Java), *C. esculenta* (New Guinea; Malaysia [Sandakan]).....*D. distinctus distinctus* Ferris
- Temple width  $\geq 0.54$ , abdomen width usually  $\geq 0.78$ , and often  $\geq 31$  setae in each brush on sternite V. Ex *Collocalia esculenta* (Malaysia [Ampang Reservoir])....  
.....*D. distinctus timjonesi* ssp.n.

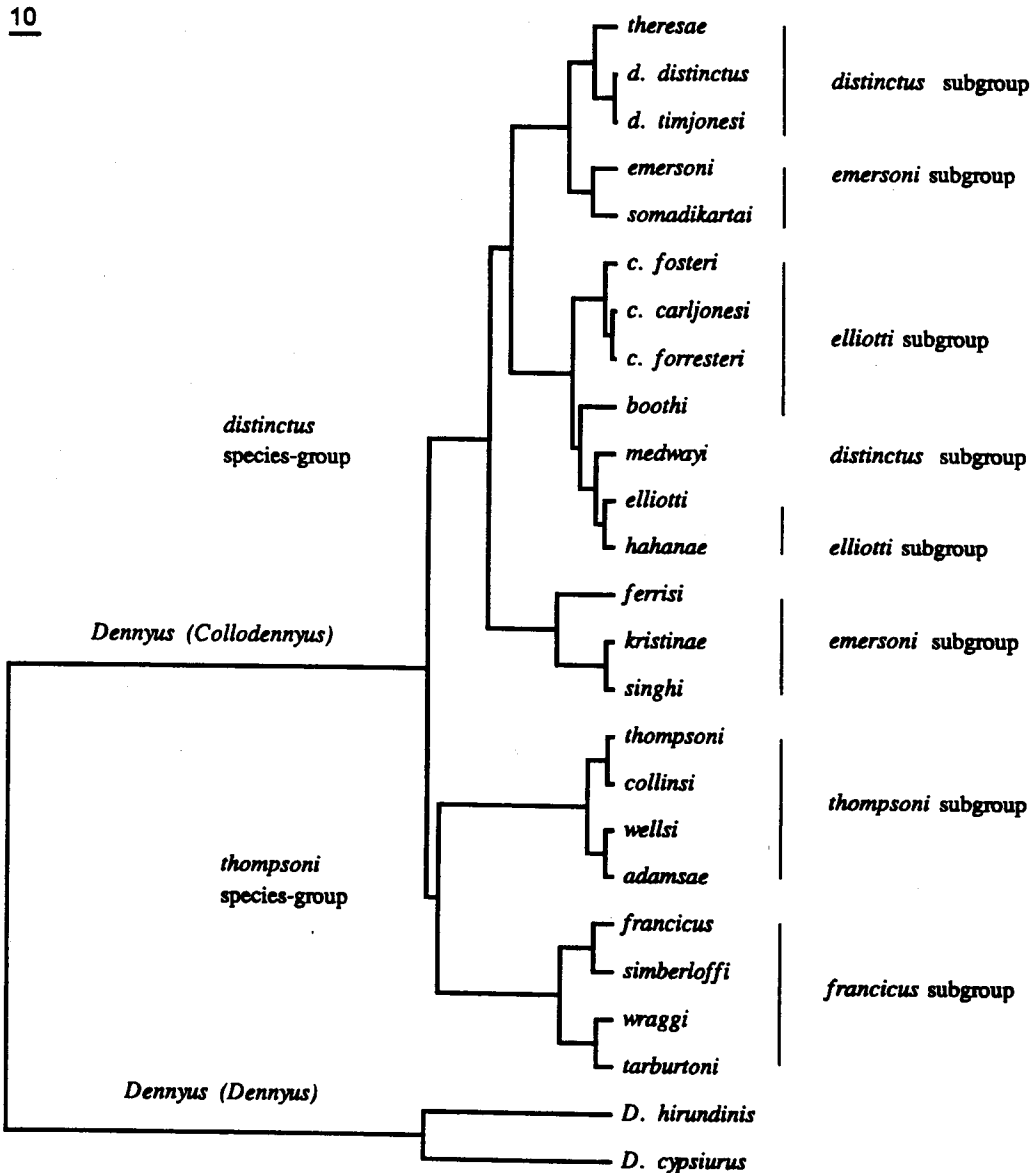


Fig. 24. Dendrogram for female *Dennyus* lice obtained by average linkage cluster analysis pairwise distance matrix computed using the first five principal components extracted from 29 variables (Table 1).

- |   |  |
|---|--|
| <p>5. Subgenital plate with 6 medioanterior setae (Fig. 8); temple width &lt;0.55 ..... <i>D.theresae</i> sp.n.</p> <p>— Subgenital plate without medioanterior setae (Fig. 9); temple width &gt;0.57 ..... <i>D.medwayi</i> Ledger</p> <p>6. Most of tergites II–VI with &lt;15 setae (Fig. 11) (<i>elliotti</i> species-subgroup) ..... 7</p> <p>— Each tergite II–VI with ≥15 setae (<i>emersoni</i> species-subgroup) ..... 12</p> <p>7. Anus ≤0.22 wide ..... <i>D.boothi</i> sp.n.</p> <p>— Anus ≥0.24 wide ..... 8</p> <p>8. Over 35 total setae on sternite VI (Fig. 12); sternite VI with ≥1 medioanterior seta, sternite V usually with ≥2 such setae (<i>D.carljonesi</i> sp.n.) ..... 9</p> | <p>— Fewer than 35 total setae on sternite VI; sternite VI without medioanterior setae, sternite V with only 0–1 such setae ..... 11</p> <p>9. Often 3–4 setae on sternite I; 1–3 anterior setae on sternite VII; temple width ≥0.59; from Seychelles ..... <i>D.c.fosteri</i> ssp.n.</p> <p>— Only 2 setae on sternite I; usually no anterior setae on sternite VII; temple width usually &lt;0.59; from Mauritius and Malaysia ..... 10</p> <p>10. Subgenital plate usually with &lt;16 marginal setae; often ≥6 total setae anterior to ventral anal fringe; abdomen length &gt;1.68; from Malaysia ..... <i>D.c.carljonesi</i> Clayton, Price &amp; Page</p> |
|---|--|

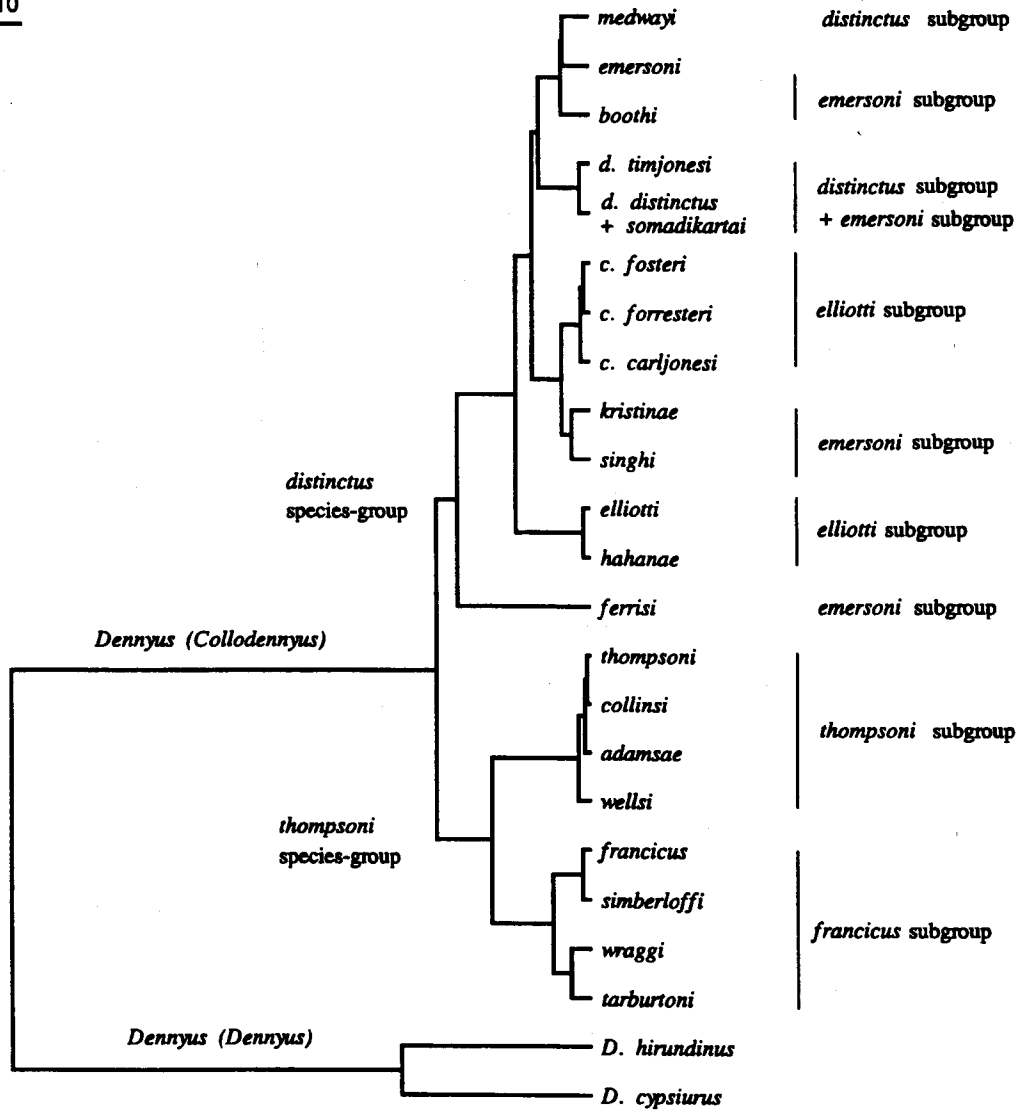
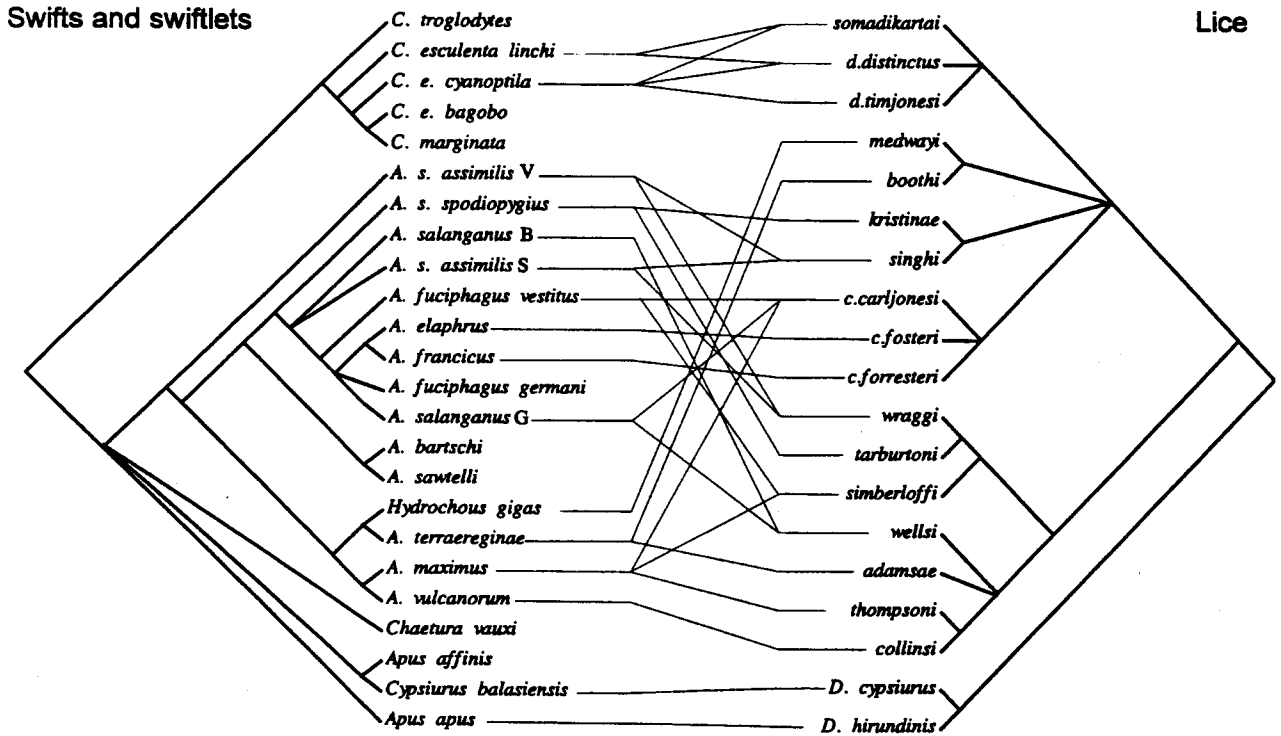


Fig. 25. Dendrogram for male *Dennyus* lice obtained as in Fig. 24 but from 22 variables (Table 1).

- 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 seta.....*D.hahanae* 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  $\leq 19$  setae; subgenital plate with  $\leq 18$  marginal setae; from Western Samoa.....*D.kristinae* sp.n.
- Tergites II–III each with  $\geq 20$  setae; subgenital plate  $\geq 19$  marginal setae (Fig. 13); from Fiji..*D. singhi* sp.n.
- 16. Anus  $\geq 0.32$  wide; abdomen generally narrow, elongate, with abdomen length/abdomen width 1.7–2.2 (Fig. 17) (*thompsoni* species-subgroup).....17
- Anus  $\leq 0.30$  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 *Dennyus* 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 *Dennyus* 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 louse is connected to its host(s) by a thin line (see Table 2).

- (*francicus* species-subgroup).....20
- 17. Anus  $\leq 0.35$  wide.....*D.adamsae* sp.n.
- Anus  $\geq 0.36$  wide.....18
- 18. Abdomen length  $> 1.72$ ; total length  $> 2.67$ .....
- .....*D.collinsi* sp.n.
- Abdomen length  $< 1.70$ ; total length  $< 2.65$ .....19
- 19. Total of  $> 43$  setae in brushes on sternite VI;  $\geq 18$  (mean = 20.0) marginal subgenital plate setae.....
- .....*D.thompsoni* Ledger
- Total of  $< 43$  setae in brushes on sternite VI;  $\leq 18$  (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  $\geq 4$  setae between very long setae.....22
- 21. Tergite V with  $> 20$  setae; sternite III with  $> 14$  marginal setae.....*D.tarburtoni* sp.n.
- Tergite V with  $< 19$  setae; sternite III with  $< 14$  marginal setae.....*D.wraggi* sp.n.
- 22. Temple width  $\geq 0.54$ ; anus width  $\geq 0.24$ ; total length  $\geq 2.15$ .....*D.simberloffii* sp.n.
- Temple width  $< 0.54$ ; anus width  $< 0.24$ ; total length  $< 2.10$ .....*D.francicus* Thompson

**Males**

The male of *D.theresae* 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  $\geq 0.52$ ; from Malaysia or Mauritius [*D.carljonesi* sp.n. (in part)].....4
- Temple width  $\leq 0.51$ ; from elsewhere.....5
4. Genitalia length  $\geq 0.69$ ; from Malaysia.....*D.c.carljonesi* Clayton, Price & Page (in part)
- Genitalia length  $< 0.69$ ; from Mauritius.....*D.c.forresteri* ssp.n. (in part)
5. Genitalia length  $\leq 0.61$ ; total anterior setae on sternites



- II–III  $\geq 9$ ; from Philippine Is. .... *D.elliotti* Ledger  
 — Genitalia length  $\leq 0.62$ ; total anterior setae on sternites II–III  $\leq 7$ ; from New Guinea ..... *D.hahnae* sp.n.
6. Genitalia length  $\geq 0.69$  and  $\geq 27$  total setae on sternite IV ..... 7  
 — Genitalia length  $\leq 0.68$ , or, if longer, then  $\leq 26$  total setae on sternite IV ..... 8
7. Each of tergites I–VII with  $\geq 17$  setae; sternites V–VI without medioanterior setae ..... *D.ferrisi* Ledger  
 — Each of tergites I–VII with  $\leq 16$  setae; sternites V–VI each with  $\geq 2$  medioanterior setae ..... *D.kristinae* sp.n.
8. Total of  $\leq 14$  anterior setae on sternites II–IV; ex *H.gigas* or *A.terraereginae* ..... 9  
 — Total of  $\geq 15$  anterior setae on sternites II–IV; ex other host taxa ..... 10
9. Temple width  $\geq 0.55$ ; head length  $\geq 0.47$ ; metathorax width  $\geq 0.53$ ; ex Malaysian *Hydrochous* .....  
 — ..... *D.medwayi* Ledger  
 — Temple width  $< 0.53$ ; head length  $\leq 0.46$ ; metathorax width  $< 0.52$ ; ex Australian *Aerodramus* *D.boothi* sp.n.
10. Total of  $\leq 27$  setae on tergites III–IV ..... 11  
 — Total of  $\geq 28$  setae on tergites III–IV ..... 14
11. Genitalia length  $\leq 0.61$ ; from Thailand .....  
 — ..... *D.emersoni* Ledger  
 — Genitalia length  $\geq 0.62$ ; from Malaysia, Mauritius, Seychelles [*D.carljonesi* sp.n. (in part)] ..... 12
12. Genitalia length  $\geq 0.69$ ; temple width  $\leq 0.55$ , metathorax width  $\leq 0.54$ ; from Malaysia .....  
 — ..... *D.c.carljonesi* Clayton, Price & Page (in part)  
 — Genitalia length  $< 0.69$ ; temple width  $\geq 0.55$ , metathorax width  $\geq 0.54$ ; from Mauritius or Seychelles ..... 13
13. Head length  $\geq 0.47$ ; sternite I with 2–3 setae; from Seychelles ..... *D.c.fosteri* ssp.n.  
 — Head length  $\leq 0.46$ ; sternite I with only 2 setae; from Mauritius ..... *D.c.forresteri* ssp.n. (in part)
14. Ex *Aerodramus* from Fiji ..... *D.singhi* sp.n.  
 — Ex *Collocalia* from elsewhere ..... 15
15. Genitalia length  $\leq 0.66$ ; from Malaysia (Sandakan), Java, New Guinea ..... *D.d.distinctus* Ferris  
 — ..... *D.somadikartai* sp.n.  
 — Genitalia length  $\geq 0.65$ ; from Malaysia (Ampang Reservoir) ..... *D.d.timjonesi* ssp.n.
16. Relatively narrow, elongate abdomen, with abdomen length/abdomen width 1.7–2.1 (*thompsoni* species-subgroup) ..... 17  
 — Relatively short, rounded abdomen, with abdomen length/abdomen width 1.3–1.5 (*francicus* species-subgroup) ..... 20
17. Sternite IV with  $\geq 10$  marginal setae, less often 9; genitalia length  $\geq 0.68$ ; ex *A.brevirostris vulcanorum* from West Java ..... *D.collinsi* sp.n.  
 — Sternite IV with  $\leq 9$  marginal setae, rarely 10; genitalia length usually  $\leq 0.68$ ; ex other *Aerodramus* from elsewhere ..... 18
18. Ex *Aerodramus terraereginae* from N. Queensland .....  
 — ..... *D.adamsae* sp.n.  
 — Ex *A.maximus*, *A.fuciphagus*, *A.salanganus*, or *A.vanikorensis* from elsewhere ..... 19
19. With total  $\geq 34$  (mean = 39.1) setae in brushes on sternite VI; genitalia  $\geq 0.64$  (mean = 0.661) long; ex *A.maximus* or *A.fuciphagus* ..... *D.thompsoni* Ledger  
 — With total  $\leq 39$  (mean = 33.9) setae in brushes on sternite VI; genitalia  $\leq 0.65$  (mean = 0.641) long; ex *A.salanganus* or *A.vanikorensis* ..... *D.wellsi* sp.n.
20. Terminal tergite with total of only 2 setae aligned between very long setae ..... 21  
 — Terminal tergite with total of  $\geq 4$  setae aligned between very long setae ..... 22
21. With  $\geq 18$  setae on each of tergites VII–VIII .....  
 — ..... *D.tarburtoni* sp.n.  
 — With  $\leq 17$  setae on each of tergites VII–VIII .....  
 — ..... *D.wraggi* sp.n.
22. Terminal tergite with total of only 4 setae between very long setae; tergite V with  $> 18$  setae; ex *A.spodiopygius* ..... *D.francicus* Thompson  
 — Terminal tergite with total of  $\geq 5$  setae between very long setae; tergite V with  $< 18$  setae; ex *A.maximus* ....  
 — ..... *D.simberloffii* sp.n.

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