

A review of *Dennyus* (Phthiraptera: Menoponidae) parasitic on the avian genera *Apus* and *Cypsiurus*

by

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The ten species of *Dennyus* that have been described from swifts belonging to the genera *Apus* and *Cypsiurus* are dealt with. Reasons are given for considering five of them (*Nitzschia minor* Kellogg & Paine, 1914; *Dennyus truncatiformis* Mokhehle, 1951; *D. africanus* Büttiker, 1954; *D. maritimus* Büttiker, 1954; *D. minutus* Büttiker, 1954) to be synonyms of *D. hirundinis* (Linnaeus) *sens. lat.* A sixth species (*D. clayae* Nakagawa, 1959) is represented by insufficient material for any conclusions to be reached. The remaining four species (*D. hirundinis* (Linnaeus, 1761); *D. cypsiurus* Thompson, 1948; *D. vonarxi* Büttiker, 1954; *D. aequatorialis* Ledger, 1968) are described and illustrated; a key is provided for their identification. The relationships of certain host species are discussed in the light of their *Dennyus* parasites.

INTRODUCTION

The genus *Dennyus* Neumann, 1906 is confined in its known distribution to the swifts (Aves: Apodidae). In a recent paper (Ledger, 1970) I reviewed those species parasitic on swiftlets of the genus *Collocalia*, for which group I proposed, the new sub-generic category *Collodennyus*. The present contribution is a continuation of my studies on Old World *Dennyus*, and this paper deals with the species found on *Apus* Scopoli and *Cypsiurus* Lesson. Both host genera have an exclusively Old World distribution, the single New World species of *Apus* recognized by Peters (1940), *A. andecolus*, having been transferred to *Aeronautes* by Lack (1956).

All lice studied were cleared and mounted on slides. Measurements, made with an ocular micrometer, are given in millimetres. A value in parenthesis following a statement of range represents the mean (means of setal counts are given to the nearest whole number). The host nomenclature basically follows that of Peters (1940), but taxonomic changes subsequently proposed by Lack (1956) and Brooke (1969a, 1969b, 1969c, 1970a, 1970b) have been accepted. Terminology used in the descriptions follows that of Clay (1969) as closely as possible. 'Tergocentrals' are defined as the row of setae between (but not including) the stout seta on each side of abdominal tergite I (considered as postspiracular seta I in this paper), and the rows of setae between (but not including) the postspiracular and its associated inner seta on each side of abdominal tergites II-VIII. The sternal abdominal setae may be divided into marginal (*m*) and anterior (*a*) series; additionally on V and VI there are lateral brushes of setae, the marginal components of which are not included in the marginal setal counts for these sternites.

The following initials are used in the text to indicate the collections from which

material was examined for this study: BMNH—British Museum (Natural History), London; GBT—Mr Gordon B. Thompson, Cambridge, England; KCE—Dr K. C. Emerson, Arlington, Virginia, U.S.A.; MRAC—Musée Royal de l'Afrique Central, Tervuren, Belgium; OPC—Veterinary Research Institute, Onderstepoort, South Africa; SAIMR—South African Institute for Medical Research, Johannesburg; USNM—United States National Museum, Washington, D.C.; WBC—Dr W. Büttiker, Basel, Switzerland; WEC—Dr W. Eichler, Kleinmachnow, German Democratic Republic; ZMB—Zoologisches Museum, Berlin, German Democratic Republic.

Subgenus *DENNYUS* Neumann, 1906, *sens. str.*

Nitzschia Denny, 1842 (*nec* Baer, 1827), *Mon. Anopflura Britt.*: 230.

Dennyus Neumann, 1906, *Bull. Soc. zool. Fr.* **20**: 60.

Type-species: *Pediculus hirundinis* Linnaeus, 1761.

DEFINITION. Menoponidae with the following combination of characters. *Head* without notch or slit in dorsolateral margin; ventral truncate-ovoid excavation with thickened anterior rim in dorsal margin of head anterior to eyes; without sclerotized processes arising near bases of maxillary palpi; forehead smoothly rounded between *dhs* 2-6 (fig. 3), never truncate; temporal carinae well-developed, gular plate not horseshoe-shaped. Alveoli of *dhs* 26 & 27 not closely associated; *dhs* 18 absent; 23 present and anterior to 22; *dhs* 24 & 25 both minute; 26, 27, 29 & 31 long and stout; 28 short; 30 medium and slender. One short, 1 medium setae between *dhs* 29 & 31.

Thorax with 1 pair short central pronotal setae lying just posterior to transverse carina; lateral pronotal lobes with 2 short and stout, 1 long setae each side; 3+3 long marginal pronotal setae. Prosternal plate well-developed, with 2 short anterior prosternal setae and invariably more than 2 long median prosternal setae on central part of plate. Postnotum present; 2 minute anterior mesonotal setae; 1+1 minute marginal mesonotal setae. Mesosternum with 2 short anterior setae, 4-9 posterior mesosternal setae. Anterolateral metanotal setae 3+3. Claws well-developed on all three pairs of tarsi; tibia I with a dense patch of outer submarginal setae (fig. 5); thick brushes of short to medium setae ventrally on femora III.

Abdomen without anterior tergal setae except for usual minute pair on I & II. Postspiracular setae long on I-VIII; an inner seta mediad to and closely associated with postspiraculars on II-VIII, absent on I. Terminal segment dorsally with 2 long stout, 2 short slender setae each side. Sternite I reduced, represented by a narrow plate lying between 3rd coxae; always 4 or more setae on this sternite. Sternites II-VIII in male and II-VI in female are discrete central plates; II has sclerotized anterior and lateral margins, with a pair of short setae in the anterolateral angle each side; V & VI with lateral brushes of short setae. In female VII is fused with succeeding sternites to form a large subgenital plate; posterior corners of this plate always with 4+4 medium to long setae; anteriorly on plate a median row and lateral groups of setae.

Discussion

The above definition of *Dennyus sens. str.* is based upon my experience with the Old World species only. The *Dennyus* of New World swifts are currently being studied (Parsons & Collins, in preparation), and it must be borne in mind that some of the New World species may grade into *Dennyus sens. str.* as defined above, and an expansion of the

definition may be necessary. Alternatively, the New World *Dennyus* may be found to share certain characters which will permit their grouping in a separate subgeneric category. For the present, I propose to use the subgenera *Dennyus sens. str.*, *Ctenodennyus* Ewing, 1930, *Takamatsua* Uchida, 1926 and *Collodennyus* Ledger, 1970 as convenient groupings for species which seem to be closely related. I recognize 4 species of Old World *Dennyus sens. str.*, and descriptions follow. I have been unable to reach any conclusions regarding the status of a fifth species, *Dennyus clayae* Nakagawa, 1959 (see below).

Dennyus (Dennyus) hirundinis (Linnaeus, 1761), figs 1-9

Pediculus hirundinis Linnaeus, 1761, *Fauna Suecica*, ed. 2: 479; Clay & Hopkins, 1950, *Bull. Br. Mus. nat. Hist. (Ent.)* 1: 267, figs.

Nirmus truncatus von Olfers, 1816, *De vegetativis et animatis corporibus in corporibus animatis reperiundus commentarius*. Berlin. Part 1: 91; Clay & Hopkins, 1960, *Bull. Br. Mus. nat. Hist. (Ent.)* 9: 31, figs.

Nitzschia burmeisteri Denny, 1842, *Mon. Anoplura Britt.*: 231, fig.

Nitzschia minor Kellogg & Paine, 1914, *Rec. Indian Mus.* 10: 242, fig. Host: *Apus affinis*.
Syn. nov.

Dennyus (Dennyus) truncatiformis Mokhehle, 1951, *Fort Hare Pap.* 1 (6): 341, figs.
Host: *Apus caffer*. **Syn. nov.**

Dennyus africanus Büttiker, 1954, *Acta trop.* 11: 159, fig. Host: *Apus aequatorialis bradfieldi*.
Syn. nov.

Dennyus maritimus Büttiker, 1954, *Acta trop.* 11: 160, fig. Host: *Apus unicolor*. **Syn. nov.**

Dennyus minutus Büttiker, 1954, *Acta trop.* 11: 160, fig. Host: *Apus pallidus*. **Syn. nov.**

Type-host: *Apus a. apus* (Linnaeus).

The early literature pertaining to this species has been discussed by Clay & Hopkins (1950, 1960) and all their conclusions are accepted here. A neotype series was designated by Clay & Hopkins (1950).

FEMALE. General appearance and chaetotaxy as in fig. 1. Number and position of dorsal head setae as in fig. 3. Median prosternal setae 3-7 (4); posterior mesosternal setae 6-8 (5); metasternal setae 14-22 (16); metanotal marginal setae 10-14 (12). Metathoracic pleurites with 1 long, 2 short setae each side.

Postspiraculars. Long on I-VIII, inner seta short, slender on II, increasing slightly in length on succeeding tergites, but on VIII not longer than about $\frac{1}{2}$ length of corresponding postspiracular (see fig. 8).

Pleural chaetotaxy. The following standard arrangement was found, with some individual variation, on all species of *Dennyus sens. str.* Two short spines on I; II-VIII always have, from dorsal to ventral, 1 short, 1 longer seta, with an additional number of setae making up a row on the posterior margin of each pleurite. On II there may be up to 10 such setae, short and spine-like. On succeeding pleurites these additional setae become less numerous, and there is progressive replacement of stout spines with slender setae. On VIII there are 3 slender additional setae only (total of 5 pleural setae on VIII).

Tergocentrals. I, 15-21 (18); II, 17-24 (19); III, 18-23 (19); IV, 16-24 (19); V, 15-21 (20); VI, 13-19 (16); VII, 13-17 (14); VIII, 9-10 (10). The most lateral tergocentrals on I-IV are frequently short and spine-like. Tergocentrals on VIII much as in fig. 8.

Ventral chaetotaxy. I, 4-7 (5); II 14-18 (16) *m*, 11-17 (13) *a*, sclerotized anterior margin not interrupted medially (see fig. 4); III, 14-20 (18) *m*, 20-28 (23) *a*; IV, 17-22

(20) *m*, 26–37 (31) *a*; V, 10–12 (11) *m*, 22–32 (28) *a*, lateral brushes about 70–80; VI, 9–13 (12) *m*, 14–20 (18) *a*, lateral brushes 25–35. Vulval margin with 16–26 (21) short to medium slender setae; anteriorly on subgenital plate a median row of 4–7 (4) setae and lateral groups of 4–8 (6) setae each side.

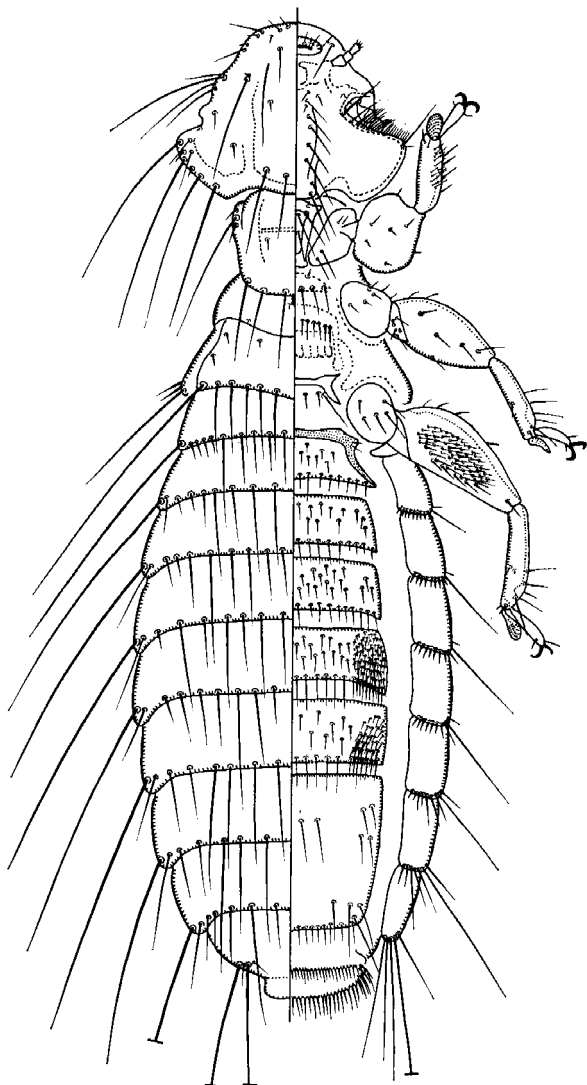


Fig. 1. *Dennyus hirundinis* (Linnaeus, 1761). Female, dorsal/ventral view.

MALE. Smaller in size, otherwise characters of head, thorax and pleurites, including chaetotaxy, agree well with the female. Abdomen as in fig. 2.

Tergocentrals. I, 12-16 (13); II, 12-17 (14); III, 13-18 (15); IV, 11-18 (15); V, 13-17 (15); VI, 12-16 (14); VII, 10-14 (12); VIII, 8-10 (10). Dorsal anal setae 16-24 (18). Tergocentrals on VIII without any one seta much longer and stouter than others in row, and normally not extending beyond tip of abdomen (fig. 9).

Ventral chaetotaxy. I, 4-5 (5); II, 9-15 (13) *m*, 7-13 (9) *a*, anterior sclerotized margin entire, as in female; III, 10-17 (14) *m*, 13-24 (18) *a*; IV, 12-20 (16) *m*, 18-27 (20) *a*; V, 7-13 (11) *m*, 12-20 (15) *a*, lateral brushes 65-75; VI, 7-10 (9) *m*, 6-16 (10) *a*, lateral brushes 25-35; VII, 4-6 (5) median marginal setae, lateral groups of 4-7 (5) each side; VIII, 6 *m*. Terminal segment with 4 submarginal setae and a marginal row of 9-15 (11) setae, those medial short, forming a ventral anal row, longer laterally and encroaching on ventral surface of terminal segment. Internal anal setae not apparent in most specimens; an undulating row of microtrichia observed in some specimens probably represents the vestiges of internal setae. Genital armature as in fig. 6; sclerite as in fig. 7; genital sac lacking large denticles.

DIMENSIONS.

	Female	Male
Preocular width	0.51-0.55 (0.54)	0.48-0.52 (0.50)
Temple width	0.69-0.73 (0.72)	0.63-0.69 (0.66)
Head length	0.49-0.52 (0.51)	0.46-0.49 (0.48)
Total length	3.0-3.5 (3.2)	2.2-2.6 (2.4)

MATERIAL EXAMINED. 6♂, 4♀ ex *Apus a. apus*, Suffolk, England (viii.1935. BMNH) (Neoparatypes of *D. hirundinis*); 1♂ ex *Apus a. apus*, Kenya (iii.1936. BMNH) (Neoparatype of *D. hirundinis*); 1♀ ex *Apus a. apus*, Asia Minor (vi.1935. BMNH) (Neoparatype of *D. hirundinis*); 2♂, 2♀ ex *Apus a. apus*, Dunwich, Suffolk, England (viii.1935. OPC); 3♂, 4♀ ex *Apus apus*, Bolanda, Tshuapa, Congo (P. Herroelin, 19.i.1955. BMNH & MRAC); 1♂, 2♀ ex *Apus a. apus*, Southern Spain (Varma, 5.iv.1961. BMNH); 1♂, 1♀ ex *Apus apus*, Battersea, London (11.vii.1957. BMNH); 1♀ ex swift, Windermere, Westmorland, England (8.viii.1929. BMNH); 1♂, 1♀ ex *Apus apus*, Bristol, England (R. S. George, 24.vii.1955. BMNH); 2♂, 1♀ ex *Micropus apus*, Oxford, England (G. B. Thompson, 27.v.1937. GBT); 1♀ ex *Micropus a. apus*, Cambridge, England (G. B. Thompson, vii.1949. GBT); 1♂, 1♀ ex *Micropus a. apus*, Northwest Lanarkshire, Scotland (P. A. Clancey, 11.vi.1938. GBT); 1♂ ex *Apus a. apus*, Denbighshire, Wales (M. Mitchell, 8.vi.1936. GBT); 1♂ ex *Apus a. apus*, Monmouthshire, England (H. M. Hallett, 18.vii.1934. GBT); 37♂, 37♀ ex *Apus apus*, Zurich, Switzerland (W. Büttiker. WBC); 1♂ ex mauersegler, Tharandt, Germany (H. Richter, 26.v.1949. ZMB); 1♀ ex *Cypselus apus*, Kowno, Russia (S. G. Iwanowski, 25.vii.1920. ZMB); 4♀, 1♂ ex *Apus apus* (ZMB).

Discussion

The above description of *Dennyus hirundinis* is based on material from the type host, *Apus apus*. In addition I have seen material, collected from a number of *Apus* species, which I find impossible to separate from *D. hirundinis* as defined above, despite

an intensive search for characters which might enable me to do so. I therefore regard these populations on hosts other than *Apus apus* as *D. hirundinis sens. lat.* Several of the populations have been named as distinct species, and I will deal with each population separately below.

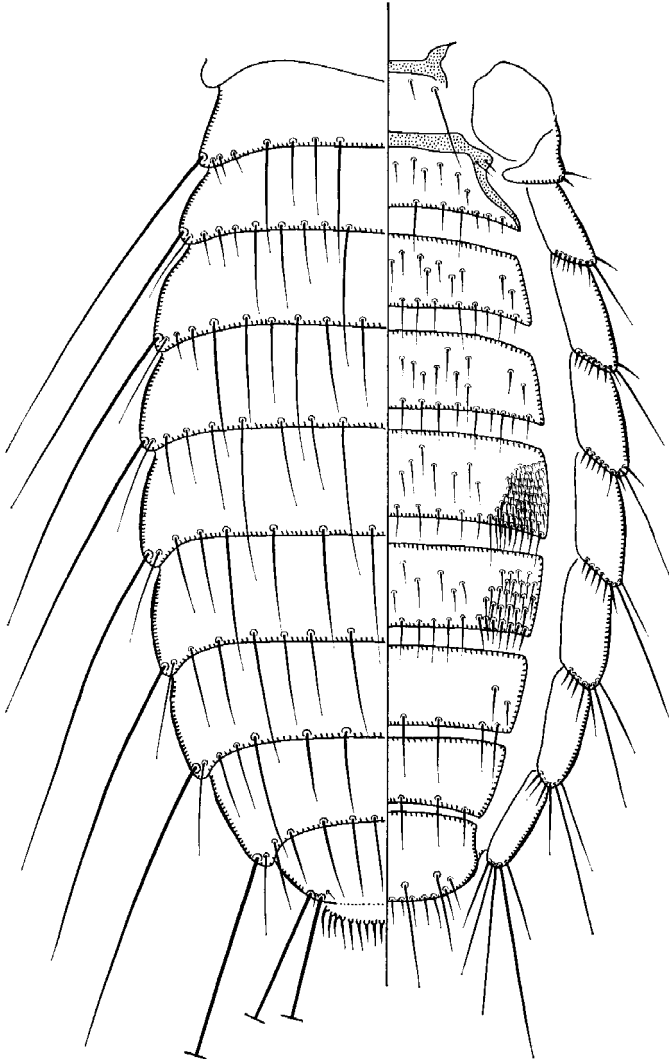


Fig. 2. *Dennyus hirundinis* (Linnaeus, 1761). Male abdomen, dorsal/ventral view.

*Dennyus hirundinis sens. lat.*1. Population on *Apus affinis* (J. E. Gray)

Nitzschia minor Kellogg & Paine, 1914 was described from material collected from specimens of *Apus affinis* in the Indian Museum, Calcutta. The measurements given in the original description are smaller than those of any adult *Dennyus* measured in the present study. Bedford (1932) first noted the similarity of *D. minor* and *D. hirundinis* and stated: "This species is very closely related to *D. truncatus* and may prove to be a synonym of that species. It was described from immature specimens taken off an Indian swift, *Colletoptera affinis* (= *Cypselus affinis*) in India". I have seen a co-type of *Nitzschia minor*, from the Ferris Collection at the University of California, Berkeley, which is a nymph. Tendeiro (1958) examined *Dennyus* from two African subspecies of *Apus affinis* and compared them with material from *Apus apus*. He concluded that although the head measurements of the material from *A. affinis* averaged slightly less than in the material from *A. apus* there was no justification for the creation of a subspecific category or any other taxonomic rank for the population from *A. affinis*. Tendeiro (1958) did not formally synonymize *Nitzschia minor* with *D. hirundinis*, and I therefore do so with the publication of this paper. The *Dennyus* parasitic on *Apus affinis* in West Africa has achieved some fame as the intermediate host of an avian filaria (Dutton, 1905); the same author reports finding that blood forms part of the diet of the louse.

During the present study I examined a good series of specimens from *A. affinis*, and I found no significant morphological characters which could possibly be used to separate the population on *A. affinis* from that on *A. apus*. A brief account of setal ranges and measurements of the *A. affinis* population follows.

FEMALE. *Tergocentrals*: I, 15-22; II, 17-24; III, 17-22; IV, 17-23; V, 14-22; VI, 13-20; VII, 11-16; VIII, 8-11. *Ventral chaetotaxy*: I, 4-6; II, 12-20 *m*, 8-16 *a*; III, 14-21 *m*, 19-26 *a*; IV, 16-23 *m*, 21-35 *a*; V, 10-13 *m*, 16-33 *a*, lateral brushes about 60-70; VI, 8-14 *m*, 12-17 *a*, lateral brushes 20-35. Vulval marginal setae 14-24 (20); anterior part of subgenital plate with 3-5 (5) median and lateral groups of 3-7 setae.

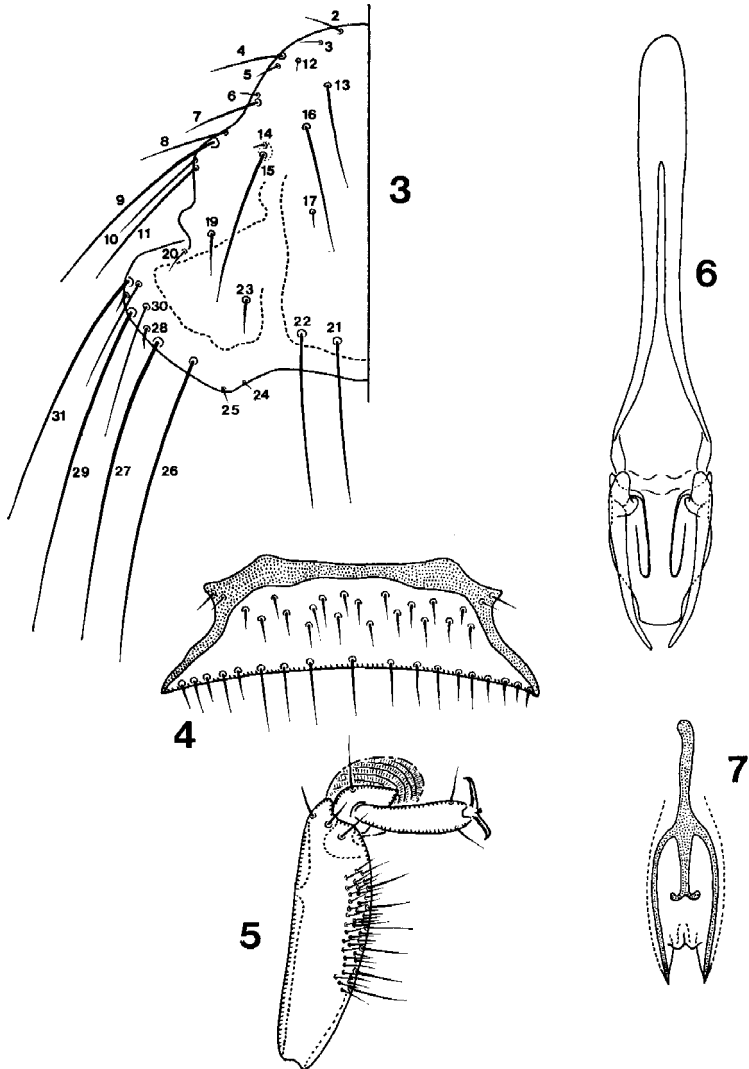
MALE. *Tergocentrals*: I, 11-16; II, 12-16; III, 12-17; IV, 14-17; V, 12-17; VI, 12-16; VII, 9-16; VIII, 8-11. *Ventral chaetotaxy*: I, 4-6; II, 10-14 *m*, 7-11 *a*; III, 13-19 *m*, 13-20 *a*; IV, 14-21 *m*, 14-21 *a*; V, 8-12 *m*, 10-17 *a*, lateral brushes about 50-60; VI, 8-12 *m*, 4-16 *a*, lateral brushes 20-30; VII, 4-6 (4) median marginal setae, lateral groups of 3-7 setae each side; VIII, 6 *m*.

DIMENSIONS.

	Female	Male
Preocular width	0.51-0.54 (0.52)	0.47-0.52 (0.49)
Temple width	0.61-0.76 (0.68)	0.60-0.68 (0.64)
Head length	0.48-0.52 (0.50)	0.44-0.49 (0.46)

MATERIAL EXAMINED. 2 ♂, 2 ♀ ex *Apus affinis*, Johannesburg, South Africa (13.iii.1953. BMNH & SAIMR); 4 ♂, 2 ♀ ex *Apus affinis*, Pretoria, South Africa (M. Markus, 22.iv.1967. SAIMR); 1 ♂, 1 ♀ ex *Apus affinis*, Pretoria, South Africa (4.xi.1930. OPC); 1 ♂ ex *Apus affinis*, Onderstepoort, South Africa (26.iv.1927. OPC); 1 ♂, 1 ♀ ex *Micropus affinis abyssinicus*, Abam, French Cameroons (J. Mouchet, BMNH); 1 ♂, 2 ♀ ex *Apus affinis subfurcatus*, Selangor, Malaya (R. A. Lever, 5.v.1952. BMNH); 1 ♂, 2 ♀ ex *Apus affinis*, Lucknow, India (BMNH); 1 ♂, 1 ♀ ex *Micropus affinis*, Indore, India

(1939. BMNH); 3 ♀ ex *Apus affinis nipalensis*, Nepal (v.1939. BMNH); 3 ♂, 2 ♀ ex *Apus affinis singalensis*, Kathiraveli, Ceylon E. P. (W. Phillips, 19.ii.1947. GBT); 3 ♂, 3 ♀ ex *Apus affinis subfurcatus*, Kasiqi, British North Borneo (30.viii.1960. USNM); 2 ♂, 2 ♀ ex *Apus affinis subfurcatus*, Kuala Lumpur, Malaya (22.v.1956. USNM); 3 ♂, 2 ♀ ex *Apus affinis*, Shih Lin, Taipei Hsien, Formosa (R. E. Kuntz, 26.vi.1958. USNM)



Figs 3-7. *Dennyus hirundinis* (Linnaeus, 1761). 3. Dorsal head setae. 4. Abdominal sternite II. 5. Tibia and tarsus, anterior leg. 6. Male genital armature. 7. Male genital sclerite.

& BMNH); 4 ♂, 3 ♀ ex *Apus affinis kuntzi*, Ta Hsi, Tao Youn Hsien, Formosa (R. E. Kuntz, 28.viii.1958. USNM); 1 ♀ ex *Apus affinis*, Khao Chang, Trat, Thailand (26.iv.1966. USNM).

2. Population on *Apus caffer* (Lichtenstein)

The name *Dennyus* (*Dennyus*) *truncatiformis* Mokhehle, 1951 was proposed for the population parasitic on *A. caffer* in the Cape Province, South Africa. In his description, the author stresses a number of points of difference between the new taxon and *D. hirundinis*; these, however, appear to be due to mounting technique. I have seen the holotype and paratypes of *D. truncatiformis*, and can find no reliable characters which could serve to distinguish the population on *A. caffer* from *D. hirundinis*. Dorsal and ventral setal counts overlap and the dimensions of the two populations appear to be identical. There are no differences in the male genitalia. I therefore have no hesitation in regarding *D. truncatiformis* a junior synonym of *D. hirundinis*.

MATERIAL EXAMINED. 2 ♂, 2 ♀ ex *Caffrapus c. caffer*, Fort Hare, Cape Province (N. Mokhehle. Zoology Department, University College of Fort Hare) (Holotype ♀ and paratypes of *D. truncatiformis*); 1 ♀ ex *Cypselus caffer*, Pirie, Kingwilliamstown, South Africa (R. Godfrey, 8.iii.1910. BMNH); 2 ♂, 1 ♀ ex *Cypselus caffer* (BMNH); 4 ♂ ex *Apus caffer*, Nbi-Nyeri, Kenya (9.i.1961. BMNH); 1 ♀ ex *Apus caffer*, Danielskuil, Cape Province (R. Joyner, 14.v.1967. SAIMR); 2 ♂ ex *Apus caffer*, Pretoria, South Africa (M. Markus, 22.iv.1967. SAIMR).

3. Population on *Apus horus* (Heuglin)

The 3 specimens from this host agree well with *D. hirundinis* in all morphological characters.

MATERIAL EXAMINED. 1 ♀ ex *Apus horus*, Magaliesberg, Transvaal, South Africa (15.ix.1955. BMNH); 2 ♂ ex *Micropus horus*, Kenya (22.vi.1943. BMNH).

4. Population on *Apus bradfieldi* (Roberts)

Dennyus africanus Büttiker, 1954 was based on material collected in South West Africa from a swift which Büttiker (1954) cited as *Apus aequatorialis bradfieldi*. Lack (1956) pointed out that *bradfieldi* did not belong in *aequatorialis*, and he considered it as a subspecies of *Apus barbatus*. Both Traylor (1960) and Brooke (1969a, 1970a) treat *bradfieldi* as a good species. An examination of a short series, comprising some of Büttiker's specimens from *A. bradfieldi*, has shown that this population also is inseparable from *D. hirundinis*. All setal counts and measurements overlap in the two populations; the shape and chaetotaxy of the prosternal plate, which Büttiker (1954) used as a diagnostic character, show no significant differences.

MATERIAL EXAMINED. 1 ♂, 4 ♀ ex *Apus aequatorialis bradfieldi*, South West Africa (A. König. WEC) (Part of type series of *D. africanus*).

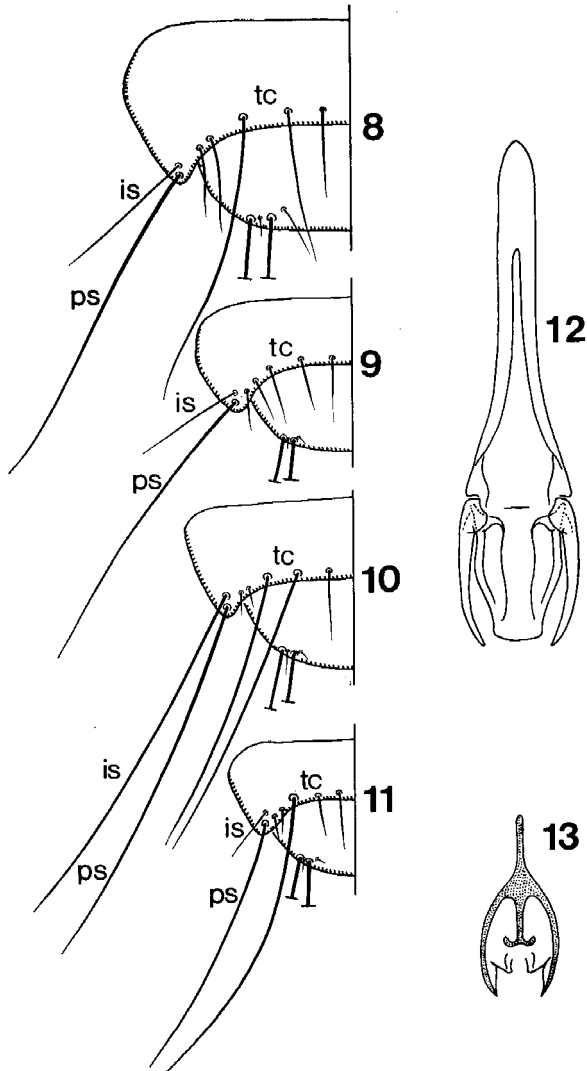
5. Population on *Apus barbatus* (Sc Slater)

The single specimen seen from this host has been identified as *D. hirundinis*.

MATERIAL EXAMINED. 1 ♀ ex *Apus barbatus*, Natal, South Africa (10.i.1951. BMNH).

6. Population on *Apus alexandri* (Hartert)

Dennyus maritimus Büttiker, 1954 was described from material taken from *Apus unicolor*, Cape Verde Islands. Lack (1956) treats *unicolor* as a race of *A. apus*, and



Figs 8–13. *Dennyus hirundinis* (Linnaeus, 1761) & *D. cypsiurus* Thompson, 1948. 8–11, terminal tergites. 8. *D. hirundinis*, female neoparatype. 9. *D. hirundinis*, male neoparatype. 10. *D. cypsiurus*, female holotype. 11. *D. cypsiurus*, male paratype. 12. *D. cypsiurus*, male genital armature. 13. *D. cypsiurus*, male genital sclerite. (is = inner seta; ps = post-spiracular seta; tc = tergo-central setae).

also regards *alexandri* as the race of *A. apus* which occurs on the Cape Verde Islands. It is therefore reasonable to suppose that Büttiker's material came from *alexandri*, which Brooke (1970b) now considers to be a good species. I have examined one pair of specimens from the type series, and although they are badly cleared they reveal sufficient details to indicate that *D. maritimus* is a junior synonym of *D. hirundinis*.

MATERIAL EXAMINED. 1 ♂, 1 ♀ ex *Apus unicolor*, Cape Verde Islands (WEC) (Part of type series of *D. maritimus*).

7. Population on *Apus pallidus* (Shelley)

Dennyus minutus Büttiker, 1954 was described from three females from *Apus p. pallidus*, Teneriffe, Canary Islands. According to Peters (1940) and Lack (1956) the race from the Canary Islands is *A. pallidus brehmorum* Hartert. Büttiker (1954) stated that the prosternal plate of *D. minutus* was distinctive; in other respects the species was said to be difficult to separate from *D. hirundinis*. I have seen a single male specimen from the collection of Dr Eichler labelled as "*Dennyus minutus* nov. spec. *Micropus pallidus*. 364a. Det. Büttiker". This specimen is in poor condition, but nonetheless it is possible to see that the details of the prosternal plate and genitalia do not differ in any way from those of *D. hirundinis*. I have also seen two females in good condition from *A. pallidus*, and a detailed examination has revealed no differences from typical *D. hirundinis*. I can therefore find no grounds for recognizing *D. minutus*, which becomes a junior synonym of *D. hirundinis*.

MATERIAL EXAMINED. 1 ♂ ex *Micropus pallidus* (364a. WEC); 2 ♀ ex *Micropus pallidus illyricus*, Santa Eulalia, Iviza, Balearic Islands (John Bernström, 3.vi.1934. GBT).

8. Population on *Apus acuticauda* (Jerdon)

I have seen a short series collected from this host in Thailand. The actual specimen from which the lice were collected has been discussed by Brooke (1969c) in his notes on *A. acuticauda*. The *Dennyus* are all over-cleared, and in one specimen the head capsule has collapsed, indicating prolonged treatment in macerating fluid. A brief description, with ranges of setal counts, follows.

FEMALE. Dorsal head chaetotaxy as for *D. hirundinis*. Median prosternal setae 4-6; posterior mesosternal setae 5-6; metasternal setae 17-22; metanotal marginal setae 12-13. *Tergocentrals*: I, 18-22; II, 18-23; III & IV, 19-22; V, 16-20; VI, 16-19; VII, 12-17; VIII, 9-11. *Ventral chaetotaxy*: I, 4-7; II, 13-19 m, 8-18 a; III, 18-20 m, 20-27 a; IV, 20-22 m, 26-42 a; V, 11-14 m, 22-32 a, lateral brushes 85-100; VI, 11-12 m, 12-22 a, lateral brushes 20-30. Vulval marginal setae 22 (1 specimen with 15), anterior part of subgenital plate with 4 median, 3-6 lateral setae each side.

MALE. 3-5 median prosternal, 4-6 posterior mesosternal, 15-21 metasternal and 10-13 metanotal marginal setae. *Tergocentrals*: I, 12-18; II, 13-18; III, 12-18; IV, 15-18; V, 14-18; VI, 13-16; VII, 13-14; VIII, 8-10; dorsal anal setae 19-28. *Ventral chaetotaxy*: I, 4-5; II, 11-16 m, 9-13 a; III, 14-17 m, 16-22 a; IV, 14-19 m, 18-25 a; V, 9-11 m, 14-23 a, lateral brushes 70-80; VI, 8-11 m, 7-14 a, lateral brushes 20-30; VII, 4-6 median marginal, 4-7 lateral setae each side; VIII, 6 m. Terminal segment with 4 submarginal, 8-13 marginal setae.

DIMENSIONS.

	Female	Male
Preocular width	0.56-0.58 (0.57)	0.51-0.54 (0.52)
Temple width	0.74-0.79 (0.76)	0.66-0.77 (0.70)
Head length	0.50-0.54 (0.52)	0.49-0.51 (0.50)
Total length	3.0-3.2 (3.1)	2.3-2.4 (2.3)

MATERIAL EXAMINED. 5 ♂, 5 ♀ ex *Apus acuticauda*, Doi Pui, Chiangmai, Thailand (B. King, 16.ii.1965. KCE).

From the above description it can be seen that setal ranges and measurements on the whole overlap those of *D. hirundinis* from the type host, except that there appear to be more setae in the sternal brushes on V, and the head appears somewhat broader in the females of the population from *A. acuticauda*. The male genitalia agree well, the sclerite is the same, but the caudal part of the basal plate in the *A. acuticauda* population appears to be slightly broader than in specimens from *A. apus*. This feature, and the larger head size in the female, may be due in part to the preparation and mounting of the specimens. I propose to regard the population on *A. acuticauda* as *D. hirundinis sens. lat.* until such time as more and better preserved material becomes available from this host.

9. *Population on Apus pacificus (Latham)*

I have seen one pair of specimens from this host. The male appears to be identical to *D. hirundinis* and the female agrees with that species in all important characters except that there are 44 vulval marginal setae. The type host of *Dennyus clayae* Nakagawa, 1959 is *Apus p. pacificus* from Japan. The characters which Nakagawa (1959) used to separate *D. clayae* from *D. hirundinis* are not reliable ones, according to my experience in the present study; these include the shape and chaetotaxy of the prosternal plate and the 3rd femora, the chaetotaxy of sternite VII in the male, and the shape of the distal part of the endomerical piece of the male genitalia. Nakagawa (1959) does not give vulval setal counts for his material. I do not intend commenting further on the status of *D. clayae* until I have seen the types, or more material from the type host.

MATERIAL EXAMINED. 1 ♀ ex *Apus pacificus*, Doi Pha Hom Pok, Chiangmai, Thailand (MAPS, 28.x.1965. USNM); 1 ♂, all data as for preceding specimen, but host labelled as *Collocalia brevirostris* (= error for *Apus pacificus*).

Dennyus (Dennyus) cypsiurus Thompson, 1948, figs 10-13

Dennyus cypsiurus Thompson, 1948, *Boln Ent. venez.* 7 (1 & 2): 4, fig.

Type-host: *Cypsiurus parvus batasiensis* (J. E. Gray).

FEMALE. General appearance as for *D. hirundinis*, but a smaller species. Dorsal head chaetotaxy and pleural chaetotaxy agree well in both species; 3-4 (3) median prosternal; 4-6 (4) posterior mesosternal; 12-17 (15) metasternal and 11-15 (13) metanotal marginal setae.

Postspiraculars. Long on I-VIII; the associated inner seta short and slender on II, increasing in length and thickness on succeeding tergites; on VIII this seta is very long and stout, similar to the postspiracular on this tergite (fig. 10).

Tergocentrals. On VIII at least 2, usually 4 tergo-centrals are much longer and stouter than others in row (fig. 10). Range: I, 18-26 (22); II, 19-25 (20); III, 19-24 (21); IV, 18-26 (21); V, 18-25 (21); VI, 15-25 (17); VII, 13-17 (14); VIII, 9-11 (10). Terminal segment as for *D. hirundinis*.

Ventral chaetotaxy. I, 4-6 (5); II, 13-18 (16) *m*, 6-11 (9) *a*, sclerotized anterior margin as for *D. hirundinis*, not interrupted medially; III, 15-20 (17) *m*, 17-23 (21) *a*; IV, 16-21 (18) *m*, 25-39 (29) *a*; V, 8-10 (9) *m*, 8-23 (20) *a*, lateral brushes 50-70; VI, 6-8 (7) *m*, 11-19 (15) *a*, lateral brushes 30-50. Vulval marginal setae 12-18 (16); anterior part of subgenital plate with a median row of 4-5 (4) and lateral groups of 4-5 (4) setae.

MALE. General appearance as for female, but smaller; 3-4 (3) median prosternal; 3-5 (4) posterior mesosternal; 10-14 (12) metasternal and 8-12 (10) metanotal marginal setae.

Postspiraculars. Long on I-VIII; the associated inner seta is medium and slender on II, and of approximately the same length and thickness on succeeding tergites, not becoming progressively longer and thicker as in female. On VIII the inner seta is slightly shorter than on VII, usually reaching to less than $\frac{1}{2}$ length of the corresponding postspiracular (see fig. 11).

Tergocentrals. On VIII one pair of tergo-centrals is normally much longer and stouter than others in the row, extending well beyond the tip of the abdomen and reaching $\frac{3}{4}$ length or more of the postspiracular seta on VIII (fig. 11). Tergocentral range: I, 12-16 (14); II, 12-19 (15); III, 13-19 (16); IV, 15-18 (16); V, 13-20 (16); VI, 13-17 (15); VII, 12-16 (13); VIII, 10-11 (10); dorsal anal setae 18-24 (22).

Ventral chaetotaxy. I, 4-5 (4); II, 11-13 (12) *m*, 4-8 (6) *a*, anterior margin as for female; III, 11-15 (13) *m*, 13-15 (14) *a*; IV, 11-14 (13) *m*, 14-21 (17) *a*; V, 6-9 (8) *m*, 7-14 (12) *a*, lateral brushes 40-60; VI, 6-9 (7) *m*, 7-14 (12) *a*, lateral brushes 25-40; VII, 3-4 (4) median marginal, 2-5 (4) lateral setae each side; VIII, 6 *m*. Terminal segment with 4 submarginal, 12-19 (14) marginal setae.

Genitalia. Very similar to *D. hirundinis*; slightly smaller. The sac and sclerite are of the same basic form in both species, but the sclerite in *D. cypsiurus* is somewhat shortened longitudinally (figs 12 & 13).

DIMENSIONS.

	Female	Male
Preocular width	0.46-0.49 (0.47)	0.42-0.44 (0.43)
Temple width	0.61-0.69 (0.66)	0.57-0.61 (0.59)
Head length	0.42-0.46 (0.45)	0.41-0.43 (0.42)
Total length	2.2-2.6 (2.4)	2.0-2.1 (2.0)

MATERIAL EXAMINED. 2 ♂, 1 ♀ ex *Cypsiurus parvus batasiensis*, Gammaduwa, Mousakande, Ceylon, C. P. (W. Phillips, 16.x.1935. GBT) (Holotype ♀, allotype ♂ and paratype ♂ of *D. cypsiurus*); 4 ♂ ex *Cypsiurus parvus batasiensis*, Bombay, India (ii.1937. BMNH); 1 ♂, 1 ♀ ex *Cypsiurus parvus*, near Hyderabad, India (J. P. Donahue, 3.viii.1961. BMNH); 2 ♂, 3 ♀ ex *Cypsiurus parvus brachypterus*, Ibembo, Uelc, Congo (Fr J. Hutsebaut, 28.x.1950. BMNH); 1 ♂, 1 ♀ ex *Cypsiurus parvus*, Banana, Congo (Mcsmackers, xi.1952. BMNH); 1 ♀ ex *Cypsiurus parvus brachypterus*, Kribi, Cameroun (V. Aellen, 13.i.1947. BMNH); 4 ♂, 8 ♀ ex *Cypsiurus parvus*, Salisbury, Rhodesia (R. P. Borrett, x.1967. SAIMR).

Discussion

Apart from its smaller size, *D. cypsiurus* is in many ways very similar to *D. hirundinis*, and on a quantitative basis of setal counts alone the two species are virtually impossible to separate, since most setal ranges overlap. However, good characters are to be found in the length and thickness of the tergo-central setae and the inner setae associated with the postspiraculars, particularly those on abdominal tergite VIII (see figs 8-11).

Brooke (1969b) regards *C. batasiensis* and *C. parvus* as separate species; I am unable to detect any differences in the *Dennyus* from the two hosts.

Dennyus (*Dennyus*) *vonarxi* Büttiker, 1954, figs 14, 15, 17, 19, 20

Dennyus von Arxi Büttiker, 1954, *Acta trop.* **11** (2): 161, figs.

Type-host: *Apus m. melba* (Linnaeus).

This and the following species are closely related and are distinguished in the male by having genitalia of a completely different type to that found in *D. hirundinis* and *D. cypsiurus*. Females of all four species resemble one another to a certain degree, but good characters have been found for their separation.

FEMALE. General appearance and chaetotaxy of head as for *D. hirundinis*, average size slightly larger. Thorax with 4-9 (7) median prosternal; 6-9 (7) posterior mesosternal; 14-20 (16) metasternal and 10-12 (11) metanotal marginal setae. Pleural chaetotaxy generally as for *D. hirundinis*.

Postspiraculars. Long on I-VIII. Inner seta medium, slender on II, increasing in length and thickness on succeeding tergites; on VIII (and usually VII) almost of same size as postspiracular.

Tergocentrals. I, 12-17 (15); II, 13-16 (15); III, 13-16 (14); IV, 14-17 (15); V, 14-16 (15); VI, 12-15 (14); VII, 11-14 (12); VIII, 6-9 (7).

Ventral chaetotaxy. I, 4-5 (5); II, 13-20 (16) *m*, 11-20 (16) *a*, anterior sclerotized margin interrupted medially (fig. 14); III, 14-20 (17) *m*, 16-27 (24) *a*; IV, 16-21 (19) *m*, 22-29 (26) *a*; V, 10-13 (12) *m*, 16-25 (20) *a*, lateral brushes 75-90; VI, 9-12 (10) *m*, 13-17 (15) *a*, lateral brushes 30-40. Vulval margin concave medially, with 26-36 (29) slender marginal setae, arranged in a single row throughout (fig. 15). Anteriorly on subgenital plate a median row of 4, lateral groups of 3-5 (4) setae.

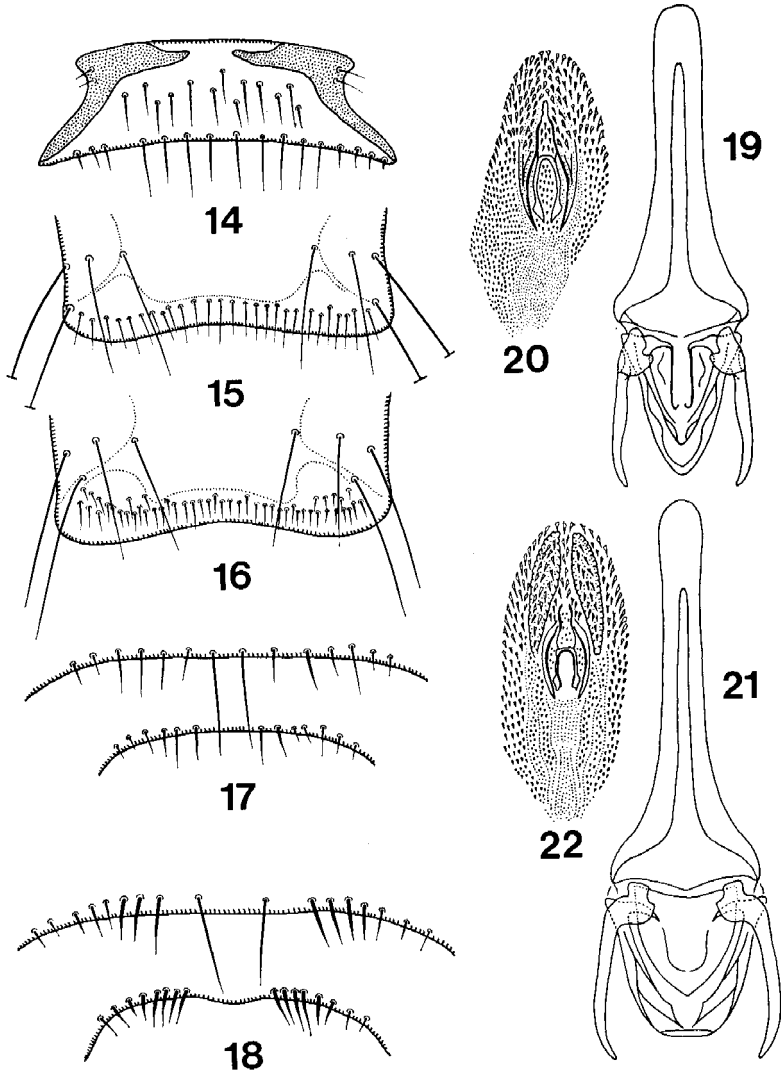
MALE. Thorax with 5-8 (6) median prosternal; 5-9 (7) posterior mesosternal; 13-21 (16) metasternal and 10-12 (10) metanotal marginal setae.

Postspiraculars. Long on I-VIII. Inner seta medium, slender on II, increasing somewhat in length on succeeding tergites to IV, then decreasing in length towards the last tergite; on VIII the inner seta is very short.

Tergocentrals. I, 11-14 (12); II, 11-14 (13); III, 12-14 (13); IV, 12-15 (14); V, 14-17 (15); VI, 15-18 (17); VII, 15-21 (18); VIII, 14-17 (15). On VII & VIII the tergo-centrals are arranged as in fig. 17. Dorsal anal setae 23-29 (26).

Ventral chaetotaxy. I, 4-5 (5); II, 12-16 (14) *m*, 9-14 (11) *a*, sclerotized anterior margin interrupted medially as in female; III, 14-17 (15) *m*, 14-19 (16) *a*; IV, 14-17 (15) *m*, 11-20 (16) *a*; V, 9-13 (11) *m*, 10-18 (13) *a*, lateral brushes 65-80; VI, 8-12 (10) *m*, 5-12 (10) *a*, lateral brushes 25-35; VII, 4-9 (7) median marginal, 3-5 (4) lateral setae each side; VIII, 6-8 (7) *m*. Terminal segment with 4 submarginal, 23-30 (27) marginal setae.

Genitalia. Basal plate short and stout, endomeran piece rather complex, with acutely rounded distal margin. Genital armature as in fig. 19, sclerite and sac as in fig. 20; genital sac with large denticles in anterior part.



Figs 14-22. *Dennyus vonarxi* Büttiker, 1954 & *D. aequatorialis* Ledger, 1968. 14. *D. vonarxi*, abdominal sternite II. 15. *D. vonarxi*, female vulval margin. 16. *D. aequatorialis*, female vulval margin. 17. *D. vonarxi*, male tergocentral setae of VII & VIII. 18. *D. aequatorialis*, male tergocentral setae of VII & VIII. 19. *D. vonarxi*, male genital armature. 20. *D. vonarxi*, male genital sclerite and sac. 21. *D. aequatorialis*, male genital armature. 22. *D. aequatorialis*, male genital sclerite and sac.

DIMENSIONS.

	Female	Male
Preocular width	0.55-0.57 (0.56)	0.52-0.54 (0.53)
Temple width	0.74-0.77 (0.73)	0.68-0.72 (0.70)
Head length	0.50-0.53 (0.52)	0.48-0.52 (0.49)
Total length	2.9-3.1 (3.0)	2.4-2.5 (2.5)

MATERIAL EXAMINED. 21 ♂, 52 ♀ ex *Apus melba*, Zurich, Switzerland (12.viii.1945. WBC) (Including 2 ♂, 4 ♀ paratypes of *D. vonarxi*); 1 ♂, 2 ♀ ex *Apus melba*, Solothurn, Switzerland (20.vi.1946. WBC); 2 ♂ ex *Apus melba*, Zurich, Switzerland (12.viii.1946. WBC); 1 ♂, 1 ♀ ex *Apus melba*, Zurich, Switzerland (W. Büttiker, 8.vii.1946. BMNH); 2 ♂, 2 ♀ ex *Tachymarptis melba marjoriae*, Waterberg, South West Africa (17.v.1937. BMNH & OPC); 2 ♂ ex *Apus melba archeri*, Somalia (A. R. Tribe, vii.1958. BMNH); 1 ♀ ex *Apus melba*, Rustenburg, Transvaal, South Africa (30.x.1960. BMNH); 1 ♂, 2 ♀ ex *Apus melba tuneti*, Kabul (iv.1947. BMNH); 1 ♂ ex *Micropus melba tuneti*, Afghanistan (v.1937. BMNH); 1 ♂, 1 ♀ ex *Micropus melba bakeri*, Indore, India (1939. BMNH); 1 ♂, 6 ♀ ex *Micropus melba bakeri*, Gammaduwa, Mousakande, Ceylon, C. P. (W. Phillips, 21.xii.1937. GBT); 1 ♂, 3 ♀ ex *Apus aequatorialis*, Wase Rock, Plateau Province, Nigeria (M. T. Horwood, 14.vi.1964. BMNH) (host error for *Apus melba*).

Discussion

The male of *D. vonarxi* is quite distinctive and requires no further discussion. Females bear a superficial resemblance to *D. hirundinis* and *D. cypsiurus*, but may be distinguished by having the sclerotized anterior margin of sternite II interrupted medially, and the vulval margin concave medially with a greater number of marginal setae, although on this last character the range grades into *D. hirundinis* at the count of 26 (maximum for *hirundinis*, minimum for *vonarxi*).

Dennyus (Dennyus) aequatorialis Ledger, 1968, figs 16, 18, 21, 22

Dennyus aequatorialis Ledger, 1968, *Novos Taxa ent.* 61: 3, figs.

Type-host: *Apus a. aequatorialis* (von Müller).

This species was based on two male specimens. Further material has since come to hand and it is now possible to describe the female. *D. aequatorialis* is closely related to *D. vonarxi*; Ledger (1968) listed characters separating the males and discussed host relationships.

FEMALE. General appearance and chaetotaxy close to *D. vonarxi*; postspiraculars and inner setae as for that species. Thorax with 5-7 (6) median prosternal; 6-9 (7) posterior mesosternal; 14-18 (16) metasternal and 11-13 (12) metanotal marginal setae.

Tergocentrals. I, 15-19 (17); II, 14-16 (15); III, 13-15 (14); IV, 13-17 (16); V, 12-16 (14); VI, 11-16 (14); VII, 12-14 (13); VIII, 8-10 (9).

Ventral chaetotaxy. I, 5-6 (6); II, 15-19 (16) *m*, 15-21 (17) *a*, sclerotized anterior margin interrupted medially, as in *D. vonarxi*; III, 17-21 (19) *m*, 20-25 (22) *a*; IV, 16-22 (19) *m*, 24-37 (30) *a*; V, 11-14 (12) *m*, 18-22 (20) *a*, lateral brushes 80-90; VI, 10-12 (11) *m*, 13-21 (16) *a*, lateral brushes 40-60. Vulval margin concave medially, heavily

sclerotized laterally with 38-54 (47) marginal setae, shorter and stouter than in *D. vonarxi*; these setae are normally arranged in a single row medially, but laterally encroach on the subgenital plate in sparse, brush-like fashion, or at least not in a single row (see fig. 16). Anteriorly on subgenital plate a median row of 4, lateral groups of 4-8 (4) setae each side.

MALE. General appearance and chaetotaxy close to *D. vonarxi*; postspiraculars and inner setae as for that species. Thorax with 5-7 (6) median prosternal; 5-9 (7) posterior mesosternal; 14-21 (16) metasternal and 10-12 (11) metanotal marginal setae.

Tergocentrals. I, 12-14 (13); II, 12-15 (13); III, 13-14 (13); IV, 13-15 (13); V, 14-15 (14); VI, 14-16 (16); VII & VIII, 16-18 (17). On VII & VIII the tergo-centrals are distinctive, medially very stout and spine-like (fig. 18). Dorsal anal setae 18-21 (20).

Ventral chaetotaxy. I, 4-5 (5); II, 12-13 (12) *m*, 10-15 (12) *a*, anterior margin as for female; III, 13-17 (15) *m*, 13-16 (14) *a*; IV, 16-19 (18) *m*, 17-18 (17) *a*; V, 10-13 (11) *m*, 11-15 (12) *a*, lateral brushes 70-90; VI, 8-10 (9) *m*, 5-8 (6) *a*, lateral brushes 30-50; VII, 4-6 (4) median marginal, 4-6 (4) lateral setae each side; VIII, 6 *m* (1 specimen with 7). Terminal segment with 4 submarginal, 29-35 (32) marginal setae.

Genitalia. Similar to *D. vonarxi*, but larger, with a longer basal plate and the distal margin of the endomeral piece truncate. Genital armature as in fig. 21, sclerite and sac as in fig. 22.

DIMENSIONS.

	<i>Female</i>	<i>Male</i>
Preocular width	0.55-0.59 (0.57)	0.54-0.56 (0.55)
Temple width	0.76-0.82 (0.78)	0.74-0.76 (0.75)
Head length	0.51-0.54 (0.52)	0.50-0.51 (0.50)
Total length	2.8-3.0 (2.9)	2.4-2.5 (2.5)

MATERIAL EXAMINED. 4 ♂, 6 ♀ ex *Apus a. aequatorialis*, Kenya (ii. & iii. 1936. BMNH); 1 ♂, 2 ♀ ex *Apus aequatorialis*, Rongai, Kenya (14.x.1964. BMNH).

Discussion

D. aequatorialis and *D. vonarxi* are obviously similar and probably evolved from the same ancestral form. Females of the two species are separated by the characters of the vulval margin (compare figs 15 & 16); males are distinguished by the form of the tergo-central setae on VII & VIII (figs 17 & 18) and by the genital armature (figs 19 & 21). Brooke (1967) has published notes on the taxonomy and distribution of the type host.

Key to adult *Dennyus* from *Apus* and *Cypsiurus*

FEMALES

- 1 Sclerotized anterior margin of sternite II entire medially (fig. 4); vulval margin not concave medially, with 26 or less vulval setae. 2
- Sclerotized anterior margin of sternite II interrupted medially (fig. 14); vulval margin concave medially, with 26 or more vulval setae. 3
- 2 Inner setae on tergite VIII of length and thickness nearly equal to postspiracular setae of that tergite (fig. 10) **cypsiurus**

- Inner setae on tergite VIII much shorter and more slender than postspiracular setae of that tergite (fig. 8)
- 3 Vulval marginal setae 38 or more, rather short and stout, laterally arranged in sparse brush-like fashion, or at least not in a single row (fig. 16)
- Vulval marginal setae 36 or less, medium and slender, normally arranged in a single row throughout (fig. 15)

hirundinis
aequatorialis
vonarxi

MALES

- 1 Genital armature as in figs 6 or 12; sclerite as in figs 7 or 13 2
- Genital armature as in figs 19 or 21; sclerite as in figs 20 or 22 3
- 2 One pair of tergo-central setae on VIII much longer and stouter than others in row, approaching length and thickness of postspiracular setae on this tergite (fig. 11)
- Tergo-central setae on VIII without any one seta much longer and stouter than others in row, normally not extending beyond tip of abdomen (fig. 9)
- 3 Tergo-central setae on VII & VIII very stout and spine-like medially (fig. 18); genital armature as in fig. 21
- Tergo-central setae on VII & VIII short medially, but not particularly stout or spine-like (fig. 17); genital armature as in fig. 19

cypsiurus
hirundinis
aequatorialis
vonarxi

HOST-PARASITE RELATIONSHIPS

As pointed out by Ledger (1968), the *Dennyus* of *Apus melba* and *A. aequatorialis* differ from the *Dennyus* on other members of the genus to a striking degree. There is thus some evidence that *A. melba* and *A. aequatorialis* evolved fairly early in the history of *Apus*, and the characters of the lice lend support to the action of Brooke (1970b) in placing *melba* and *aequatorialis* in the subgenus *Tachymarptis* Roberts, 1922. Brooke (*op. cit.*) retains all other species in the subgenus *Apus sens. str.*, and again the *Dennyus* evidence suggests that this is a sound classification, for *D. hirundinis sens. lat.* has been seen from at least 8 representatives of *Apus sens. str.*, which in turn indicates fairly recent speciation in this group.

Brooke (*op. cit.*) has suggested that evolution in the pamprodactyl Apodini (including *Apus sens. str.*, *Apus (Tachymarptis)* and *Cypsiurus*) was stimulated by tectonic movements of the late Tertiary which resulted in an abundance of vertical rock breeding sites for a group which had hitherto been largely restricted to arboreal nesting sites. *Cypsiurus* has remained restricted to the latter type of nesting site, and Brooke (*op. cit.* and pers. comm.) regards it as a relic of the stock which gave rise to *Tachymarptis* (an early off-shoot) and *Apus sens. str.* When one looks at *Dennyus cypsiurus*, however, the obvious impression is that this louse is much closer to *D. hirundinis* than are *D. vonarxi* and *D. aequatorialis*. This suggests to me that the *A. melba/aequatorialis* line may have diverged from the basic stock and utilized the new rock breeding sites before *Apus sens. str.* took to the rock faces, speciated rapidly and left *Cypsiurus* behind in the old tree-nesting environment. A note of caution must be added here, for Clay (1958) has pointed out that the degree of difference between populations of Phthiraptera is not necessarily an indication of the degree and time of isolation of their hosts; evolution of characters in the parasites does not necessarily progress at a uniform rate on different hosts. However, after considering the *Dennyus* evidence in this case I think it worthwhile to make a tentative proposal that there may have been two waves of evolutionary assault by the arboreal-nesting swift stock upon the newly formed rock nesting sites, the first led by the ancestors of *A. melba* and *A. aequatorialis*, followed later by the forerunners of present-day *Apus sens. str.*

A final observation remains to be made on the *Dennyus* of a bird long known as *Apus myoptilus* (Salvadori). De Roo (1968) recently created the monotypic genus *Schoute-*

denapus for this swift on the grounds that it has anisodactyl feet. Brooke (1970b) does not agree with previous subfamily categories in swifts, and divides the Apodidae into two subfamilies, Cypseloidinae and Apodinae (comprising three tribes, Collocaliini, Chaeturini and Apodini). The suprageneric position of *Schoutedenapus* is problematic, and has been discussed by De Roo (1968) and Brooke (1970b); the latter author suspects that this swift will prove to be an aberrant member of the Collocaliini, and quotes another authority as being of the opinion that *S. myoptilus* may well be an aberrant member of the Cypseloidinae.

I have before me a single male *Dennyus*, collected from *Schoutedenapus myoptilus* at Nanyuki, Kenya (iv.1949. BMNH). The louse resembles members of the subgenus *Ctenodennyus* Ewing, 1930 which is distinguished, amongst other characters, by the peg-like form of some of the dorsal head, thoracic and tergo-central setae. The type and only described species of *Ctenodennyus* is *spiniger* Ewing, 1930 from the New World *Cypseloides niger* (Cypseloidinae), and the specimen from *Schoutedenapus* is clearly a close relative of *D. spiniger*, indicating at first sight a host affinity with the Cypseloidinae. Unfortunately this is not conclusive because *Ctenodennyus* is also represented on *Collocalia*. I have seen a few specimens taken from members of the latter genus, and it is hoped that the results of taxonomic studies on *Ctenodennyus* (Parsons, in preparation) will shed some light on the affinities of *Schoutedenapus*. One thing seems clear; *S. myoptilus* has nothing to do with *Apus*, and the meagre *Dennyus* evidence available supports the contention that it is a relic of a very old swift fauna (De Roo, 1968).

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