

## A revision of the genus *Harrisoniella* (Mallophaga: Philopteridae)

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**Abstract** Four species of the genus *Harrisoniella* Bedford, 1929 are recognised; 2 further species are placed in synonymy. These, together with their hosts, are *H. ferox* (Giebel, 1867) (= *D. irroratae* Kéler, 1957 new synonymy; = *H. chilensis* Carriker, 1964 new synonymy) on *Diomedea melanophrys melanophrys*, *D. m. impavida*, *D. irrorata*, *D. cauta cauta*, *D. c. salvini*, and *D. bulleri*; *H. densa* (Kelllogg, 1896) on *D. albatrus* and *D. immutabilis*; *H. hopkinsi* Eichler, 1952 on *D. exulans exulans*, *D. e. chionoptera*, *D. epomophora epomophora*, and *D. e. sanfordi*; *H. copei* Timmermann, 1969 on *D. nigripes*.

A key and illustrations to adult males and females of the species are provided and a neotype is designated for *Harrisoniella ferox* (Giebel, 1867). The relationships of the hosts are discussed with respect to their lice; attention is drawn to the species of Diomedidae from which no records of *Harrisoniella* spp. exist. A bibliography of the genus and of all species, valid and synonymised, is given.

**Keywords** chewing lice; Philopteridae; *Harrisoniella*; revisions; new synonymies; type specimens; host relationships; systematics; taxonomy; *Diomedea*; Diomedidae; Mallophaga

### INTRODUCTION

The genus *Harrisoniella* Bedford, 1929 includes large lice found regularly on species of *Diomedea* (albatrosses, mollymawks). However, although conspicuous, these lice are not collected in large

numbers but they have been taken often and have attracted the attention of many workers. Not unexpectedly, they have been described by several authors, often from single specimens (even nymphs), resulting in a long history of taxonomic confusion over almost 150 years.

Most workers have dealt with single species in an ad hoc fashion, or have confined their attention to the literature (e.g., Hopkins 1946). The first reference to material which we recognise as belonging to *Harrisoniella* was made by J. R. Forster (1785) in his excellent account of albatrosses. He described, but did not name, 2 different species of lice; we have been able to confirm that one of them is *Harrisoniella hopkinsi* Eichler, 1952 (see 'Material examined'). The first attempt to revise the genus, based on an examination of material, was made by Eichler (1952), who recognised and named 4 species and designated a further 2 as "A" and "B". Kéler (1957) described what he regarded as 4 species, and gave excellent figures of the diagnostic features of males. Timmermann (1965) discussed the status of the genus and accepted Kéler's 4 species; although he did not publish a key, his is the most recent extensive account. His text figures were all taken from Kéler (1957).

The confusion over the identity of the type species of *Harrisoniella* was extensively discussed by Hopkins (1946). Nevertheless, disregarding Hopkins's very clear discussion, Kéler (1957) created the genus *Diomedicola* to receive species of the largest lice from albatrosses. Kéler (1957, 1958) retained *Harrisoniella* Bedford for another group of smaller lice — which are now included in the genus *Paraclisis* Timmermann, 1965 — from the same hosts. Hopkins & Clay (1957) reviewed the situation and made a submission to the International Commission on Zoological Nomenclature (Clay & Hopkins 1961). The Commission ruled that *Harrisoniella* be regarded in the sense of Hopkins, 1946 (International Commission on Zoological Nomenclature 1963).

Until now, nobody has had the opportunity to study a wide range of material from all hosts known to harbour *Harrisoniella*, let alone the type specimens. We have been able to examine 6 types from 7 nominal species.

Because of the confused taxonomy, we believe it desirable to include in the species synonymies all references to the material now recognised as

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**Table 1** Measurements of *Harrisoniella* spp. (means, in mm; ranges in parentheses).

	Head length*	Head width*	Total length
<i>H. ferox</i>			
Neotype ♂	1.75	1.10	8.61
24 ♂	1.643 (1.48–1.75)	1.016 (0.93–1.10)	8.200 (7.65–8.62)
23 ♀	1.747 (1.64–1.83)	1.249 (1.16–1.31)	8.320 (8.05–8.63)
<i>H. densa</i>			
15 ♂	1.781 (1.70–1.87)	1.159 (1.08–1.25)	8.655 (8.10–9.00)
18 ♀	1.883 (1.79–1.98)	1.339 (1.25–1.42)	8.424 (7.93–8.95)
<i>H. hopkinsi</i>			
31 ♂	1.794 (1.70–1.85)	1.194 (1.13–1.26)	9.168 (8.55–9.52)
37 ♀	1.854 (1.75–1.94)	1.453 (1.39–1.52)	8.843 (8.53–9.35)
<i>H. copei</i>			
11 ♂	1.735 (1.68–1.78)	1.107 (1.05–1.13)	8.463 (7.88–8.90)
10 ♀	1.771 (1.73–1.81)	1.375 (1.33–1.42)	8.213 (7.85–8.72)

\* taken at temples.

*Harrisoniella*, so that records of host-louse associations, together with their geographical ranges, may be brought into line with the current interpretation of the species.

As an illustration of the extreme confusion which exists in the literature, we mention *Pediculus diomedae* J. C. Fabricius, 1775. This name has been applied, under the genera *Lipeurus* Nitzsch, 1818; *Philoapterus* Nitzsch, 1818; *Esthiopterum* Harrison, 1916; *Harrisoniella* Bedford, 1929; and *Perineus* Thompson, 1936, to all 4 of the species herein recognised as belonging to *Harrisoniella* (see synonymies in the following pages). The species *diomedae* J. C. Fabricius, 1775 in fact does not belong in this genus at all (Clay & Hopkins 1951), but in *Paraclisis* Timmermann, 1965.

In the species synonymies, we use quotation marks (" ") for those binomial combinations in which we regard the name as having been incorrectly applied by the author(s) cited immediately after the species name. Original figures are referred to; those published again by the same or other author(s) are not listed. The entries qualified by "Listed only" have probably arisen from literature searches rather than from direct observations of specimens: many of these will thus refer to the same original material. Even where authors state that material has been examined in their work, it is obvious that access has been gained repeatedly to the same specimens.

Where specimens have not been seen by us in this work, our proposed synonymies are based on the published descriptions together with a consideration of the host from which the specimens are stated to have been taken. For bald literature lists,

we inferred the identity of the lice from the name of the host specified: we recognise four distinct *Harrisoniella* species, which we are unable to separate into clearly defined species-groups, and we find that each species is strictly limited in its host association. These are: *H. copei* Timmermann, 1969 on 1 host; *H. densa* (Kellogg, 1896) on 2 hosts; *H. hopkinsi* Eichler, 1952 on 4 hosts; and *H. ferox* (Giebel, 1867) on 6 hosts (See Table 2 — 'Host-parasite list', below). Apart from some occasions, when present evidence suggests the lice be regarded as stragglers or contaminants (see 'Material examined' for each species), we have found no host harbouring more than 1 species of *Harrisoniella*. This does not preclude the possibility that, with further collecting, species of *Harrisoniella* might be found on other hosts.

The geographical distribution of the species of *Harrisoniella* naturally reflects that of their hosts, i.e. 2 species (*H. densa* and *H. copei*) in the North Pacific Ocean, and 2 species (*H. ferox* and *H. hopkinsi*) in the Southern Hemisphere, with *H. ferox* extending to the Galápagos Islands and the north-western coast of South America on *Diomedea irrorata*.

It is our experience that adult specimens of *Harrisoniella* are not abundant on an individual host. Despite albatrosses being among the largest birds, few specimens (rarely more than 6) of *Harrisoniella* are taken from 1 bird as against other genera, such as the quite large and conspicuous *Docophoroides* and the smaller *Paraclisis*, which may be very numerous (some hundreds) on each host searched. Nymphs of *Harrisoniella* may, however, be more numerous.

Specimens of *Harrisoniella* are found mainly on the wing feathers, but they are agile and liable to move when disturbed, or when the host dies.

#### Abbreviations used for institutions and collections

AMNZ — Auckland Institute and Museum, Auckland, New Zealand;  
 ANIC — Australian National Insect Collection, CSIRO, Canberra, Australia;  
 BASE — British Antarctic Survey, Cambridge, England;  
 BMNH — British Museum (Natural History), London, England;  
 BPBM — Bernice P. Bishop Museum, Honolulu, Hawaii;  
 CISC — California Insect Survey, Division of Entomology and Parasitology, University of California, Berkeley, California;  
 CMNZ — Canterbury Museum, Christchurch, New Zealand;  
 INCO — Museo de Zoología, Universidad de Concepción, Concepción, Chile;  
 KCEC — K. C. Emerson Collection, Sanibel, Florida, U.S.A.;  
 MAMU — Macleay Museum, University of Sydney, Sydney, Australia;  
 MNSC — Museo Nacional de Historia Natural, Santiago, Chile;  
 NMNZ — National Museum, Wellington, New Zealand;  
 NZAC — New Zealand Arthropod Collection, DSIR, Auckland, New Zealand;  
 REEC — R. E. Elbel Collection, Salt Lake City, Utah, U.S.A.;  
 RLCP — R. L. C. Pilgrim Collection, housed in NMNZ;  
 SAIRM — South African Institute for Medical Research, Johannesburg, South Africa;  
 SAMA — South Australian Museum, Adelaide, Australia;  
 USNM — United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.;  
 WRAI — Walter Reed Army Institute of Research, Washington, D.C., U.S.A.;  
 ZMHU — Zoologisches Museum, Humboldt Universität, Berlin, East Germany (D.D.R.).

## SYSTEMATICS

### Genus *Harrisoniella* Bedford

Bedford, 1929: 529. — Hopkins, 1946: 4. — Eichler, 1952: 40. — Hopkins & Clay, 1952: 165. — Hopkins & Clay, 1957: 308. — Clay & Hopkins, 1961: 195. — Edwards, 1961: 127–128. — International Commission Zoological Nomenclature, 1963: 178. — Carriker, 1964: 2. — Blagoveshchenskii, 1964: 322 (in part). — Timmermann, 1965: 90. — Timmermann, 1966: 86. — Clay & Moreby, 1967: 162. — Emerson, 1972b: 10.

Type species *Lipeurus ferox* Giebel, 1867 (by subsequent designation in International Commission Zoological Nomenclature 1963: 178).

*Diomedicola* Kéler, 1957: 496. — Eichler, 1963: 174, 188.

Type species *Lipeurus ferox* Giebel, 1867 (by original designation).

The diagnosis given by Bedford (1929) is satisfactory except that we do not find the "... dark median transverse band." on the sternites of either male or female specimens which we have examined, including the female specimen listed by Bedford (see Fig. 2) and at least 1 male which we believe Bedford had seen (see Fig. 1). Although he did not list any male in his paper, he included a measurement and a description of the "male copulatory apparatus" in his diagnosis.

In 1957, Kéler erected the genus *Diomedicola* to contain the species *ferox*, *hopkinsi*, *densa*, *irroratae*, and *grandis*. The inclusion of the last-named species led him to a broader diagnosis of his genus than is now required for the 4 species recognised here (*grandis* has been removed to *Haffneria* Timmermann, 1966 — see below). Kéler nevertheless drew attention to useful taxonomic characters, in both sexes, of the antennae, terminalia, and genitalia.

Timmermann (1965) published a generic description with which we agree except that, on examination of more specimens, we find that the male and female tergites are not consistent with his observations. We consider these structures to have no taxonomic value.

*Lipeurus grandis* Piaget, 1880, a smaller louse species parasitic on skuas (genera *Stercorarius*, *Catharacta*), has occasionally been referred to as *Harrisoniella grandis*; this species was removed by Timmermann (1966) to be the type species of his new genus *Haffneria* and will not be further considered in this paper.

**Diagnosis.** Very large, elongate, dark brown lice. Head longer than broad; antennae dimorphic.

**MALE** (Fig. 1). Head: lateral margins behind antennae almost straight, diverging posteriorly; greatest width near posterior corners. Antenna: segment I greatly swollen, bearing an anteriorly-directed toothlike projection (Fig. 1, 3–6); segments IV and V much shorter and narrower than segment III, set slightly proximal to tip of segment III, which is produced into a small hook. Thorax: prothorax rectangular, broader than long; pterothorax trapezoidal, about as broad as long. Abdomen: 8th (penultimate) visible segment strongly narrowing, with 6 pairs of long tergal setae located as in Fig. 7–10; 9th (last) visible segment spatulate (Fig. 8, 10), or produced into a terminal cone (Fig. 7, 9), its tergite with a median lack of sclerotisation flanked by pronounced thickenings; genitalia elongate, slender, well chitinised, except the basal plate anteriorly (Fig. 11–14); parameres united, with 4 pairs of pores (Fig. 15–18).

**FEMALE** (Fig. 2). Head: lateral margins behind antennae slightly swollen; greatest width about midway between antennae and posterior margin (Fig. 19, 20). Antenna: filiform (Fig. 2, 19, 20); width gradually decreasing from segment I to III; IV and V abruptly narrower. Thorax: as in male. Abdomen: last 2 segments tapering to a subtriangular form; subgenital plate with a submarginal fringe of 8 long setae (Fig. 21, 22); ventral wall of genital chamber with an area of conspicuous polygonal microstructures (p.m.) (Fig. 23–26); in front of this area, the ventral wall has 2 folds projecting antero-ventrally (a.f. and p.f., Fig. 27), the limits of these folds usually showing as lines in whole mounts.

Measurements of head length, head width, and total length of slide-mounted specimens of the 4 species are given in Table 1.

**Remarks.** The hyaline margin of the clypeal signature is sometimes not visible in slide preparations as it may become deflected or bent; Carriker was misled by such distortions to the extent of considering and drawing them in his original description of *H. chilensis* (see Carriker 1964, fig. 4, 5). Our measurements of head lengths, used in calculating length:width ratios, include the hyaline margin.

The position and, to a lesser extent, the number of the setae on the ventral segments are subject to minor variation in both sexes. The 4 pairs of distal pores (Fig. 15–18) on the male genitalia are not always completely symmetrical in any one specimen, but the characteristic spacing of the series is maintained within each species.

In examining the shape of the terminal abdominal cone in males (Fig. 7, 9), care must be taken to include the hyaline (true) lateral margin of the last segment; if this is not observed, the proportions and shape of the last segment will be incorrectly interpreted. It is sometimes difficult to see, so that only the pigmented portions are readily visible; this may have led Taschenberg (1882: 147; pl. V, fig. 1) to regard his male specimen of *H. hopkinsi* as being *H. ferox*.

#### KEY TO SPECIES OF HARRISONIELLA:

##### Adults only

- 1 Antennal segment I greatly enlarged and with a toothlike projection. (Fig. 1, 3–6). Ventral terminalia as in Fig. 28 ..... MALES. 2
- 1' Antennal segment I not greatly enlarged and without a toothlike projection (Fig. 2, 19, 20). Ventral terminalia as in Fig. 22.

##### FEMALES. 5

- 2 Toothlike projection (including its swollen base) of antennal segment I occupying more than  $\frac{1}{2}$  of segment length (Fig. 4). Last abdominal segment as in Fig. 8, and genitalia as in Fig. 12, 16 (On *Diomedea albatrus* and *D. immutabilis*) ..... *H. densa*
- 2' Toothlike projection (including its base) of antennal segment I occupying no more than  $\frac{1}{2}$  of segment length (Fig. 3, 5, 6). Last abdominal segment and genitalia not with above combination ..... 3
- 3 Ratio of lengths of antennal segments III:IV+V more than 1.70; antenna as in Fig. 5. Last abdominal segment as in Fig. 9, and genitalia as in Fig. 13, 17. (On *Diomedea exulans exulans*, *D. exulans chionopectera*, *D. epomophora epomophora*, and *D. epomophora sanfordi*) ..... *H. hopkinsi*
- 3' Ratio of lengths of antennal segments III:IV+V not more than 1.70; antenna as in Fig. 3, 6. Last abdominal segment and genitalia not with above combination ..... 4
- 4 Antenna as in Fig. 3. Distal half of last abdominal segment (from alveolus of long lateral setae, l.l.s.) tapering, slightly longer than broad (Fig. 7). Genitalia as in Fig. 11; distal pores (4 pairs) situated as in Fig. 15. (On *Diomedea melanophrys melanophrys*, *D. melanophrys impavida*, *D. cauta cauta*, *D. cauta salvini*, *D. irrorata*, and *D. bulleri*) ..... *H. ferox*
- 4' Antenna as in Fig. 6. Distal half of last abdominal segment (from alveolus of long lateral setae, l.l.s.) not tapering, much longer than broad (Fig. 10). Genitalia as in Fig. 14; distal pores (4 pairs) situated as in Fig. 18. (On *Diomedea nigripes*) ..... *H. copei*
- 5 Length:width ratio of head greater than 1.35 (Fig. 19) ..... 6
- 5' Length:width ratio of head less than 1.35 (Fig. 20) ..... 7
- 6 Genital chamber as in Fig. 23. Ratio of lengths of antennal segments II+III:IV+V less than 2.40. (On *Diomedea melanophrys melanophrys*, *D. melanophrys impavida*, *D. cauta cauta*, *D. cauta salvini*, *D. irrorata*, and *D. bulleri*) ..... *H. ferox*
- 6' Genital chamber as in Fig. 24. Ratio of lengths of antennal segments II+III:IV+V greater than 2.40 (Fig. 19). (On *Diomedea albatrus* and *D. immutabilis*) ..... *H. densa*
- 7 Submarginal fringe of 8 long setae on subgenital plate interrupted by a median gap about as wide as that between the outermost seta and the next one (Fig. 21). Genital chamber as in

Fig. 25. (On *Diomedea exulans exulans*, *D. exulans chionopectera*, *D. epomophora epomophora*, and *D. epomophora sanfordi*)

- ..... *H. hopkinsi*
- 7' Submarginal fringe of 8 long setae on subgenital plate not interrupted by such a median gap (Fig. 22). Genital chamber as in Fig. 26. (On *Diomedea nigripes*) ..... *H. copei*

#### *Harrisoniella ferox* (Giebel, 1867) (Fig. 1–3, 7, 11, 15, 23)

*Lipeurus ferox* Giebel, 1867: 195. (Type host: *Diomedea melanophrys* Temminck, 1828). Holotype lost/destroyed. Neotype designated below.

*Lipeurus ferox*; Giebel, 1874: 235.

*Lipeurus ferox*; Piaget, 1880: 333.

*Lipeurus ferox*; Kellogg, 1908: 39 (in part *L. ferox* Giebel, 1867; in part *L. densus* Kellogg, 1896; in part *H. hopkinsi* Eichler, 1952; in part *H. copei* Timmermann, 1969). Listed only.

*Esthiopterum ferox* (Giebel, 1867); Harrison, 1916: 134. Listed only.

*Lipeurus ferox*; Lahille, 1920: 45 (in part *L. ferox*; in part *H. hopkinsi* Eichler, 1952). Listed only.

"*Harrisoniella diomedea*" Bedford, 1929: 529 (not *Pedicularius diomedea* J. C. Fabricius, 1775).

"*Harrisoniella diomedea*" (sic) Bedford, 1932: 334 (not *P. diomedea* J. C. Fabricius, 1775) (in part *L. ferox*; in part *H. hopkinsi* Eichler, 1952). Listed only.

*Perineus ferox* (Giebel 1867); Harrison, 1937: 29.

*Harrisoniella ferox* (Giebel, 1867); Thompson, 1938b: 486. Listed only.

*Harrisoniella ferox*; Thompson, 1939a: 245. Listed only.

"*Harrisoniella diomedea*" Thompson, 1939b: 210, 215 (not *P. diomedea* J. C. Fabricius, 1775) (in part *L. ferox*; in part *L. densus* Kellogg, 1896; in part *H. copei* Timmermann, 1969). Listed only.

*Harrisoniella ferox*; Hopkins, 1946: 7.

*Harrisoniella ferox*; Eichler, 1952: 40.

*Harrisoniella ferox*; Hopkins & Clay, 1952: 165. Listed only.

*Harrisoniella ferox*; Clay, 1957: 2. Listed only.

*Diomedicola ferox* (Giebel, 1867); Kéler, 1957: 502, fig. 1, 4, 8, 9.

*Diomedicola irroratae* Kéler, 1957: 508, fig. 3C, 10C. (Type host: *Diomedea irrorata* Salvin, 1883). Holotype ♂ in BMNH, slide no. 1913–450/1. New synonymy.

*Harrisoniella ferox*; Hopkins & Clay, 1957: 308.

*Harrisoniella ferox* (sic) (Giebel, 1867); Orfila, 1959: 518. Listed only.

*Harrisoniella ferox*; Clay & Hopkins, 1961: 198.

*Harrisoniella ferox*; International Commission Zoological Nomenclature, 1963: 178.

*Harrisoniella chilensis* Carriker, 1964: 6, fig. 4–7, 7A (Type host: *Prionocella antarctica* (Stephens, 1826) = *Fulmarus glacialis* (Smith, 1840)). Holotype ♂ in MNSC, slide no. 1269 (= slide 00905 C.U.V. in Carriker). New synonymy.

*Harrisoniella ferox*; Carniker, 1964: 8.

*Harrisoniella irroratae* (Kéler, 1957); Carriker, 1964: 10.

*Harrisoniella ferox*; Holdgate, 1965: 397. Listed only.

*Harrisoniella ferox*; Timmermann, 1965: 94.

*Harrisoniella irroratae*; Timmermann, 1965: 95.

*Harrisoniella ferox*; Timmermann, 1966: 86.

*Harrisoniella ferox*; Clay & Moreby, 1967: 168. Listed only.

*Harrisoniella chilensis*; Clay & Moreby, 1967: 168. Listed only.

*Harrisoniella chilensis*; Emerson, 1967: 86. Listed only.

*Harrisoniella irroratae*; Timmermann, 1969: 248, fig. 2b.

*Harrisoniella ferox*; Clay & Moreby, 1970: 217. Listed only.

*Harrisoniella chilensis*; Clay & Moreby, 1970: 217. Listed only.

*Harrisoniella ferox*; Gressitt, 1970: 327. Listed only.

*Harrisoniella chilensis*; Gressitt, 1970: 327. Listed only.

*Harrisoniella ferox*; Emerson, 1972a: 83. Listed only.

*Harrisoniella ferox*; Emerson, 1972b: 14. Listed only.

*Harrisoniella ferox*; Watson, 1975: 90. Listed only.

*Harrisoniella chilensis*; Camoussieght, 1980: 34. Listed only.

*Harrisoniella ferox*; Ledger, 1980: 113. Listed only.

*Harrisoniella ferox*; Pilgrim & Palma, 1982: 6. Listed only.

*Harrisoniella irroratae*; Maunder, 1983: 7.

**Diagnosis.** MALE as in Fig. 1. Antenna: as in Fig. 3, with toothlike projection of segment I arising close to proximal end of segment, its distal margin irregular; segment II about one-third longer than segment III; segment III about one-half longer than segments IV+V combined. Abdomen: dorsal aspect of terminalia as in Fig. 7; 8th visible tergite partly sub-divided by a median unscerotised area; 9th visible tergite with sclerotisation almost parallel-sided in its distal half, but with a hyaline membranous lateral margin producing an overall conical shape. Genitalia: as in Fig. 11; 4 pairs of pores, almost equally spaced, grouped towards distal end; endomeral plate truncated (Fig. 15).

**FEMALE** as in Fig. 2. Head: length:width ratio greater than 1.35. Antenna: ratio of lengths of segments II+III:IV+V less than 2.40. Subgenital plate: submarginal fringe of 8 long setae not interrupted by a median gap. Genital chamber: as in Fig. 23; area of larger polygonal microstructures (p.m.) with a deeply concave, well defined anterior limit, in front of which are some less conspicuous, smaller microstructures; anterior fold (a.f.) of ventral wall well defined by an anterior and a posterior line, together forming a crescent.

##### Material examined

**Ex *Diomedea melanophrys*:** Dyers Is., Cape Province, South Africa, 1919, 1♂ (SAIMR) and Cape Town, South Africa, Jul 1923, 1♀ (SAIMR) (these 2 specimens are presumably those referred to by Bedford, 1929; see above, p. 147); South Africa, Oct 1925, 1♂, 1♀ (G. B. Thompson Collection, BMNH); Durban, Natal, South Africa, Jul 1953, 3♀ (SAIMR); Flinders Is., Tasmania, 26 Aug 1968, 1♀ (ANIC).

- Ex *D. melanophrys melanophrys*: Wellington, New Zealand, 27 Feb 1935, 1♂ (NMNZ); Belfast, N.Z., 28 Mar 1971, 2♀ (RLCP).
- Ex *D. melanophrys impavida*: Campbell I., N.Z., 2 Dec 1975, 1♀ (NMNZ).
- Ex *D. cauta cauta*: Albatross I., Tasmania, 29 Jan 1973, 2♂, 1♀ (BMNH); same locality, 1 Feb 1973, 1♀ (BMNH); same locality, Jan 1981, 8♂, 6♀ (NMNZ); Disappointment I., Auckland Is., N.Z., 15 Feb 1973, 1♂ (RLCP); South West Cape, Auckland I., N.Z., 21 Feb 1973, 1♀ (NZAC); Waitarere Beach, N.Z., 13 Oct 1978, 3♂, 3♀ (NMNZ); Glenelg, Australia, 1♀ (SAMA).
- Ex *D. cauta salvini*: Kaikoura, N.Z., 23 Dec 1974, 2♂ (RLCP); Nelson, N.Z., Jan 1975, 1♀ (NZAC); Wellington, N.Z., 28 Aug 1977, 1♂, 1♀ (NMNZ); Proclamation I., Bounty Is., N.Z., 19 Nov 1978, 1♂, 2♀ (NMNZ); Hawke's Bay, N.Z., 1♂ (NMNZ).
- Ex *D. bulleri*: Sisters Is., Chatham Is., N.Z., 7 Feb 1973, 1♀ (NZAC); Bay of Plenty, N.Z., 2 Jul 1980, 1♂ (NMNZ).
- Ex *D. irrorata*: Lobos de Tierra, South America, 20 May 1912, 1♂ holotype of *Diomedicola irroratae* (BMNH, 1913-450/1); Hood I., Galápagos Is., 27 Apr 1925, 3♂, 1♀ (NMNZ); same locality, 11 Jun 1961, 2♀ (BMNH); Galápagos Is., 19 May 1974, 1♂, 1♀ (BMNH); same locality, no date, 1♂, 1♀ (Meinertzhagen Collection, BMNH).

#### Stragglers and contaminants

- Ex *Diomedea epomophora sanfordi*: Wellington, N.Z., 27 Jul 1953, 1♂ (NMNZ).
- Ex *Macronectes halli*: Makara Beach, N.Z., 18 Oct 1977, 1♂, 1♀ (NMNZ).
- Ex *Fulmarus glacialis*: off Valparaíso, Chile, 22 Jun 1962, 1♂ holotype of *Harrisoniella chilensis* (MNSC, 1269).

**Designation of neotype.** Searches and enquiries made at several appropriate museums in England, the United States, and Germany have failed to locate the holotype of *Harrisoniella ferox*; it is presumed lost in the destruction of the Giebel Collection at Halle during World War II (J. M. Martens, pers. comm.). Because of the extreme confusion in the identification of lice in the genus *Harrisoniella*, and because *H. ferox* is the type species of the genus, it is advisable to designate a neotype.

We designate as neotype the slide-mounted male (Fig. 1) taken from *Diomedea melanophrys*, Dyers Is., Cape Province, South Africa, 1919, in the Onderstepoort Collection, deposited at the South African Institute for Medical Research, Johannesburg, South Africa. The characters of the neotype are entirely consistent with the description of the holotype provided by Giebel and no locality was given for the original specimen.

We designate as neoparatypes: 1♂, 6♀ from *Diomedea melanophrys*, and 1♂, 2♀ from *D. melanophrys melanophrys*, with data as listed in 'Material examined', above.

**Remarks.** No significant differences were found among populations of *Harrisoniella ferox* (29♂, 32♀) from the 6 species/subspecies of hosts (i.e. excluding stragglers and contaminants). There are some minor variations in the form of the toothlike projection on segment I of the male antenna, in that the outline of its distal (concave) side has a variable number of irregularities.

Giebel's account (1867) is fairly long but the relevant diagnostic description is meagre. He did, however, draw attention to the outstanding character of the first segment of the male antenna, though he is in error in referring to 3 further segments rather than 4; he perhaps failed to distinguish 2 segments (IV-V) in the small antennal tip.

Kéler (1957) adequately described and figured the female of *H. ferox* from the type host, and referred to the polygonal microstructure and folding in the ventral wall of the genital chamber (his "Wabensskulptur" and "Mondfalte"). In the same paper he described *H. irroratae* (as *Diomedicola irroratae*) from 2 males taken from *Diomedea irrorata*. It is perhaps unfortunate that Kéler did not have any males of *Harrisoniella* from the type host of *H. ferox* or he might well have recognised that only 1 species was involved; he may have cautiously assumed that the lice from a new host were to be treated as a new taxon.

Carriker (1964) described *H. chilensis* from 2 adult specimens obtained from *Fulmarus glacialis* collected off the coast of Chile. The holotype male is in rather poor condition but it agrees with the neotype and all other male specimens of *H. ferox* examined. The allotype female is in better condition than the male but it differs from females of *H. ferox* in diagnostic features. However, it agrees with the females of *H. hopkinsi* Eichler, and we identify it as that species. We have not found any *Harrisoniella* on more than 30 specimens of *Fulmarus glacialis* examined, yet we have recovered many examples of 4 other species of Mallophaga from them. *Fulmarus glacialis* breeds on Antarctica and its outlying islands, but disperses north to the western coast of South America, as do several species of *Diomedea*, including *D. melanophrys* (type host of *H. ferox*) (Harper & Kinsky 1978). Although Carriker emphasised that "... great care was taken to prevent straggling of the parasites from one host to another.", the evidence from all other collections strongly suggests that no species of *Harrisoniella* is regularly found on *F. glacialis*.

From the foregoing, we conclude that the male louse found by Carriker was a straggler. Carriker's allotype female, which is not conspecific with the holotype male of *chilensis*, we believe is more likely to have been a contaminant. One of the normal

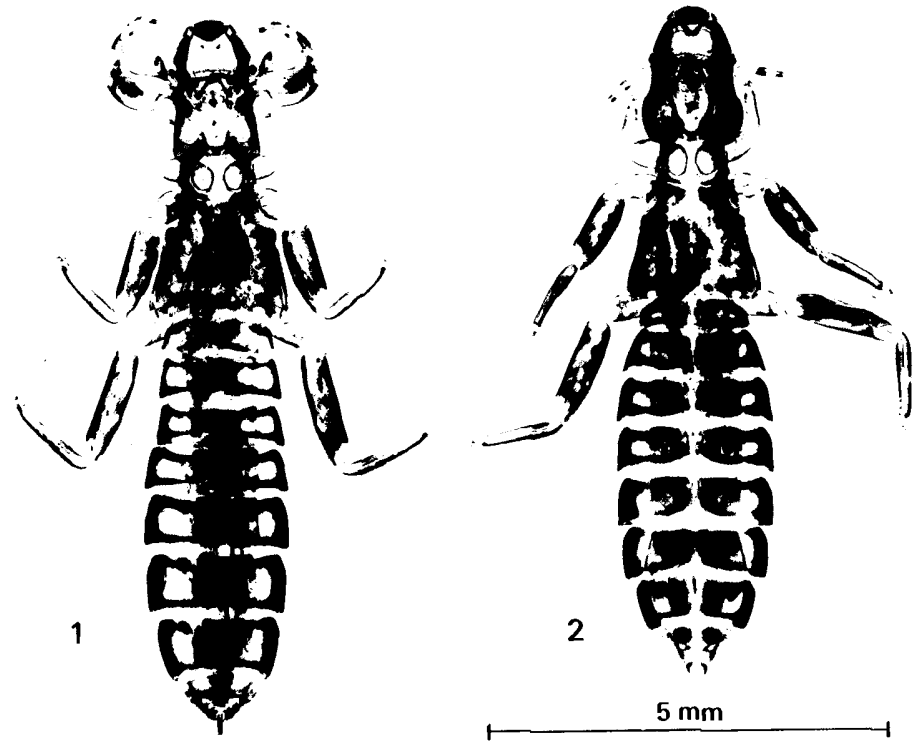


Fig. 1, 2 *Harrisoniella ferox*: 1, male neotype; 2, female neoparatype (Cape Town, South Africa, July 1923).

hosts of *Harrisoniella hopkinsi* is *Diomedea epomophora* and it is significant that at least 1 specimen of the latter was included among the birds from which lice were reported by Carriker (1964: 12).

#### *Harrisoniella densa* (Kellogg, 1896)

(Fig. 4, 8, 12, 16, 19, 24, 28)

- "*Lipeurus diomedea*" Glioli, 1864: 19, pl. IB, fig. 1, 2 (not *Pediculus diomedea* J. C. Fabricius, 1775).
- Lipeurus densa* Kellogg, 1896: 114, pl. VII, fig. 1, 2. (Type host: *Diomedea albatrus* Pallas, 1769). Holotype nymph, presumed lost.
- "*Lipeurus ferox*" Kellogg, 1896: 127, pl. IX, fig. 1, 2 (not *L. ferox* Giebel, 1867).
- Lipeurus densa*, Kellogg & Chapman, 1899: 96.
- "*Lipeurus ferox*" Kellogg & Chapman, 1899: 97 (not *L. ferox* Giebel, 1867).
- "*Lipeurus ferox*" Kellogg, 1899b: 59, 82, 83 (not *L. ferox* Giebel, 1867). Listed only.

- "*Lipeurus diomedea*" (sic) Kellogg, 1899b: 59 (not *P. diomedea* J. C. Fabricius, 1775). Listed only.
- Lipeurus densa*, Kellogg, 1899b: 59, 82 (in part *L. densa* Kellogg, 1896; in part *H. copei* Timmermann, 1969). Listed only.
- Lipeurus densa*, Kellogg, 1908: 38 (in part *L. densa*; in part *H. copei* Timmermann, 1969). Listed only.
- "*Lipeurus ferox*" Kellogg, 1908: 39 (in part *L. densa*; in part *L. ferox* Giebel, 1867; in part *H. hopkinsi* Eichler, 1952; in part *H. copei* Timmermann, 1969). Listed only.
- "*Lipeurus ferox*" Mjöberg, 1910: 83, 199 (not *L. ferox* Giebel, 1867).
- "*Lipeurus ferox*" Kellogg & Paine, 1910: 125 (not *L. ferox* Giebel, 1867) (in part *L. densa*; in part *H. copei* Timmermann, 1969).
- Lipeurus densa*, Kellogg & Paine, 1910: 125.
- Esthiopterum densum* (Kellogg, 1896); Harrison, 1916: 133. Listed only.
- Lipeurus densa*, Uchida, 1917: 201 (in part *L. densa*; in part *H. copei* Timmermann, 1969).
- Perineus densa* (Kellogg, 1896); Harrison, 1937: 29.
- Harrisoniella densa* (Kellogg, 1896); Thompson, 1938b: 484. Listed only.

*Harrisoniella densa*; Thompson, 1939a: 245. Listed only.

"*Harrisoniella diomedae*" Thompson, 1939b: 210, 214 (not *P. diomedae* J. C. Fabricius, 1775) (in part *L. densus*; in part *L. ferox* Giebel, 1867; in part *H. copei* Timmermann, 1969). Listed only.

*Harrisoniella densa*; Hopkins, 1946: 7.

*Harrisoniella* sp. Thompson, 1948: 200 (in part *L. densus*; in part *H. copei* Timmermann, 1969).

"*Harrisoniella ferox*" Zimmerman, 1948: 279 (not *L. ferox* Giebel, 1867) (in part *L. densus*; in part *H. copei* Timmermann, 1969).

*Harrisoniella densa*; Eichler, 1952: 40, fig. 5.

*Harrisoniella densa*; Hopkins & Clay, 1952: 165. Listed only.

*Diomedicola densus* (Kellogg, 1896); Kéler, 1957: 506, fig. 3D, 10D.

*Diomedicola densus*; Kéler, 1958: 378.

*Harrisoniella densa*; Malcomson, 1960: 184. Listed only.

*Harrisoniella densa*; Emerson, 1962: 11, 12. Listed only.

"*Harrisoniella ferox*" Butler & Usinger, 1963: 20 (not *L. ferox* Giebel, 1867) (in part *L. densus*; in part *H. copei* Timmermann, 1969). Listed only.

*Harrisoniella* sp. Butler & Usinger, 1963: 20. (in part *L. densus*; in part *H. copei* Timmermann, 1969). Listed only.

*Harrisoniella densa*; Carriker, 1964: 8.

*Harrisoniella densa*; Emerson, 1964: 70 (in part *L. densus*; in part *H. copei* Timmermann, 1969). Listed only.

*Harrisoniella densa*; Timmermann, 1965: 95, pl. VI, fig. 2, 3.

*Harrisoniella densa*; Amerson & Emerson, 1971: 2, 24. Listed only.

*Harrisoniella densa*; Emerson, 1972a: 83. Listed only.

*Harrisoniella densa*; Emerson, 1972b: 12, 14. Listed only.

*Harrisoniella densa*; Ward & Downey, 1973: 394.

**Diagnosis.** MALE Antenna: as in Fig. 4, with toothlike projection of segment I including a swollen base occupying at least proximal half of segment, its tip not hooked and situated at about mid-length of segment; segment II about twice as long as segment III; segment III about twice as long as segments IV+V combined. Abdomen: dorsal aspect of terminalia as in Fig. 8; 8th visible tergite undivided; 9th visible segment well sclerotised, markedly spatulate, without a conspicuous hyaline membranous lateral margin (Fig. 28). Genitalia: as in Fig. 12; 3 pairs of pores approximately equally spaced, grouped proximally, and 1 (distal) pair separated by a greater distance; endomerteral plate with an obtusely pointed tip (Fig. 16).

**FEMALE** Head: as in Fig. 19; length:width ratio greater than 1.35. Antenna: ratio of lengths of segments II+III:IV+V greater than 2.40. Subgenital plate: submarginal fringe of 8 long setae not interrupted by a median gap. Genital chamber: as in Fig. 24; area of large polygonal microstructures (p.m.) limited anteriorly by a sharp line which is

variable in shape, either almost straight, or convex with a median indentation; anterior fold (a.f.) of ventral wall with at least 1 well-defined, slightly curved, line.

#### Material examined

Ex *Diomedea albatrus*: Chemulpo, Korea, 1♂ (USNM, 124780); North Pacific, 1♂ (Meinertzhagen Collection, BMNH); Japan, 2♀ (Meinertzhagen Collection, BMNH).

Ex *D. immutabilis*: Laysan I., Hawaiian Is., 1902, 1♂, 2♀ (Hopkins Collection, BMNH); same locality, 9 Apr 1923, 1♂ (Tanager Expedition, BPBM); same locality, 11 Apr 1923, 1♂, 1♀ (Tanager Expedition, BMNH); Midway Atoll, Hawaiian Is., 7 Apr 1949, 1♂, 4♀ (BPBM); Sand I., Midway Atoll, Hawaiian Is., 11–13 Jan 1957, 1♂, 1♀ (USNM); same locality, 23 Apr 1957, 1♂, 1♀ (USNM); Midway Atoll, Hawaiian Is., 2–16 Dec 1959, 1♂, 4♀ (BPBM WRAI); Honolulu, Hawaiian Is., 27 Feb 1962, 1♂, 2♀ (BPBM); Midway Atoll, Hawaiian Is., 19 Feb 1963, 1♂, 1♀ (USNM); Sand I., Midway Atoll, Hawaiian Is., 25 Jan 1964, 1♀ (BPBM); Midway Atoll, Hawaiian Is., 15 Apr 1969, 8♀ (BPBM: NMNZ); Pearl & Hermes Reef, Hawaiian Is., 28 May 1969, 1♂, 11♀ (BPBM: NMNZ); Laysan I., Hawaiian Is., 15–16 May 1979, 1♀ (KCEC); Midway Atoll, Hawaiian Is., 26 Nov 1980, 1♂, 2♀ (RLCP); same locality, no date, 7♂, 6♀ (BPBM: NMNZ); Laysan I., Hawaiian Is., no date, 2♂ (NMNZ).

#### Stragglers and contaminants

Ex *Diomedea nigripes*: Ocean I., Hawaiian Is., 22 Apr 1923, 1♀ (Tanager Expedition, BMNH); Midway Atoll, Hawaiian Is., 14 Jan 1964, 2♀ (BPBM); same locality, 4 Feb 1964, 4♂, 3♀ (BMNH: USNM REEC).

Ex *Puffinus pacificus cuneatus* (?): Laysan I., Hawaiian Is., 13 Apr 1923, 1♀ (Tanager Expedition, BPBM).

**Note.** It could be argued that there have been sufficient samples and specimens of *H. densa* found on *Diomedea nigripes* that this species may be regarded as a regular host for *H. densa*. However, from the number of specimens of *H. densa* available from *Diomedea immutabilis*, and the number of specimens of *H. copei* available from *D. nigripes* (q.v. below, p.160), and because not only do these 2 species of albatrosses have breeding localities in common (Jouanin & Mougouin, 1979), but on several occasions the same people have collected lice from the 2 species during the same field trip, we are confident that the specimens listed above as stragglers and contaminants should not be regarded otherwise.

**Remarks.** No significant differences were found among populations of *Harrisoniella densa* (22♂, 47♀) from the 2 species of hosts (i.e. excluding stragglers and contaminants).

Kellogg (1896:114) described *H. densa* (as *Lipeurus densus*) from a single second instar nymph

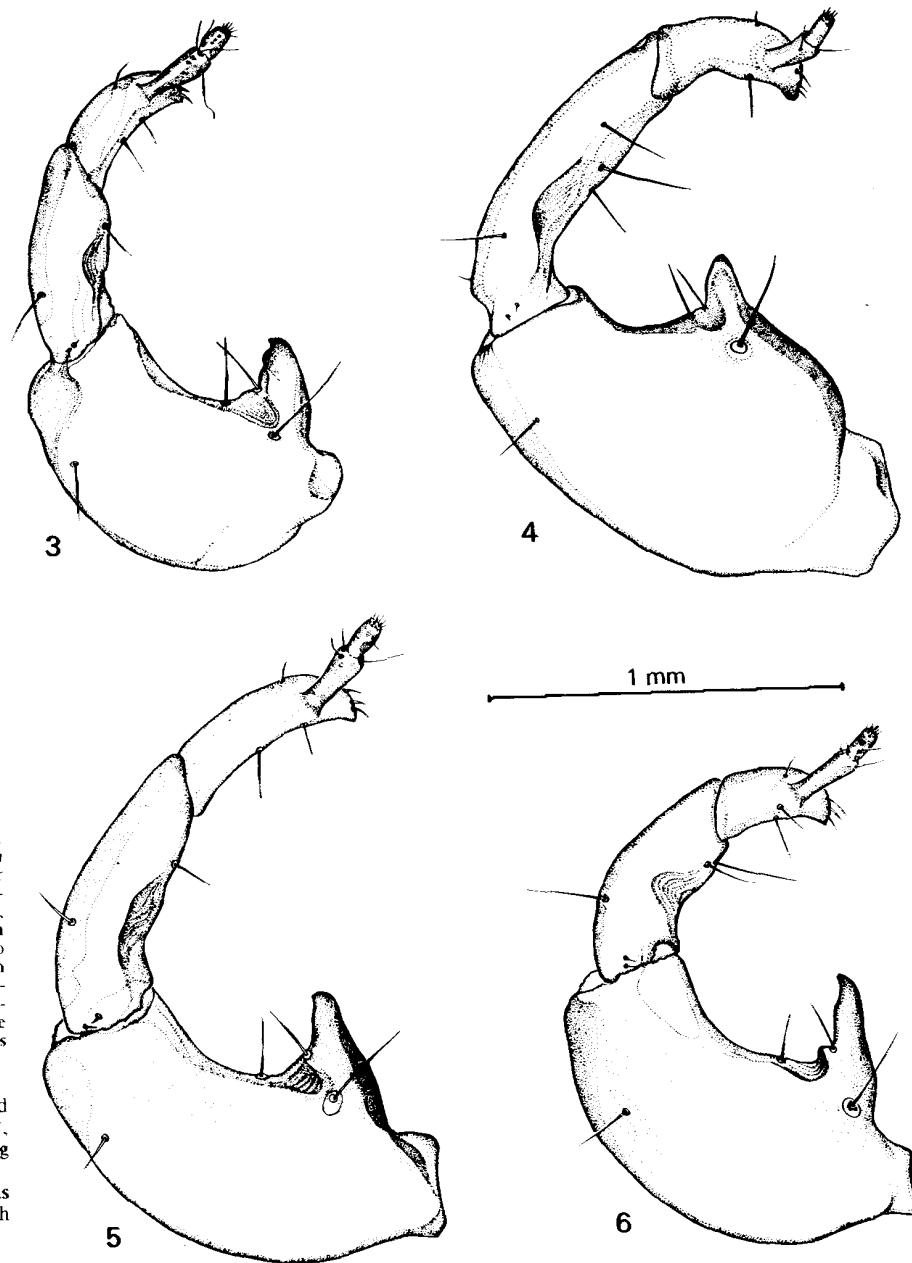


Fig. 3–6 (opposite page) Male antennae, dorsal view: 3, *Harrisoniella ferox*; 4, *H. densa*; 5, *H. hopkinsi*; 6, *H. copei*.

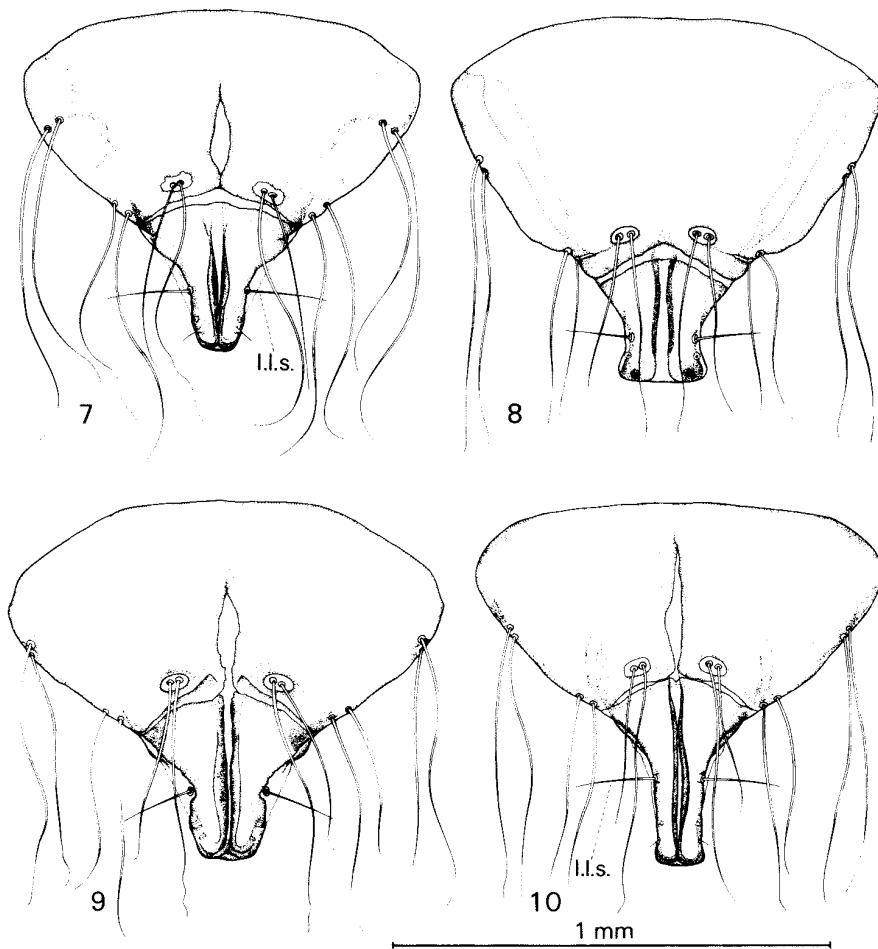


Fig. 7-10 Male terminalia, dorsal view: 7, *Harrisoniella ferox*; 8, *H. densa*; 9, *H. hopkinsi*; 10, *H. copei*. (l.l.s., long lateral setae).

taken from *Diomedea albatrus*, which he believed to be a female and, as Hopkins (1946: 6) pointed out, continued to identify subsequent collections of nymphs as adults of this species. We follow Hopkins (1946: 7) and subsequent authors in regarding all specimens of *Harrisoniella* from *D. albatrus* as belonging uniformly to 1 species. Kellogg's name is thereby applicable to this species; although it was

first applied to an immature individual and the type specimen is possibly lost, it is not necessary to designate a neotype at this stage.

Curiously, Kellogg (1896: 127, pl. IX, fig. 1,2) identified adult male and female specimens taken from *Diomedea albatrus* as *H. ferox* but, from an examination of his text and his diagnostically accurate male figure, the specimens are clearly identical



Fig. 11-14 Male genitalia: 11, *Harrisoniella ferox*; 12, *H. densa*; 13, *H. hopkinsi*; 14, *H. copei*.

with those from all other *D. albatrus* hosts; these lice are therefore *H. densa* and Kellogg has unconsciously provided the first good illustration of the male of this species. Kellogg himself (1896: 129) expressed doubt as to whether the male specimen should be attributed to *ferox*, but he continued to identify further adults from *D. albatrus* and other hosts as *ferox*. Comparison of the relevant sections of text in Kellogg (1896: 114, 127) reveals that the nymph of his *densa* n.sp. and the adults of his *ferox* material are from the same individual host birds.

Kellogg & Chapman (1899) recorded "Two females and a male from a Short-tailed Albatross, *Diomedea albatrus*" as *Lipeurus densus*. We have examined these specimens (CISC collection) and

have found that they are third instar nymphs. However, they would have produced 2 females and 1 male as they already show sexual dimorphism in the antennae. We agree with Kellogg & Chapman in regarding these nymphs as *H. densa*.

Kellogg & Paine (1910) reported some *Lipeurus ferox* from *Diomedea nigripes* and *Diomedea immutabilis* collected at Erben Bank and Laysan I. by J. O. Snyder and W. K. Fisher in 1902. We have examined 1 male and 2 females ex *D. immutabilis*, Laysan I. with the same collecting data, and have identified them as *H. densa*. Thompson (1948) reported a small sample of adult and immature specimens which he refrained from determining beyond the generic level. We have gained access to

part of this collection and find that 2 males and 1 female from *Diomedea immutabilis* are *H. densa*. Of Thompson's 2 specimens from *D. nigripes*, the male is *H. copei* Timmermann, 1969 (q.v. below, p. 158), whereas the female is *H. densa* and is regarded as a straggler or contaminant.

### *Harrisoniella hopkinsi* Eichler, 1952

(Fig. 5, 9, 13, 17, 21, 25, 27)

- "*Philopecterus diomedae*" Dufour, 1835: 671, pl. XXI, fig. 1, 2 (not *Pediculus diomedae* J. C. Fabricius, 1775).  
 "Lipeurus *ferox*" Taschenberg, 1882: 145, pl. V, fig. 1, 1a (not *L. ferox* Giebel, 1867).  
 "Lipeurus *diomedae*" Osborn in Howard, 1890: 189 (not *P. diomedae* J. C. Fabricius, 1775).  
 "Lipeurus *ferox*" Kellogg, 1908: 39 (in part *H. hopkinsi* Eichler, 1952; in part *L. ferox* Giebel, 1867; in part *L. densus* Kellogg, 1896; in part *H. copei* Timmermann, 1969). Listed only.  
 "Lipeurus *ferox*" Neumann, 1911: 20 (not *L. ferox* Giebel, 1867).  
 "Lipeurus *diomedae*" (sic) Enderlein, 1912: 138, 156 (not *P. diomedae* J. C. Fabricius, 1775).  
 "Lipeurus *ferox*" Neumann, 1913: 192 (not *L. ferox* Giebel, 1867).  
 "Lipeurus *densus*" Waterston, 1914: 311 (not *L. densus* Kellogg, 1896).  
 "Lipeurus *ferox*" Waterston, 1914: 311 (not *L. ferox* Giebel, 1867).  
 "Lipeurus *densus*" Kellogg, 1914: 85 (not *L. densus* Kellogg, 1896).  
 "Esthiopterum *diomedae*" Harrison, 1916: 133 (not *P. diomedae* J. C. Fabricius, 1775). Listed only.  
 "Lipeurus *densus*" Enderlein, 1917: 244, fig. 8 (not *L. densus* Kellogg, 1896).  
 "Lipeurus *diomedae*" (sic) Enderlein, 1917: 245 (not *P. diomedae* J. C. Fabricius, 1775).  
 "Lipeurus *ferox*" Lahille, 1920: 45 (in part *H. hopkinsi*; in part *L. ferox* Giebel, 1867). Listed only.  
 "Lipereus (sic) *densus*" Lahille, 1920: 48 (not *L. densus* Kellogg, 1896). Listed only.  
 "Harrisoniella *diomedae*" (sic) Bedford, 1932: 334 (not *P. diomedae* J. C. Fabricius, 1775) (in part *H. hopkinsi*; in part *L. ferox* Giebel, 1867). Listed only.  
 "Perineus *diomedae*" Harrison, 1937: 29 (not *P. diomedae* J. C. Fabricius, 1775).  
 "Harrisoniella *diomedae*" Thompson, 1938a: 5, pl. I (not *P. diomedae* J. C. Fabricius, 1775).  
 "Harrisoniella *diomedae*" Thompson, 1938b: 484 (not *P. diomedae* J. C. Fabricius, 1775). Listed only.  
 "Harrisoniella *ferox*" Clay, 1940: 298 (not *L. ferox* Giebel, 1867).  
 "Harrisoniella *diomedae*" (sic) Séguy, 1944: 370, fig. 24, 550, 551 (not *P. diomedae* J. C. Fabricius, 1775).  
 "Perineus *diomedae* Harrison"; Hopkins, 1946: 7.  
 "Harrisoniella *diomedae* Thompson"; Hopkins, 1946: 7.  
 "Esthiopterum *diomedae* Harrison"; Clay & Hopkins, 1951: 34.  
 "Lipeurus *ferox*" Kéler, 1952: 204 (not *L. ferox* Giebel, 1867).

- Harrisoniella hopkinsi* Eichler, 1952: 40, fig. 1 (Type host: *Diomedea exulans* Linnaeus, 1758). Holotype ♂ in ZMHU, slide no. 1289/449, 1914a.  
*Harrisoniella thompsoni* Eichler, 1952: 41, fig. 4 (Type host: *Diomedea epomophora* Lesson, 1825). Nomen novum for the species figured by Thompson, 1938a: 5, pl. I. Holotype ♂ in BMNH, slide no. 1980-40.  
*Harrisoniella* spec. B Eichler, 1952: 42, fig. 3.  
*Harrisoniella hopkinsi*, Hopkins & Clay, 1953: 438. Listed only.  
*Harrisoniella thompsoni*, Hopkins & Clay, 1953: 438. Listed only.  
*Harrisoniella hopkinsi*, Brinck, 1955: 417, 421.  
*Diomedicola hopkinsi* (Eichler, 1952); Kéler, 1957: 504, fig. 1B, 3AB, 7, 10B.  
*Harrisoniella hopkinsi*, Orfila, 1959: 518. Listed only.  
*Harrisoniella thompsoni*, Orfila, 1959: 518. Listed only.  
*Harrisoniella hopkinsi*, Carriker, 1964: 4, fig. 1, 2, 3.  
*Harrisoniella hopkinsi*, Clay, 1964: 231, 233.  
*Harrisoniella hopkinsi*, Gressitt, 1964: 538. Listed only.  
*Harrisoniella hopkinsi*, Gressitt et al., 1964: 523. Listed only.  
*Harrisoniella hopkinsi*, Timmermann, 1965: 94.  
*Harrisoniella hopkinsi*, Timmermann, 1966: 86.  
*Harrisoniella* sp. Watson, 1967: 72. Listed only.  
*Harrisoniella hopkinsi*, Clay & Moreby, 1967: 162, 168, fig. 84, 116, 126.  
*Harrisoniella hopkinsi*, Clay & Moreby, 1970: 217. Listed only.  
*Harrisoniella hopkinsi*, Gressitt, 1970: 327. Listed only.  
*Harrisoniella hopkinsi*, Amerson & Emerson, 1971: 22, 24. Listed only.  
*Harrisoniella hopkinsi*, Gollner-Scheiding, 1973: 35. Listed only.  
*Harrisoniella hopkinsi*, Watson, 1975: 88. Listed only.  
*Harrisoniella hopkinsi*, Wise, 1977: 61. Listed only.  
*Harrisoniella hopkinsi*, Ledger, 1980: 113. Listed only.  
*Harrisoniella hopkinsi*, Pilgrim & Palma, 1982: 5. Listed only.

**Diagnosis.** MALE Antenna: as in Fig. 5, with toothlike projection of segment I arising close to proximal end of segment, its tip with slightly sinuous margins; segment II about one-third longer than segment III; segment III nearly twice as long as segments IV+V combined. Abdomen: dorsal aspect of terminalia as in Fig. 9; 8th visible tergite partly subdivided by a median un sclerotised area; 9th visible tergite with sclerotisation slightly spiculate, but with a hyaline membranous lateral margin producing an overall conical shape. Genitalia: as in Fig. 13; 3 pairs of pores about equally spaced, grouped distally, and 1 (proximal) pair separated by a greater distance; endomeral plate truncated (Fig. 17).

**FEMALE** Head: length:width ratio less than 1.35. Antenna: ratio of lengths of segments II+III:IV+V more than 2.40. Subgenital plate: as in Fig. 21; submarginal fringe of 8 long setae interrupted by a median gap about as wide as that between the outermost seta and the next one. Genital chamber: as in Fig. 25; area of large polygonal microstructures

(p.m.) limited anteriorly by a concave line or extending slightly in front of the line; anterior fold (a.f.) of ventral wall well defined by an anterior and a posterior line, together forming a crescent.

#### Material examined

- Ex *Diomedea exulans*:** South Atlantic Ocean, near Cape of Good Hope (about 36°50' S, 11°00' E), 24 Oct 1772, 1♂, 1♀ (MAMU) (these specimens were collected by the Rev. Johann Reinhold Forster, naturalist to Captain James Cook's second voyage around the world, in HMS *Resolution*; see Hoare 1982: 179); South Atlantic Ocean, between South-west Africa and South America, 30 Oct 1901, 1♂ holotype of *H. hopkinsi* (ZMHU, 1289/449, 1914a); no locality, 1913, 1♀ (BASE); Kaitiua, N.Z., 20 Feb 1921, 2♀ (NZAC; BMNH); Indian Ocean, off South Africa, 9 Aug 1922, 1♂, 1♀ (Hopkins Collection, BMNH); 36°51' S, 23°05' E, 23 Oct 1929, 1♂, 1♀ (BMNH); no locality, 3 Mar 1931, 2♂, 1♀ (SAMA); New Zealand, 28 Jun 1935, 1♂, 1♀ (NMNZ); Wellington, N.Z., 13 Jun 1967, 1♂ (NMNZ); Malabar, New South Wales, Australia, 14 Sep 1968, 1♂ (ANIC); same locality, 20 Sep 1969, 1♂ (ANIC); same locality, 10 Jun 1972, 1♂, 2♀ (ANIC); same locality, 19 Jul 1972, 2♀ (ANIC); Christchurch, N.Z., 14 Mar 1975, 1♀ (RLCP); Taranaki, N.Z., 28 Jan 1980, 1♀ (NMNZ); Tristan da Cunha, no date, 1♂ (Thompson Collection, BMNH); South Atlantic Ocean, no date, 4♂, 3♀ (SAIMR; Meinerzhagen Collection, BMNH); Falkland Is., no date, 2♂ (Meinerzhagen Collection, BMNH); 50°20' S, 61°18' W, no date, 1♂ (BASE); South Atlantic Ocean, no date, 1♀ (R. C. Murphy, 1380, CISC).
- Ex *D. exulans exulans*:** Wellington, N.Z., Jun 1959, 2♀ (NMNZ); Timaru, N.Z., Jul 1967, 1♂ (RLCP); Bahía de Concepción, Chile, 1 Apr 1976, 4♂, 3♀ (NMNZ); INCO; Dargaville, N.Z., 5 Jun 1976, 1♂ (NMNZ); Wainuiomata, N.Z., 26 Mar 1977, 1♂, 1♀ (NMNZ); Antipodes Is., N.Z., 24 Nov 1978, 3♂, 5♀ (NMNZ).
- Ex *D. exulans chionopectera*:** 36°51' S, 23°05' E, 23 Oct 1929, 1♂, 3♀ (SAMA); no locality, 29 Oct 1929, 1♀ (SAMA); Tasman Sea, 27 May 1968, 1♂ (NMNZ); Taumutu, Canterbury, N.Z., 10 Oct 1974, 1♂, 1♀ (RLCP).
- Ex *D. epomophora*:** New Zealand, 7 Apr 1922, 1♂ (NZAC); same locality, 1934, 1♂ holotype of *Harrisoniella thompsoni* (Thompson Collection, BMNH, 1980-40); Arahura, N.Z., 29 Jul 1974, 2♂, 5♀ (RLCP); Auckland Is., N.Z., no date, 1♀ (CMNZ).
- Ex *D. epomophora epomophora*:** Wellington, N.Z., 5 May 1952, 1♂, 1♀ (NMNZ); same locality, 2 Oct 1959, 1♂, 3♀ (NMNZ); Kaikoura, N.Z., 15 Dec 1963, 1♂ (RLCP); Fitzroy Bay, N.Z., 11 Jun 1965, 1♂ (NMNZ); Campbell I., N.Z., 2 Dec 1967, 1♀ (NMNZ); same locality, 15 Jun 1968, 1♀ (NMNZ); Kaikoura, N.Z., 26 May 1968, 1♂, 1♀ (RLCP); Oamaru, N.Z., 11 Apr 1970, 1♂, 3♀ (RLCP); Wainuiomata River, N.Z., 2 Aug 1972, 3♂, 3♀ (NMNZ); Wellington, N.Z., 12 Oct 1974, 2♂, 2♀ (NMNZ); AMNZ; Wairarapa, N.Z., 11 Jul 1976, 3♀ (NMNZ);

Kaikoura, N.Z., 27 Sep 1976, 1♀ (NMNZ); Lake Ferry, Wairarapa, N.Z., 2♂, 2♀ (NMNZ); Campbell I., N.Z., 24 Dec 1979, 1♂, 1♀ (NMNZ).

- Ex *D. epomophora sanfordi*:** Wellington, N.Z., 27 Jul 1953, 1♀ (NMNZ); same locality, 9 Mar 1954, 9♂, 9♀ (NMNZ; AMNZ; RLCP); Ocean Beach, Hawkes Bay, N.Z., 28 Mar 1967, 1♀ (NMNZ); Orongorongo River, N.Z., 14 Apr 1968, 1♀ (NMNZ); Middle Sister I., Chatham Is., N.Z., 19 Nov 1973, 1♂, 3♀ (NMNZ); same locality, 20 Nov 1973, 1♂ (NZAC); Makara Beach, N.Z., 28 Oct 1981, 10♂, 8♀ (NMNZ); Forty Fours Rocks, Chatham Is., N.Z., 1 Dec 1983, 1♂ (NMNZ).

#### Stragglers and contaminants

**Ex *Diomedea melanophrys*:** Manly, New South Wales, Australia, 13 Jul 1954, 1♂ (ANIC); South Pacific, no date, 1♂ (BMNH).

**Ex *D. cauta cauta*:** Auckland I., N.Z., 21 Feb 1973, 1♂ (NZAC).

**Ex *D. bulleri*:** Sister I., Chatham Is., N.Z., 12 Feb 1974, 3♀ (NZAC).

**Ex *Fulmarus glacialisoides*:** off Valparaíso, Chile, 22 Jun 1962, 1♀ allotype of *Harrisoniella chilensis* (MNSC, 1270).

**Host unknown:** New South Wales, Australia, 1839, 2♀ (MAMU); St Paul I., Indian Ocean, 1875, 1♂, 1♀ (BMNH) (these specimens were collected by Mister Gaston de l'Isle, as member of the mission "Passage de Vénus sur le Soleil" 1874-1875, probably from *Diomedea exulans*; see Vélain (1877) and Jouanin (1953); New Zealand, no date, 2♀ (RLCP).

**Remarks.** No significant differences were found among the populations of *H. hopkinsi* (74♂, 89♀) from the 4 subspecies of hosts (i.e. excluding stragglers and contaminants).

Taschenberg (1882: 145) drew particular attention to the characteristic shape of the clypeal signature in the male; the holotype male agrees with Taschenberg's account in this respect, but we find that the shape is very variable in the material examined.

Kellogg (1914) reported "one adult female and one young male" of *Lipeurus densus* ex *Diomedea exulans* from the South Atlantic Ocean. We have examined these specimens and have identified them as 1 adult female and 1 third instar nymph of *H. hopkinsi*. This appears to be the only time that Kellogg identified an adult specimen of *Harrisoniella* as *L. densus*. It has been pointed out already that he consistently regarded all nymphs as *L. densus* and all adults as *L. ferox*, from all host species.

Enderlein (1917) reported, as *Lipeurus diomedae*, 2 specimens taken from *Diomedea exulans* between South-west Africa and South America in 1901, of which the male was made the holotype of *H. hopkinsi* by Eichler in 1952.

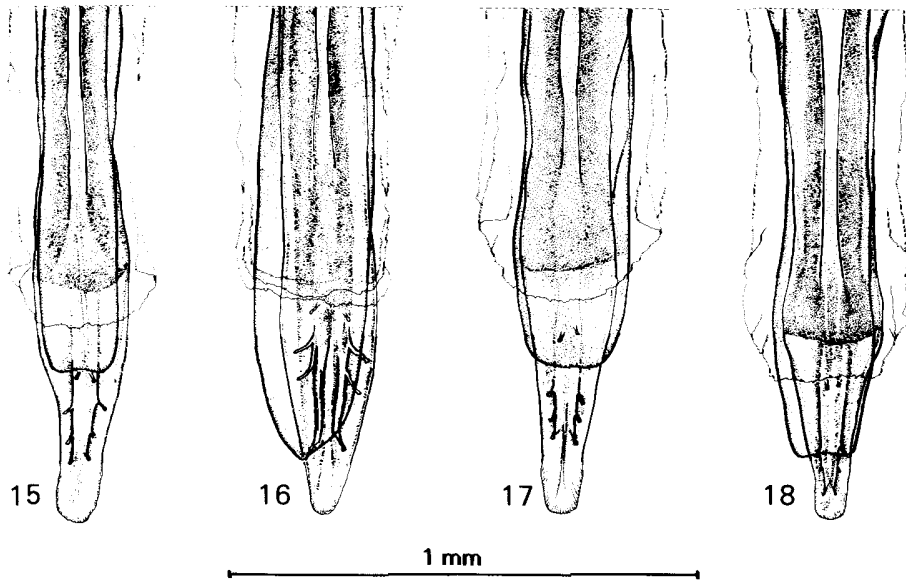


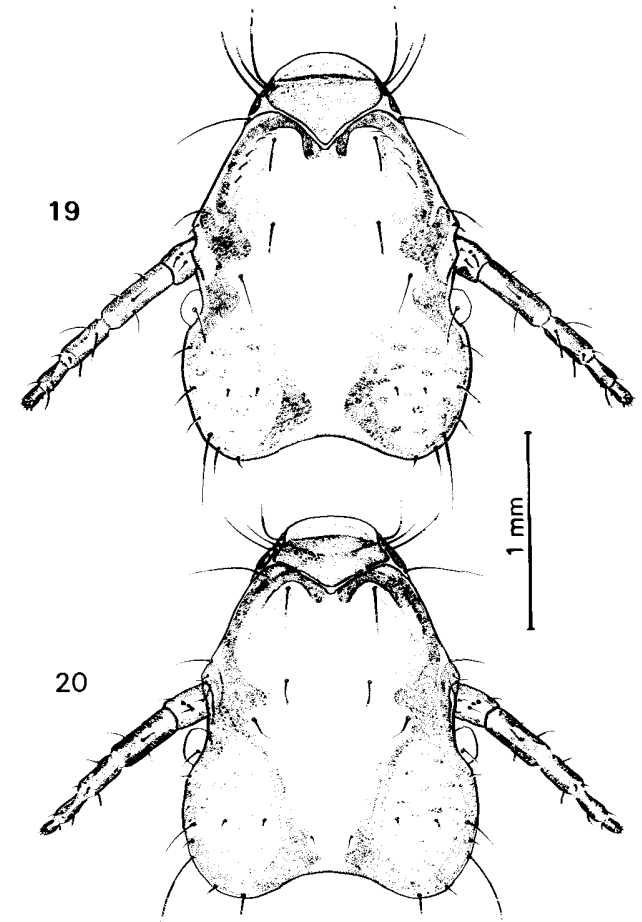
Fig. 15–18 Distal end of male genitalia (armature of genital sac omitted): 15, *Harrisoniella ferox*; 16, *H. densa*; 17, *H. hopkinsi*; 18, *H. copei*.

***Harrisoniella copei* Timmermann, 1969**  
(Fig. 6, 10, 14, 18, 20, 22, 26)

- “*Lipeurus densus*” Kellogg, 1899a: 28, pl. III, fig. 2 (not *L. densus* Kellogg, 1896).  
 “*Lipeurus densus*” Kellogg, 1899b: 59, 82 (in part *H. copei* Timmermann, 1969; in part *L. densus* Kellogg, 1896). Listed only.  
 “*Lipeurus ferox*” Kellogg & Kuwana, 1900: 154 (not *L. ferox* Giebel, 1867).  
 “*Lipeurus densus*” Kellogg & Kuwana, 1900: 154 (not *L. densus* Kellogg, 1896).  
 “*Lipeurus ferox*” Kellogg & Chapman, 1902: 22 (not *L. ferox* Giebel, 1867). Listed only.  
 “*Lipeurus ferox*” Kellogg, 1906: 318 (not *L. ferox* Giebel, 1867).  
 “*Lipeurus densus*” Kellogg, 1908: 38 (in part *H. copei*; in part *L. densus* Kellogg, 1896). Listed only.  
 “*Lipeurus ferox*” Kellogg, 1908: 39 (in part *H. copei*; in part *L. ferox* Giebel, 1867; in part *L. densus* Kellogg, 1896; in part *H. hopkinsi* Eichler, 1952). Listed only.  
 “*Lipeurus ferox*” Kellogg & Paine 1910: 125 (not *L. ferox* Giebel, 1867) (in part *H. copei*; in part *L. densus* Kellogg, 1896).  
 “*Lipeurus densus*” Uchida, 1917: 201 (in part *H. copei*; in part *L. densus* Kellogg, 1896).  
 “*Lipeurus ferox*” Uchida, 1917: 204 (not *L. ferox* Giebel, 1867).  
 “*Esthiopterum diomedae*” Zunker, 1932: 292, 294 (not *Pediculus diomedae* J. C. Fabricius, 1775). Listed only.

- “*Harrisoniella diomedae*” Thompson, 1939b: 210, 214 (not *P. diomedae* J. C. Fabricius, 1775) (in part *H. copei*; in part *L. ferox* Giebel, 1867; in part *L. densus* Kellogg, 1896). Listed only.  
 “*Esthiopterum diomedae*” Cope, 1940: 117, fig. 54–66 (not *P. diomedae* J. C. Fabricius, 1775).  
 “*Lipeurus densus* Kellogg, 1899”: Hopkins, 1946: 7 (not *L. densus* Kellogg, 1896).  
*Harrisoniella* sp. Thompson, 1948: 200 (in part *H. copei*; in part *L. densus* Kellogg, 1896).  
 “*Harrisoniella ferox*” Zimmerman, 1948: 279 (not *L. ferox* Giebel, 1867) (in part *H. copei*; in part *L. densus* Kellogg, 1896).  
*Harrisoniella* spec. A Eichler, 1952: 42, fig. 2.  
 “*Harrisoniella densa*” Emerson, 1962: 12 (not *L. densus* Kellogg, 1896). Listed only.  
 “*Harrisoniella ferox*” Butler & Usinger, 1963: 20 (not *L. ferox* Giebel, 1867) (in part *H. copei*; in part *L. densus* Kellogg, 1896). Listed only.  
*Harrisoniella* sp. Butler & Usinger, 1963: 20 (in part *H. copei*; in part *L. densus* Kellogg, 1896). Listed only.  
 “*Harrisoniella densa*” Emerson, 1964: 70 (in part *H. copei*; in part *L. densus* Kellogg, 1896). Listed only.  
*Harrisoniella copei* Timmermann, 1969: 247, fig. 2a, 3. (Type host: *Diomedea nigripes* Audubon, 1839).  
**Holotype** ♂ in BPBM, slide no. 8864.  
*Harrisoniella copei*: Emerson, 1972a: 83. Listed only.  
*Harrisoniella copei*: Emerson, 1972b: 13. Listed only.  
*Harrisoniella copei*: Ward & Downey, 1973: 394.  
*Harrisoniella copei*: Tenorio, 1979: 12. Listed only.

Fig. 19, 20 Female heads, dorsal view: 19, *Harrisoniella densa*; 20, *H. copei*.



**Diagnosis.** MALE Antenna: as in Fig. 6, with toothlike projection of segment I arising close to proximal end of segment, its tip slender, with slightly sinuous margins; segment II about twice as long as segment III; segment III about same length as segments IV+V combined. Abdomen: dorsal aspect of terminalia as in Fig. 10; 8th visible tergite partly subdivided by a median unsclerotised area; 9th visible segment well sclerotised, its distal half roughly parallel-sided, with an inconspicuous hyaline membranous lateral margin. Genitalia: as in

Fig. 14; 3 pairs of pores about equally spaced, grouped distally, and 1 (proximal) pair separated by a greater distance; endomeral plate truncated (Fig. 18).

**FEMALE** Head: as in Fig. 20; length:width ratio less than 1.35. Antenna: ratio of lengths of segments II+III:IV+V less than 2.40. Subgenital plate: as in Fig. 22; submarginal fringe of 8 long setae not interrupted by a median gap. Genital chamber: as in Fig. 26; area of larger polygonal microstructures



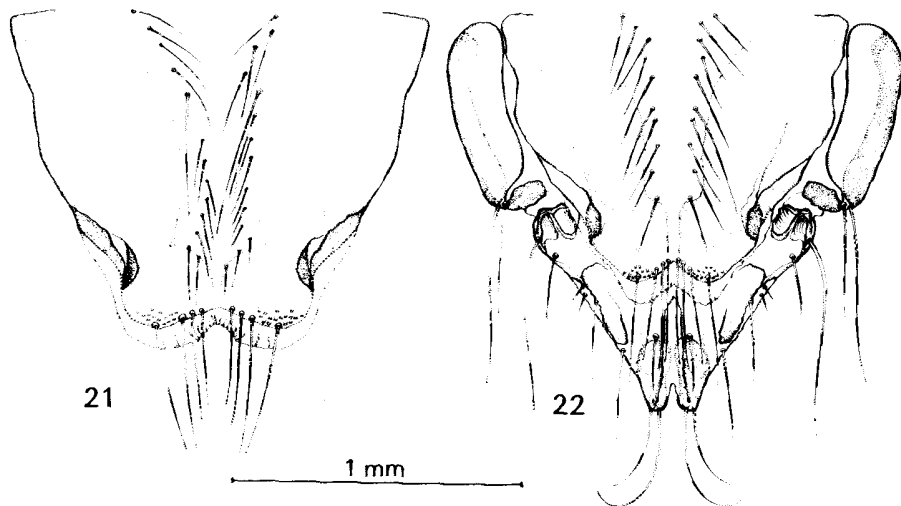


Fig. 21 *Harrisoniella hopkinsi*, female subgenital plate. 22 *Harrisoniella copei*, female terminalia, ventral view.

(p.m.) merging gradually into an anterior area of smaller polygons, over a shallow concave front; anterior and posterior folds of ventral wall weakly developed.

#### Material examined

Ex *Diomedea nigripes*: Clarion I., eastern Pacific Ocean, 1901, 1♀ (Hopkins Collection, BMNH); Ocean I., Hawaiian Is., 22 Apr 1923, 1♂ (Tanager Expedition, BMNH); Midway Atoll, Hawaiian Is., 2–16 Dec 1959, 5♂, 6♀ (BPBM; WRAD); same locality, 14 Jan 1964, 5♂, 8♀ (BMNH; BPBM; NMNZ); same locality, 30 Jan 1964, 1♂ holotype of *H. copei* (BPBM, 8864); same locality, 4 Feb 1964, 1♂, 2♀ (BMNH); Pacific Ocean, 4 Feb 1964, 1♀ (USNM); same locality, 5 Apr 1964, 1♂ (USNM); Midway Atoll, Hawaiian Is., 7–8 May 1979, 1♀ (KCEC); Laysan I., Hawaiian Is., 15–16 May 1979, 1♂ (KCEC); Midway Atoll, Hawaiian Is., 19 Dec 1980, 1♂ (RLCP); Hawaiian Is.: no date, 1♀ (Meinertzhagen Collection, BMNH).

#### Stragglers and contaminants

Ex *Diomedea immutabilis*: Honolulu, Hawaiian Is., 27 Feb 1962, 3♀ (BPBM; NMNZ).  
Ex *D. irrorata*: Galapagos Is., no date, 2♀ (Meinertzhagen Collection, BMNH); Peru, no date, 1♂ (Meinertzhagen Collection, BMNH).

**Remarks.** Timmermann (1969: 248, fig. 2a) emphasised the shape of the terminal segment of the male abdomen as a diagnostic character for this species. We agree that the outline of this region is different from that of the remaining species in being *not tapered*, however, in material examined by us, the expansion of the extreme tip is variable or may be absent. The representations of this region by Cope (1940: fig. 64A, 65D, of “*Esthiopterum diomedea*”) are schematic and show a degree of expansion not seen by us.

In the genital chamber of the female, the anterior and posterior folds of the ventral wall are less developed than in the other species, and are variable in that the folds may show as discontinuous lines.

Kellogg (1899a) described “A single male from a Black-footed Albatross, *Diomedea nigripes*”. We have examined this specimen (CISC collection) and have found that it is a third instar nymph, which would have produced a male. Kellogg (1899a) assumed that this was the male of *Lipeurus densus* (now *Harrisoniella densa*) but we regard it as *H. copei* because of its host. Similarly, we have seen 3 nymphs — 2 third instar and 1 second instar — (CISC collection) ex *Diomedea nigripes* from Pt

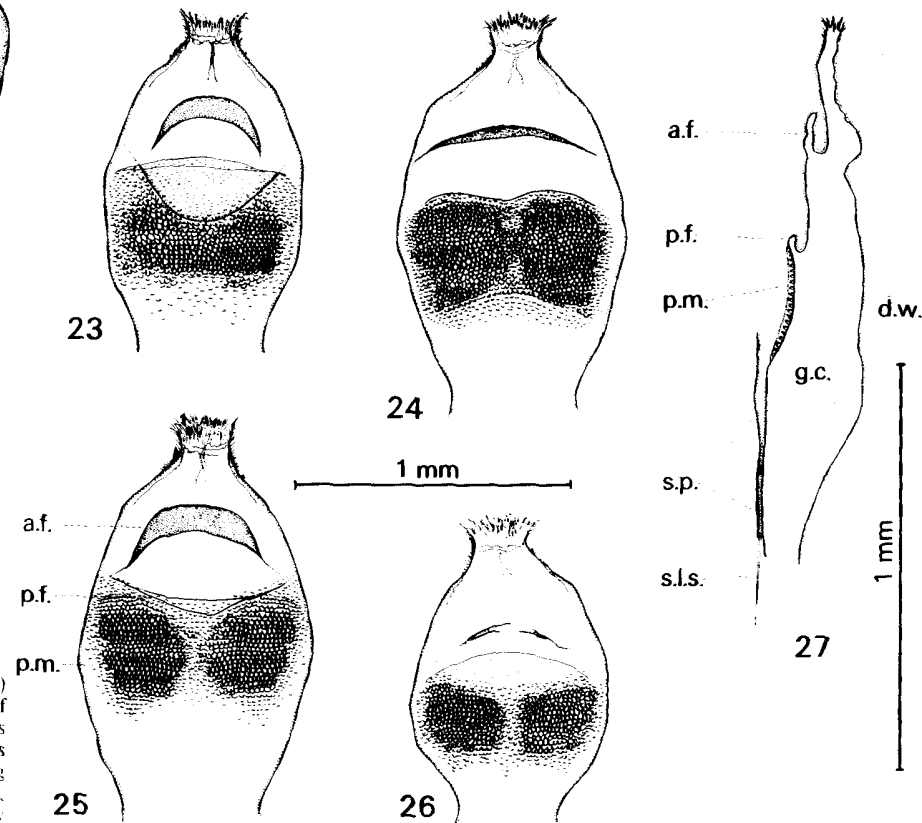


Fig. 23–27 Female genital chambers: 23–26, whole mounts, ventral view. (23) *Harrisoniella ferox*, (24) *H. densa*, (25) *H. hopkinsi*, (26) *H. copei*; 27, longitudinal section, *H. hopkinsi* (a.f., anterior fold; p.f., posterior fold; p.m., polygonal microstructures; s.p., subgenital plate; s.l.s., submarginal long seta; g.c., genital chamber; d.w., dorsal wall).

Barrow, Alaska, which were identified and published by Kellogg & Kuwana (1900) as *Lipeurus densus*. We regard them as *H. copei*.

Kellogg (1906) recorded *Lipeurus ferox* from *Diomedea nigripes* collected at Clarion I. by R. Beck in 1901. We have examined 1 female from that collection and have identified it as *H. copei*.

Thompson (1948) reported, as *Harrisoniella* sp., 2 specimens taken from *D. nigripes* from Ocean I. We have examined these: the male proved to be *H. copei*, the female is *H. densa* (q.v. above, p. 151).

#### REMARKS ON THE RELATIONSHIPS WITHIN THE GENUS *DIOMEDEA*, BASED ON THE DISTRIBUTION OF THE SPECIES OF *HARRISONIELLA*, AND OTHER LICE GENERA

To some degree, the distribution of the lice species follows the subdivision of the genus *Diomedea* into subgenera (Jouanin & Mougou 1979) (see Table 2 — ‘Host-parasite list’).

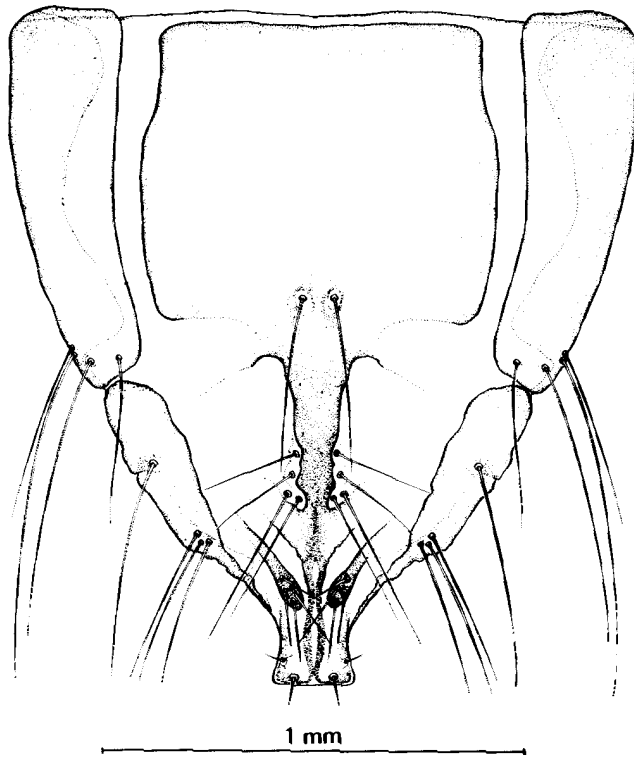


Fig. 28 *Harrisoniella densa*, male terminalia, ventral view.

*Harrisoniella hopkinsi* is confined to the great albatrosses, subgenus *Diomedea*, all of which bear this louse. *H. ferox*, however, parasitises hosts of 2 subgenera of smaller albatrosses, the mollymawks, *Thalassarche* and *Thalassogeron*; but *H. ferox* is also found on *D. irrorata*, currently regarded as belonging to the subgenus *Phoebastria*. This lack of correlation between *Harrisoniella* species and the subgenus *Phoebastria* is further shown by there being 2 more lice, *H. densa* and *H. copei* on the 3 other species of *Phoebastria*. A comparable pattern emerges from a consideration of other genera of philopterid lice found on these hosts (Table 3).

The distribution of lice species outlined above and in Table 3 suggests that *Thalassogeron* should

not be recognised as distinct from *Thalassarche*, a view implied by Timmermann (1965: 216) as a result of his findings on the Mallophaga. The distribution also shows the special position of *Diomedea irrorata*, and makes its inclusion in the subgenus *Phoebastria* doubtful.

We are unaware of any specimen of *Harrisoniella* collected from the following members of the family Diomedidae: *Diomedea chrysostoma* Forster, 1785; *D. chlororhynchos* Gmelin, 1789; *D. amsterdamensis* Roux, Jouventin, Mougín, Stahl, & Weimerskirch, 1983; *Phoebetria fusca* (Hilseberg, 1822) and *P. palpebrata* (Forster, 1785). We would be pleased to examine samples from these hosts.

Table 2 HOST-PARASITE LIST (Hosts listed following Jouanin & Mougín (1979)).

<b>Subgenus <i>Diomedea</i></b>	
<i>Diomedea exulans exulans</i> Linnaeus, 1758.....	<i>Harrisoniella hopkinsi</i>
<i>Diomedea exulans chionopectera</i> Salvin, 1895.....	<i>Harrisoniella hopkinsi</i>
<i>Diomedea epomophora epomophora</i> Lesson, 1825.....	<i>Harrisoniella hopkinsi</i>
<i>Diomedea epomophora sanfordi</i> (Murphy, 1917).....	<i>Harrisoniella hopkinsi</i>
<b>Subgenus <i>Phoebastria</i></b>	
<i>Diomedea irrorata</i> Salvin, 1883.....	<i>Harrisoniella ferox</i>
<i>Diomedea albatrus</i> Pallas, 1769.....	<i>Harrisoniella densa</i>
<i>Diomedea nigripes</i> Audubon, 1839.....	<i>Harrisoniella copei</i>
<i>Diomedea immutabilis</i> Rothschild, 1893.....	<i>Harrisoniella densa</i>
<b>Subgenus <i>Thalassarche</i></b>	
<i>Diomedea melanophrys melanophrys</i> Temminck, 1828.....	<i>Harrisoniella ferox</i>
<i>Diomedea melanophrys impavida</i> Mathews, 1912.....	<i>Harrisoniella ferox</i>
<b>Subgenus <i>Thalassogeron</i></b>	
<i>Diomedea cauta cauta</i> Gould, 1841.....	<i>Harrisoniella ferox</i>
<i>Diomedea cauta salvini</i> (Rothschild, 1893).....	<i>Harrisoniella ferox</i>
<i>Diomedea bulleri</i> Rothschild, 1893.....	<i>Harrisoniella ferox</i>

Table 3 Species distribution of the lice genera *Docophoroides*, *Paraclisis*, and *Perineus* on albatrosses of the genus *Diomedea*. Hosts listed following Jouanin & Mougín (1979).

Albatross	<i>Docophoroides</i> *	Genera of lice <i>Paraclisis</i> *	<i>Perineus</i> *
<b>Subgenus <i>Diomedea</i></b>			
<i>D. exulans exulans</i>	<i>D. brevis</i>	<i>P. hyalina</i>	<i>P. concinnoides</i>
<i>D. exulans chionopectera</i>	<i>D. brevis</i>	<i>P. hyalina</i>	<i>P. concinnoides</i>
<i>D. epomophora epomophora</i>	<i>D. brevis</i>	<i>P. hyalina</i>	<i>P. concinnoides</i>
<i>D. epomophora sanfordi</i>	<i>D. brevis</i>	<i>P. hyalina</i>	<i>P. concinnoides</i>
<b>Subgenus <i>Phoebastria</i></b>			
<i>D. irrorata</i>	<i>D. irroratae</i> <i>D. levequei</i>	<i>P. miriceps</i>	<i>P. oblongus</i>
<i>D. albatrus</i>	<i>D. pacificus</i>	<i>P. giganticola</i>	<i>P. concinnus</i>
<i>D. nigripes</i>	<i>D. ferrisi</i>	<i>P. confidens</i>	<i>P. concinnus</i>
<i>D. immutabilis</i>	<i>D. niethammeri</i>	<i>P. giganticola</i>	<i>P. concinnus</i>
<b>Subgenus <i>Thalassarche</i></b>			
<i>D. melanophrys melanophrys</i>	<i>D. harrisoni</i> <i>D. simplex</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<i>D. melanophrys impavida</i>	<i>D. simplex</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<b>Subgenus <i>Thalassogeron</i></b>			
<i>D. cauta cauta</i>	<i>D. harrisoni</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<i>D. cauta salvini</i>	<i>D. harrisoni</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<i>D. cauta eremita</i>	<i>D. harrisoni</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<i>D. chrysostoma</i>	<i>D. simplex</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<i>D. chlororhynchos</i>	<i>D. simplex</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>
<i>D. bulleri</i>	<i>D. harrisoni</i>	<i>P. diomedae</i>	<i>P. circumfasciatus</i>

\*Records of lice taken from: Clay (1957); Kéler (1957); Timmermann (1965); Ward & Downey (1973); Pilgrim & Palma (1979, 1982).

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