A revision of the genus *Naubates* (Insecta: Phthiraptera: Philopteridae)*

Ricardo L. Palma¹ and Robert L. C. Pilgrim²†

**Abstract**  Ten species of the genus *Naubates* Bedford, 1930 are recognised, including two new species: *N. (Guenterion) ultimae* n. sp. from *Pterodroma ultima*, and *N. (Guenterion) lessonii* n. sp. from *Pterodroma lessonii*. The genus *Naubates* is subdivided into two subgenera: the subgenus *Naubates* sensu stricto containing three species, and the new subgenus *Guenterion* n. sg. containing seven species. Keys, together with measurements and illustrations, are provided to both male and female adults of all the species, including *Naubates thieli* Timmermann, 1965 which is illustrated for the first time. A key to the subgenera is also provided. A lectotype is designated for *Lipeurus prioni* Enderlein, 1908. The morphological relationships of *Naubates* species and their host distribution are discussed with respect to the current classification of their host taxa.

**Keywords**  Phthiraptera; Philopteridae; *Naubates*; revision; new taxa; lectotype; systematics

**INTRODUCTION**

The genus *Naubates* Bedford, 1930 includes elongate lice of medium size, found regularly on petrels, prions, and shearwaters of the Procellarii genera *Pterodroma*, *Halobaena*, *Pachyptila*, *Procellaria*, and *Puffinus*.

Hopkins & Clay (1952) listed eight species under *Naubates*, six of which we recognise as valid (*N. major* (Kellogg & Chapman, 1899) is a pre-occupied name and a synonym of *N. (N.) harrisoni* Bedford, 1930; *N. testaceus* (Taschenberg, 1882) is a synonym of *N. (N.) fuliginosus* (Taschenberg, 1882)). In the course of revising the genus, Timmermann (1961, 1965) described two new species. Since those papers were published, there has been no overall account of the genus. Collections available to us include two new species which are described below, bringing the total number of species to 10; they have enabled us to produce a key to their identification.

Specimens of *Naubates* are found predominantly on the wing feathers. The abundance and frequency of *Naubates* species on their hosts appear to be inversely related to those of other wing-lice species of the genus *Halipeurus* Thompson, 1936: species of *Naubates* living on *Halobaena*, *Pachyptila*, and *Procellaria* hosts (all of which lack *Halipeurus*; see Pilgrim & Palma 1982) are more abundant and frequent than those living on *Pterodroma* and *Puffinus*

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* University of Canterbury Snares Islands Expedition Paper 59.
* Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand.
* Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch, New Zealand.
* Honorary Research Associate, Museum of New Zealand Te Papa Tongarewa.

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hosts. Most species of the latter two hosts are parasitised by *Halipeurus* lice and, in some species of both genera, no *Naubates* have been found despite examination of large numbers of birds.

We use the term “stragglers” to qualify lice which are found occasionally on a bird which is not their regular host (q.v. below), even though the occurrence is from field collecting. Stragglers are the result of a “natural contamination”, i.e., a transference of lice from their regular host to a non-regular host species (q.v. below) without human intervention (while in close contact during breeding, feeding, roosting, etc.).

We use the term “contaminants” to qualify lice which are found occasionally on a bird which is not their regular host (q.v. below) because of presumed human error. Contaminants are the result of a transference of lice from their regular host to a different host species by human agency (while handling birds in the field or the laboratory, collecting from host skins kept together in museum collections, mislabelling of samples, etc.).

We qualify a host species as a “regular host” for a given louse species when that host is naturally and often infested with that louse species. This association is the result of a transference of lice between host individuals of the same species (while mating, brooding, feeding the young, roosting, etc.).

We qualify a host species as a “non-regular host” for a given louse species when that host is associated with lice qualified as stragglers or contaminants.

In the species synonymies, we use quotation marks (“ ”) for those binomial combinations which we regard as having been incorrectly applied by the author(s) cited immediately after the species name.

The nomenclature of the hosts follows that given by Jouanin & Mougin (1979).

**ABBREVIATIONS USED FOR INSTITUTIONS AND COLLECTIONS**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>American Museum of Natural History, New York, USA.</td>
</tr>
<tr>
<td>AMNZ</td>
<td>Auckland Institute and Museum, Auckland, New Zealand.</td>
</tr>
<tr>
<td>AMSA</td>
<td>Australian Museum, Sydney, Australia.</td>
</tr>
<tr>
<td>ANIC</td>
<td>Australian National Insect Collection, CSIRO, Canberra, Australia.</td>
</tr>
<tr>
<td>BMNH</td>
<td>British Museum (Natural History), London, England.</td>
</tr>
<tr>
<td>BPBM</td>
<td>Bernice P. Bishop Museum, Honolulu, Hawaii, USA.</td>
</tr>
<tr>
<td>CISC</td>
<td>California Insect Survey, Division of Entomology and Parasitology, University of California, Berkeley, California, USA.</td>
</tr>
<tr>
<td>CMNZ</td>
<td>Canterbury Museum, Christchurch, New Zealand.</td>
</tr>
<tr>
<td>GNMS</td>
<td>Göteborg Naturhistoriska Museet, Göteborg, Sweden.</td>
</tr>
<tr>
<td>KCEM</td>
<td>K. C. Emerson Entomology Museum, Oklahoma State University, Stillwater, Oklahoma, USA.</td>
</tr>
<tr>
<td>MFMP</td>
<td>Museu Municipal do Funchal, Madeira, Portugal.</td>
</tr>
<tr>
<td>MONZ</td>
<td>Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.</td>
</tr>
<tr>
<td>MZUC</td>
<td>Museo de Zoología, Universidad de Concepción, Concepción, Chile.</td>
</tr>
<tr>
<td>NZAC</td>
<td>New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand.</td>
</tr>
<tr>
<td>OCSA</td>
<td>Onderstepoort Collection, Veterinary Research Institute, Onderstepoort, South Africa.</td>
</tr>
<tr>
<td>QVTA</td>
<td>Queen Victoria Museum and Art Gallery, Launceston, Tasmania, Australia.</td>
</tr>
<tr>
<td>REEC</td>
<td>R. E. Elbel Collection, Salt Lake City, Utah, USA.</td>
</tr>
<tr>
<td>RLCR</td>
<td>R. L. C. Pilgrim Collection, housed in MONZ.</td>
</tr>
<tr>
<td>SAIMR</td>
<td>South African Institute for Medical Research, Johannesburg, South Africa.</td>
</tr>
<tr>
<td>SAMA</td>
<td>South Australian Museum, Adelaide, South Australia.</td>
</tr>
</tbody>
</table>
Fig. 1–2  *Naubates* (*Naubates*) *harrisoni* (ex *Puffinus huttoni*). **Fig. 1** male; **Fig. 2** female.

SAMS  South African Museum, Cape Town, South Africa.

TMTA  Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia.

UQIC  University of Queensland Insect Collection, Brisbane, Australia.

USNM  United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

ZFMK  Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

ZMHU  Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Germany.

ZUAC  Instituto de Zoología, Universidad Austral de Chile, Valdivia, Chile.
SYSTEMATICS

Family *Philopteridae* Burmeister, 1838

Genus *Naubates* Bedford, 1930

**DIAGNOSIS:** Medium-sized, elongate, dark-brown lice (Fig. 1–2, 34, 68–73). Head: longer than broad; marginal carinae divided into pre- and post-marginal carinae; dorsal carinae with broad, widely separated, posterior prolongations; ventral carinae very prolonged posteriorly; clypeal suture well defined; clypeal signature sharply demarcated and well pigmented (Fig. 3–9). Antennae dimorphic: in the male segment I swollen, occupying about half the total length of the antenna; segment III with a distal sclerotised knob; segments IV and V slender, filiform, set at an angle (Fig. 1, 3–5, 7, 34, 68, 70, 72). The female antenna is filiform with segment II longest, segment I slightly shorter, segments III, IV, V subequal and each shorter than I; segment I slightly wider than remainder (Fig. 2, 6, 8–9, 69, 71, 73).

Measurements of head length (including hyaline margin), head width, and total length of slide-mounted specimens of the 10 species are given in Tables 1–4.

**REMARKS:** In his revision of the genus, Timmermann (1961) separated the then seven known species into two distinct species groups, *fuliginosus*-group and *clypeatus*-group, based on characters of the head, prosternum, and abdomen. We find that, of these characters, only those of the head (except the temporal setae) and the prosternum are consistent; but they are so reliable and diagnostic that we propose his species-groups be considered as subgenera.

**KEY TO SUBGENERA OF NAUBATES**

(Adults only)

1 Clypeal signature without a depression; posterior prolongations of dorsal carinae reach level of mandibles (Fig. 1–2, 7–9, 34) .......................................................... *Naubates*  
   Clypeal signature with sharply-defined \( \bigcirc \) or \( \bigcirc \) shaped ventral depression (Fig. 3–6, 10–13); posterior prolongations of dorsal carinae do not reach level of mandibles (Fig. 3–6, 68–73) .......................................................... *Guenterion*

**Subgenus Naubates sensu stricto**

*Naubates* Bedford, 1930: 167.

Type species: *Esthiopterum fuliginosum* (Taschenberg, 1882) (by original designation)


*Naubates* Bedford, 1930; Timmermann 1961, p. 176 (as *fuliginosus*-group).

*Naubates* Bedford, 1930; Timmermann 1965, p. 118 (as *fuliginosus*-group).

**DIAGNOSIS:** Post-marginal carinae with inner margins lightly curved but without pronounced emargination; posterior prolongations of dorsal carinae reaching level of mandibles; ventral carinae slender, smoothly curved, slightly expanded at posterior end; clypeal signature without ventral depression (Fig. 1–2, 7–9, 34). Prosternal plate elongated-oval, its long axis anteroposterior (Fig. 19–20).

**REMARKS:** The three species in this subgenus are very consistent with respect to several characters in addition to those described in the above diagnosis. These are: the shapes of the

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*Fig. 3–9* Heads, dorsal views. *Fig. 3* male *Naubates* (*Guenterion*) *damma*; *Fig. 4* male *Naubates* (*G.*) *pterodromi*; *Fig. 5* male *Naubates* (*G.*) *clypeatus*; *Fig. 6* female *Naubates* (*G.*) *clypeatus*; *Fig. 7* male *Naubates* (*N.*) *fuliginosus*; *Fig. 8* female *Naubates* (*N.*) *fuliginosus*; *Fig. 9* female *Naubates* (*N.*) *thieli*. Abbreviations: a.m.s.1, first anterior marginal setae; a.m.s. 2, second anterior marginal setae; t.s., temporal setae.
clypeal signature (Fig. 7–9), and the male antenna (Fig. 1, 7, 34); the number (six) and length
(four very long, one medium, one short) of the posterolateral setae on the pteronotum; the
relative lengths of the male abdominal segments, with the 3rd and 4th (visible) being the
shortest (Fig. 1, 34) and forming the region where the abdomen is bent upwards during
copulation.

**KEY TO SPECIES OF SUBGENUS NAUBATES**

(Adults only)

1 First antennal segment swollen, and at least as long as segments II–V together (Fig. 1, 7, 34).

   Genitalia as in Fig. 26–28 .......................................................... MALES ........................................ 2

2 First antennal segment not swollen, much shorter than segments II–V together (Fig. 2, 8–9).

   Terminalia as in Fig. 29–30 .......................................................... FEMALES .................................. 4

2 Parameres slender, closely apposed distally and occupying no greater width than the basal
plate (Fig. 26). Ventral terminalia as in Fig. 31 .................................. *N. (N.) fuliginosus*

   Parameres massive, widely separated throughout and occupying greater width than the
basal plate (Fig. 27–28). Ventral terminalia not as above .......................... 3

3 Genitalia as in Fig. 27, and terminalia as in Fig. 32 .......................... *N. (N.) harrisoni*

   Genitalia as in Fig. 28, and terminalia as in Fig. 33 .......................... *N. (N.) thieli*

4 Total length of last two abdominal segments (8th + 9th visible) equal to or more than the
maximum width of 8th visible segment (Fig. 29). Subgenital plate as in Fig. 35

   ...............................................................................................................

   .......................................................... *N. (N.) fuliginosus*

5 Subgenital plate as in Fig. 36. Trabeculae prominent, more than half the length of first
antennal segment (Fig. 38) ............................................................. *N. (N.) harrisoni*

   Subgenital plate as in Fig. 37. Trabeculae not prominent, less than half the length of first
antennal segment (Fig. 39) ............................................................. *N. (N.) thieli*

*Naubates (Naubates) fuliginosus* (Taschenberg, 1882)

(Fig. 7–8, 19, 26, 29, 31, 35)

*Lipeurus fuliginosus* Taschenberg, 1882: 156, pl. IV, fig. 3 (Type hosts: *Diomedea exulans*
Linnaeus, 1758 and *Diomedea chlororhynchos* Gmelin, 1789; both in error). Syntypes δ♀
presumed lost.

*Lipeurus testaceus* Taschenberg, 1882: 135, pl. V, fig. 3 (Type host: *Daption capense*
Linnaeus, 1758); in error). Syntypes, nymphs, presumed lost.

*Lipeurus fuliginosus*; Kellogg 1914, p. 85 (in part *Naubates (N.) fuliginosus* Taschenberg,
1882; in part *Naubates (G.) pterodromi* Bedford, 1930).

*Lipeurus fuliginosus*; Waterston 1914, p. 311 (in part *Naubates (N.) fuliginosus* Taschenberg,
1882; in part *Naubates (G.) pterodromi* Bedford, 1930).

*Esthiopterum fuliginosum* (Taschenberg, 1882); Harrison 1916, p. 134. Listed only.

*Esthiopterum testaceum* (Taschenberg, 1882); Harrison 1916, p. 142. Listed only.

*Naubates fuliginosus* (Taschenberg, 1882); Bedford 1930, p. 168, fig. 9, 11, 15, 16a.

*Naubates testaceus* (Taschenberg, 1882); Thompson 1938, p. 492.


*Naubates fuliginosus*; Timmermann 1961, p. 177, fig. 1, 3, pl. I, fig. a–b.

*Naubates fuliginosus*; Timmermann 1965, p. 118, fig. 53, 55, pl. IV, fig. 1–2.

**DIAGNOSIS:** Male head as in Fig. 7, with four long temporal setae on each side; ocular seta as long as the first (anterior) temporal seta. Abdomen: terminalia approximately triangular, its ventral aspect as in Fig. 31, with a patch of numerous central setae of similar length irregularly scattered on the subgenital plate. Genitalia as in Fig. 26; parameres slender, slightly asymmetrical, occupying approximately half the total length.

Female head as in Fig. 8, with one short and three long temporal setae on each side; ocular seta as long as the first (anterior) temporal seta. Abdomen: terminalia as in Fig. 29, with total
length of last two abdominal segments equal to or more than the maximum width of 8th visible segment; subgenital plate as in Fig. 35.

MATERIAL EXAMINED: Ex Procellaria aequinoctialis: 2 ♂, 2 ♀, St Sebastian Bay, Cape Province, South Africa, 25 Apr 1912 (GNMS); 2 ♂, South Atlantic, 1912–13 (CISC; USNM); 1 ♂, near Isla Masatierra, Juan Fernandez Is, Chile, 1913 (AMNH); 3 ♂, 1 ♀, South Africa, Aug 1915 (BMNH); 1 ♂, 1 ♀, Lambert’s Bay, Cape Province, South Africa, 9 Feb 1917 (OCSA); 2 ♂, 2 ♀, Perú, 16 Jul 1922 (KCEM; USNM); 2 ♀, 55°11’S, 55°55’E, 3 Feb 1930.
(SAMA); 4 ♂, 3 ♀, 62°04′S, 87°24′E, 27 Mar 1947 (BMNH); 1 ♂, 1 ♀, NW Cape Columbine, South Africa, 26 Sep 1951 (ZMHU); 2 ♂, 3 ♀, Pacific Ocean off Chile, 12 Apr 1965 (KCEM; USNM); 3 ♂, same locality, 15 Apr 1965 (USNM); 1 ♂, 1 ♀, Perth, Western Australia, 1974 (BMNH); 1 ♂, 2 ♀, South Atlantic Ocean (41°S, 13°E), Aug 1985 (MONZ); 3 ♂, 3 ♀, Valdivia, Chile, 17 Dec 1987 (MONZ); 1 ♂, Table Bay, South Africa, no date (BMNH); 1 ♀, Australia, no date (BMNH).

Ex Procellaria aequinoctialis aequinoctialis: 1 ♂, 1 ♀, Cape Hen, South Africa, 1901 (BMNH; SAMS); 3 ♂, 2 ♀, off Lambert’s Bay, Cape Province, South Africa, 31 Oct 1917 (BMNH); 5 ♂, 4 ♀, same locality, 5 Nov 1917 (BMNH); 1 ♂, 1 ♀, Murray I., Royal Sound, Kerguelen Is, Indian Ocean, 23 Feb 1930 (BMNH); 1 ♂, 1 ♀, Campbell I., NZ, 22 Feb 1947 (MONZ); 19 ♂, 16 ♀, SW Africa, May 1949 (BMNH; SAIMR); 3 ♂, 2 ♀, Kidney I., E Falkland Is, South Atlantic Ocean, 31 Dec 1958 (BMNH); 2 ♂, South Georgia I., South Atlantic Ocean, 31 Jan 1961 (BMNH); 1 ♂, Grytviken Peninsula, South Georgia I., South Atlantic Ocean, 12–14 Nov 1963 (BPBM); 2 ♂, 2 ♀, Ewing I., Auckland Is, NZ, 15 Jan 1963 (BMNH; BPBM); 3 ♂, 1 ♀, Antipodes Is, NZ, 4 Feb 1969 (RLCP); 3 ♂, 2 ♀ same locality, 21 Feb 1969 (BMNH; NZAC); 1 ♂, Spencerville, Canterbury, NZ, 14 Jan 1973 (RLCP); 3 ♂, 3 ♀, Disappointment I., Auckland Is, NZ, 15 Feb 1973 (MONZ; RLCP); 10 ♂, 10 ♀, Wellington, NZ, 19 Apr 1976 (MONZ); 6 ♂, 6 ♀, 60 miles SE off Snares Is, NZ, 22 Jan 1977 (MONZ); 9 ♂, 9 ♀, Antipodes Is, NZ, 23 Nov 1978 (MONZ); 2 ♂, 3 ♀, Île Grek, Golf du Morbihan, Kerguelen Is, Indian Ocean, 24 Jan 1985 (MONZ); 1 ♂, 1 ♀, New Zealand, no date (MZUC); 2 ♂, 2 ♀, Possession I., Crozet Is, Indian Ocean, no date (BMNH); 1 ♂, 4 ♀, Crozet Is, Indian Ocean, no date (BMNH); 3 ♂, 3 ♀, Kerguelen Is, Indian Ocean, no date (BMNH); 2 ♂, 2 ♀.

Table 1  Measurements (in mm) of seven species of Naubates (means; ranges in parentheses). Head width is maximum, at temples. Head length is maximum from hyaline margin to posterior limit of temple.

<table>
<thead>
<tr>
<th>Species</th>
<th>Head width (in mm)</th>
<th>Head length (in mm)</th>
<th>Total length (in mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Naubates (N.) thieli</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 ♂♂</td>
<td>0.613 (0.60–0.63)</td>
<td>0.961 (0.94–1.03)</td>
<td>4.087 (3.89–4.25)</td>
</tr>
<tr>
<td>10 ♀♀</td>
<td>0.632 (0.61–0.65)</td>
<td>0.990 (0.97–1.00)</td>
<td>3.978 (3.85–4.07)</td>
</tr>
<tr>
<td>Naubates (G.) clypeatus</td>
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<tr>
<td>15 ♂♂</td>
<td>0.397 (0.39–0.41)</td>
<td>0.646 (0.63–0.68)</td>
<td>2.492 (2.35–2.58)</td>
</tr>
<tr>
<td>15 ♀♀</td>
<td>0.455 (0.45–0.46)</td>
<td>0.708 (0.68–0.73)</td>
<td>2.925 (2.86–3.01)</td>
</tr>
<tr>
<td>Naubates (G.) prioni</td>
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<tr>
<td>60 ♂♂</td>
<td>0.373 (0.35–0.39)</td>
<td>0.621 (0.58–0.65)</td>
<td>2.402 (2.22–2.53)</td>
</tr>
<tr>
<td>60 ♀♀</td>
<td>0.437 (0.40–0.47)</td>
<td>0.699 (0.67–0.73)</td>
<td>2.755 (2.55–2.96)</td>
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<tr>
<td>Naubates (G.) heteroproctus</td>
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<tr>
<td>15 ♂♂</td>
<td>0.593 (0.57–0.62)</td>
<td>0.914 (0.88–0.94)</td>
<td>3.762 (3.65–4.09)</td>
</tr>
<tr>
<td>15 ♀♀</td>
<td>0.609 (0.59–0.65)</td>
<td>0.900 (0.87–0.93)</td>
<td>3.522 (3.36–3.72)</td>
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<tr>
<td>Naubates (G.) pterodromi</td>
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<tr>
<td>45 ♂♂</td>
<td>0.556 (0.53–0.58)</td>
<td>0.858 (0.80–0.88)</td>
<td>3.436 (3.23–3.55)</td>
</tr>
<tr>
<td>45 ♀♀</td>
<td>0.593 (0.57–0.62)</td>
<td>0.858 (0.83–0.89)</td>
<td>3.422 (3.26–3.52)</td>
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<tr>
<td>Naubates (G.) lessonii</td>
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<tr>
<td>15 ♂♂</td>
<td>0.591 (0.58–0.62)</td>
<td>0.909 (0.90–0.94)</td>
<td>3.633 (3.52–3.80)</td>
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<td>15 ♀♀</td>
<td>0.617 (0.60–0.65)</td>
<td>0.901 (0.88–0.92)</td>
<td>3.461 (3.40–3.55)</td>
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<tr>
<td>Holotype ♂</td>
<td>0.59</td>
<td>0.91</td>
<td>3.55</td>
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<tr>
<td>Naubates (G.) ultimae</td>
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</tr>
<tr>
<td>15 ♂♂</td>
<td>0.553 (0.53–0.57)</td>
<td>0.881 (0.85–0.92)</td>
<td>3.723 (3.56–3.92)</td>
</tr>
<tr>
<td>15 ♀♀</td>
<td>0.559 (0.54–0.57)</td>
<td>0.864 (0.84–0.88)</td>
<td>3.454 (3.35–3.56)</td>
</tr>
<tr>
<td>Holotype ♂</td>
<td>0.57</td>
<td>0.92</td>
<td>3.92</td>
</tr>
</tbody>
</table>
Table Bay, South Africa, no date (BMNH); 1♀, South Africa, no date (BMNH); 2♀, South America, no date (BMNH); 2♀, Falkland Is, South Atlantic Ocean, no date (BMNH); 14♂, 19♀, South Georgia I., South Atlantic Ocean, no date (BMNH).

Ex *Procellaria westlandica*: 2♂, Greymouth, NZ, 20 Jun 1935 (RLCP); 4♂, 4♀, Cook Strait, NZ, 15 Jul 1954 (MONZ); 1♂, 2♀, Barrytown, Westland, NZ, 31 Aug 1957 (BMNH); 5♂, 5♀, same locality, 5 May 1960 (MONZ); 2♂, Lyall Bay, Wellington, NZ, 16 May 1961 (MONZ); 1♂, 2♀, Punakaiki, Westland, NZ, 15 Jul 1969 (MONZ); 2♂, 1♀, Rae’s Valley, Barrytown, Westland, NZ, 21 Jul 1970 (RLCP); 1♂, 1♀, Barrytown, Westland, NZ, 2 Aug 1970 (RLCP); 1♂, 1♀, same locality, 29 Nov 1970 (RLCP); 3♂, Paroa Beach, Westland, NZ, 21 Jul 1974 (RLCP); 19♂, 19♀, Punakaiki, Westland, NZ, 10 May 1975 (AMNZ; BMNH; KCEM; RLCP; ZFMK); 1♂, 1♀, Ruru, Greyouth, NZ, 28 Nov 1975 (RLCP); 7♂, 1♀, Cobden, NZ, 18 Dec 1976 (RLCP); 1♂, 1♀, Punakaiki River Mouth, Westland, NZ, 13 Apr 1977 (MONZ); 5♂, 5♀, Punakaiki, Westland, NZ, 10 Oct 1977 (MONZ); 2♂, 2♀, Barrytown, Westland, NZ, 20 Dec 1977 (MONZ); 5♂, 1♀, Punakaiki, Westland, NZ, 20 May 1978 (MONZ); 1♂, 9♀, Island Bay, Wellington, NZ, 9 Jul 1978 (MONZ); 2♂, Punakaiki, Westland, NZ, 21 May 1980 (MONZ).

Ex *Procellaria parkinsoni*: 6♂, 6♀, Kinleith, NZ, 31 May 1965 (MONZ; RLCP); 1♂, Little Barrier I., NZ, 11 Dec 1968 (MONZ); 8♂, 8♀, same locality, 23 Feb 1969 (MONZ); 6♂, 6♀, off Great Barrier I., NZ, Mar 1977 (MONZ); 1♂, Little Barrier I., NZ, 18 May 1978 (NZAC); 4♂, 4♀, St Heliers Bay, Auckland, NZ, 25 May 1987 (MONZ); 6♂, 3♀, Waikanae Beach, Wellington, NZ, 8 Oct 1988 (MONZ; AMNZ); 7♂, 5♀, Pt Fitzroy, Great Barrier I., NZ, 10 Feb 1989 (MONZ); 4♂, 2♀, Otorohanga, Waikato, NZ, 6 May 1989 (MONZ; AMNZ); 3♂, 3♀, Little Barrier I., NZ, 10 Jun 1991 (MONZ); 2♂, 1♀, New Zealand, no date (BMNH); 2♀, no locality, no date (BMNH).

Ex *Procellaria cinerea*: 2♂, South Atlantic Ocean, 1912–13 (CISC; USNM); 1♂, Campbell I., NZ, 3 Jun 1944 (RLCP); 2♀, same locality, Jun 1945 (BMNH); 5♂, 1♀, Antipodes Is, NZ, 4 Nov 1950 (MONZ); 3♂, 1♀, Wellington, NZ, 16 Aug 1952 (MONZ); 2♀, Gough I., South Atlantic Ocean, 23 Feb 1956 (BMNH); 2♂, Antipodes Is, NZ, 13 Feb 1969 (RLCP); 4♂, 3♀, Reef Pt, Antipodes Is, NZ, 23 Feb 1969 (BMNH; NZAC); 5♂, 2♀, Antipodes Is, NZ, 26 Feb 1969 (MONZ; BMNH; RLCP); 1♂, 1♀, Feilding, Manawatu, NZ, 6 Jan 1972 (MONZ); 2♂, 1♀, Karori Stream, Wellington, NZ, 8 May 1977 (MONZ); 3♂, 7♀, Antipodes Is, NZ, 18 Nov 1978 (MONZ); 4♂, 7♀, Isthmus, Macquarie I., Australia, Apr 1984 (MONZ; QVTA); 1♂, 1♀, Antipodes Is, NZ, no date (BMNH); 6♂, 5♀, South Pacific Ocean, no date (BMNH); 2♂, no locality, no date (BMNH).

**STRA GGLERS AND CONTAMINANTS: **Ex *Diomedea exulans*: 2♀, South Georgia I., South Atlantic Ocean, Nov 1901 (BMNH).

Ex *Diomedea melanophris*: 1♂, no locality, no date (SAMS).

Ex *Diomedea chlororhynchos*: 1♂, no locality, no date (BMNH).

Ex *Phoebetria fusca*: 1♀, South Atlantic Ocean, no date (BMNH).

Ex *Phoebetria palpebrata*: 1♂, 2♀, 62°29'S, 91°26'E, 14 Jan 1947 (BMNH).

Ex *Macronectes giganteus*: 1♂, South Atlantic Ocean, 1912–13 (CISC); 1♂, South Georgia I., South Atlantic Ocean, no date (BMNH).

Ex *Pterodroma brevirostris*: 1♀, Kerguelen Is, Indian Ocean, no date (BMNH).

Ex *Pterodroma mollis mollis*: 1♂, North Atlantic Ocean, no date (BMNH).

Ex *Calonectris leucomelas*: 1♂, Japan, no date (BMNH).

Ex *Puffinus gravis*: 1♂, Cape of Good Hope, South Africa, no date (BMNH).
Fig. 26–28  Male genitalia, dorsal views. Fig. 26 *Naubates (N.)* fuliginosus; Fig. 27 *Naubates (N.)* harrisoni; Fig. 28 *Naubates (N.)* thieli.
DISCUSSION: No significant qualitative differences were found among populations of *Naubates* (*Naubates*) *fuliginosus* (279♂, 242♀) from the four species of regular hosts (i.e., excluding stragglers and contaminants). Specimens from *Procellaria cinerea* are smallest in all dimensions (Table 2); specimens from *P. westlandica* and from *P. aequinoctialis* spp. are similar to each other but proportionately larger than those from *P. cinerea*; while specimens from *P. parkinsoni* are intermediate—they are about as slender as those from *P. cinerea* but reach the length of those from *P. westlandica* and *P. aequinoctialis*. The number of central setae on the male subgenital plate varies from c. 20 to c. 40 without clear correlation with host association. The male genitalia in specimens from *P. westlandica* and *P. aequinoctialis* spp. are c. 50% broader than in those from the other two hosts, especially with respect to the distal end of the basal plate and the bases of the parameres. We do not consider that these quantitative differences among the lice populations justify taxonomic separation.

It is clear from the material examined that, apart from a few stragglers and contaminants, *N. (N.) fuliginosus* has been found only on hosts of the genus *Procellaria*. We strongly suggest that Taschenberg’s attribution (1882, p. 157) of *Diomedea exulans* and *D. chlororhynchos* as hosts of *N. (N.) fuliginosus* is incorrect, though he has been followed by a number of authors. In the course of extensive and intensive examination of lice samples from all known species of *Diomedea* (see Horning et al. 1980; Pilgrim & Palma 1982; Palma & Pilgrim 1984, 1988; Palma 1999), we have never found evidence that species of this genus of birds could be considered as regular hosts of *N. (N.) fuliginosus*, or indeed of any other species of *Naubates*. Our conclusion is that Taschenberg’s specimens, collected by A. B. Meyer,
either were stragglers from a *Procellaria* host, or resulted from an incorrect host-louse association due to human error following collection.

Taschenberg (1882, p. 135) described *Lipeurus testaceus* from nymphs (which he interpreted as females) collected by A. B. Meyer from “*Procellaria capensis*” (now *Daption capense* (Linnaeus, 1758)). Since the types of *L. testaceus*, as also those of *N. (N.) fuliginosus*, are presumed destroyed with the Halle collection during World War II (J. M. Martens pers. comm. 1976), we had necessarily to rely on indirect evidence to associate the nymphs described as *L. testaceus* with a currently valid species of *Naubates*. Examination of Taschenberg’s pl. V, fig. 3 shows that, on the evidence of size and proportions, as well as sclerotisation and shape of the abdominal plates, the specimen illustrated was a third instar nymph. Comparison with third instar nymphs from all elongate lice genera known to occur on Procellariiformes, shows it to belong unquestionably in the genus *Naubates*. Nymphs of *Pseudonirmus gurlti* (Taschenberg, 1882), a regular louse of *Daption capense*, are readily distinguishable from Taschenberg’s figure of *L. testaceus*. To this extent we agree with Hopkins & Clay (1952, p. 235) in placing *L. testaceus* in *Naubates*, but we do not believe that *Daption capense* is a regular host for this or any species of *Naubates*: our examination of many samples from this host has never revealed specimens belonging to this louse genus (Horning et al. 1980; Pilgrim & Palma 1982; Palma 1999). We therefore maintain again that Taschenberg’s specimens are stragglers or contaminants.

With regard to the species identity of the nymphs described as *L. testaceus*, comparison of Taschenberg’s figure (1882, pl. V, fig. 3) against nymphal specimens of all the species of *Naubates* here recognised as valid, shows them to be *N. (N.) fuliginosus*. This identification is based on the following features: dimensions (those given by Taschenberg (1882, p. 136) are too great for third instar nymphs of *Naubates* (G.) *clypeatus* (Giebel, 1874); *N. (G.) prioni* (Enderlein, 1908) or *N. (G.) damma* Timmermann, 1961); size and proportions of the abdomen (different from those in third instar nymphs of *N. (N.) harrisoni* Bedford, 1930; *N. (G.) pterodromi* Bedford, 1930; *N. (G.) heteroproctus* Harrison, 1937; *N. (N.) thieli* Timmermann, 1965 or *N. (G.) ultimae* new species). We conclude that the types of *L. testaceus* were nymphs of *N. (N.) fuliginosus*. It is significant that Taschenberg’s material included not only adults, which he described as *L. fuliginosus*, but also nymphs which he described as *L. testaceus*; that both samples were collected by the same person; and that both were stragglers or contaminants.

Harrison (1916, p. 142) had already synonymised *N. testaceus* with *N. (N.) fuliginosus* (both listed in the genus *Esthiopterum*) though without explanation. Bedford (1932, p. 334) agreed with Harrison’s synonymy; however, several subsequent authors continued to regard *N. testaceus* as a valid species (e.g., Thompson 1938; Hopkins & Clay 1952; Clay & Moreby 1967, 1970). Timmermann (1961, p. 174) stated that *N. testaceus* was described from a nymph, and that *Naubates* did not normally occur on *Daption capense*. Timmermann (1965, p. 119) included this petrel as an accidental host for *N. (N.) fuliginosus* without specific mention of *N. testaceus*; we interpret this as an implied synonymy.

Brinck (1955, p. 417) listed several specimens taken from *Procellaria aequinoctialis* as “*Naubates* sp. nov. R. L. EDWARDS (in press)” but, to the best of our knowledge, Edwards has never published such a new species. In the Göteborg Naturhistoriska Museet (see material examined) we have located four of the specimens referred to by Brinck and we have identified them as *N. (N.) fuliginosus*. Presumably, Edwards failed to recognise these specimens as *N. fuliginosus* because of the initial confusion regarding the true regular hosts of this louse species.

There are several other purported hosts published for *N. (N.) fuliginosus*: *Sterna paradisaea*, *Macronectes giganteus*, *Pterodroma mollis*, and *Pt. incerta* in Kellogg (1914, p. 85–86);
Diomedea melanophrys and Oceanites oceanicus in Waterston (1914, p. 311); Calonectris leucomelas, Puffinus gravis, and Pterodroma brevirostris in Timmermann (1965, p. 119); Pheboetria palpebrata and Ph. fusca in Clay & Moreby (1970, p. 217). We regard all these host associations with *N. (N.) fuliginosus* as incorrect, some being the result of natural or human contaminations, others being cases of misidentifications of the lice. We have examined the specimens from several procellariiform hosts collected by R. C. Murphy in the South Atlantic Ocean and reported by Kellogg (1914, pp. 85–86) as *L. fuliginosus*; also, we have examined six of the nine specimens reported by Waterston (1914, p. 311) as *L. fuliginosus*, collected from procellariiform hosts. In both instances, we have identified them as a mixture of *N. (N.) fuliginosus* and *N. (G.) pterodromi* (for details, see Material examined of these two species). Further, we have examined two of the specimens reported by Clay & Moreby (1970, p. 217) as *N. fuliginosus* on *Diomedea exulans* from Macquarie Island; both specimens had been misdetermined: they are *N. (G.) lessonii* n. sp. In addition, the association of this latter species of louse with *Diomedea exulans* is almost certainly the result of contamination: it is significant that the same collector took *N. (G.) lessonii* from *Pterodroma lessonii* at Macquarie Island only two days previously (see Material examined). For other misapplications of the name *fuliginosus* see under *N. (N.) harrisoni* synonymy and discussion.

**Naubates (Naubates) harrisoni** Bedford, 1930

(Fig. 1–2, 20, 27, 30, 32, 36, 38)


*Esthiopterum majus* (Kellogg & Chapman, 1899) (not *Lipeurus major* Piaget, 1880: 346); Harrison 1916, p. 138. Listed only.

*Naubates harrisoni* Bedford, 1930: 168, fig. 12, 14, 16b (Type host: *Puffinus gravis* O’Reilly, 1818). Holotype ♂ in SAMS.

*Naubates fuliginosus major* (Kellogg & Chapman, 1899) (not *Lipeurus major* Piaget, 1880: 346); Thompson 1938, p. 486. Listed only.

“*Naubates fuliginosus*” Thompson 1939a: 211 (not *Lipeurus fuliginosus* Taschenberg, 1882).


*Naubates harrisoni*; Timmermann 1961, p. 180, fig. 4.

*Naubates harrisoni*; Timmermann 1965, p. 119, fig. 56, 58.

*Naubates harrisoni*; Pilgrim & Palma 1982, p. 11, 12. Listed only.

**DIAGNOSIS:** Male as in Fig. 1. Head with three long temporal setae on each side; ocular setae less than half the length of the temporal setae. Abdomen: terminalia approximately trapezoidal, its ventral aspect as in Fig. 32, with two longitudinal para-median rows, each of five or six setae of various lengths, on the subgenital plate. Genitalia as in Fig. 27; parameres massive, markedly asymmetrical, occupying no more than ⅓ total length, with prominent inwardly projecting processes at their proximal ends; genital sac with a strongly pigmented sclerite
bearing a sharp point at one distal corner; basal plate approximately parallel-sided for most of its length, and with a narrow, longitudinal median stripe.

Female head as in Fig. 2, with three long temporal setae on each side; ocular setae less than half the length of the temporal setae; trabeculae prominent, more than half the length of first antennal segment (Fig. 38). Abdomen: terminalia as in Fig. 30, with total length of last two abdominal segments (8th + 9th visible) less than maximum width of 8th visible segment; subgenital plate as in Fig. 36.

MATERIAL EXAMINED: Ex Puffinus gravis: 2 ♂, 2 ♀, Mar del Plata, Argentina, Oct 1914 (AMNH); 3 ♂, 60 miles NW of Cape Town, South Africa, 29 Sep 1926 (BMNH); Holotype ♂, allotype ♀, paratypes 2 ♂, Cape Town, South Africa, 1929 (BMNH; OCMA; SAMS); 1 ♀, Tristan da Cunha, 17 Dec 1937 (BMNH); 1 ♀, W Greenland, Aug 1955 (BMNH); 1 ♂, 1 ♀, Cocoa Beach, Brevard Country, Florida, USA, 17 Jun 1972 (KCEM); 2 ♂, 1 ♀, Little Cumberland I., Camden County, Georgia, USA, 10 Jun 1973 (KCEM); 1 ♀, Vero Beach, Indian River County, Florida, USA, 18 Jun 1978 (KCEM); 2 ♂, 6 ♀, Port Saunders, Newfoundland, Canada, 23 Jun 1978 (MONZ); 4 ♂, 3 ♀, Cape St Mary’s, Newfoundland, Canada, 29 Jun 1978 (MONZ; RLCP); 1 ♂, 1 ♀, Vero Beach, Indian River County, Florida, USA, 15 Jun 1979 (KCEM); 1 ♂, Atlantic Ocean (42°26′N, 69°18′W), 9 Sep 1982 (MONZ); 2 ♂, 4 ♀, Gough I., South Atlantic Ocean, Nov 1985 (MONZ); 3 ♂, 3 ♀, Montauk Pt, Long I., USA, no date (CISC); 1 ♂, 3 ♀, South Atlantic Ocean, no date (BMNH).

Ex Puffinus pacificus: 2 ♂, New Britain, Pacific Ocean, 1927 (BMNH); 1 ♀, Eastern I., Midway Atoll, Central Pacific, 15 Jul 1962 (RLCP); 2 ♂, 1 ♀, Terrace, Raoul I., Kermadec Is, NZ, 16 Jan 1963 (BMNH; BPBM); 3 ♂, 1 ♀, Johnston Atoll, Pacific Ocean, 20 Aug 1963 (BMNH; REEC); 1 ♂, 1 ♀, Pacific Ocean, 13 Sep 1963 (KCEM); 1 ♂, 4 ♀, Pacific Ocean, 15 Sep 1963 (KCEM; USNM); 4 ♀, Sand I., Johnston Atoll, Pacific Ocean, 2 Nov 1963 (REEC; USNM); 1 ♂, 3 ♀, Johnston Atoll, Pacific Ocean, same date (BMNH); 2 ♀, Laysan I.,

Fig. 29–30 Female terminalia, dorsal views. Fig. 29 Naubates (N.) fuliginosus; Fig. 30 Naubates (N.) harrisoni.
Hawaiian Is, 7 Dec 1963 (BMNH; BPBM); 18 ♂, 20 ♀, Pacific Ocean, 2 Apr–5 Sep 1964 (KCEM; USNM); 1 ♂, 1 ♀, Kure Atoll, Hawaiian Is, 26 Sep 1964 (USNM); 1 ♂, 4 ♀, same locality, 5 Oct 1964 (USNM); 2 ♀, Green L., Kure Atoll, Hawaiian Is, 7 Oct 1964 (USNM); 1 ♀, same locality, 13 Oct 1964 (USNM); 1 ♂, Kure Atoll, Hawaiian Is, 14 Oct 1964 (USNM); 1 ♀, Pacific Ocean (15°12′N, 174°01′W), 16 Dec 1964 (USNM); 1 ♂, 1 ♀, Pacific Ocean (19°40′N, 159°23′W), 11 May 1965 (USNM); 1 ♂, 1 ♀, Phoenix I., Phoenix Is, Pacific Ocean, 28 May 1965 (USNM); 1 ♀, Pacific Ocean (06°20′N, 153°14′W), 10 Jun 1965 (USNM); 1 ♂, Pacific Ocean (06°35′N, 152°54′W), same date (USNM); 1 ♀, Pacific Ocean (07°24′N, 159°52′W), 12 Jun 1965 (USNM); 1 ♀, Pacific Ocean (07°28′N, 160°7′W), same date (USNM); 1 ♂, 3 ♀, Pacific Ocean (08°54′N, 162°58′W), 13 Jun 1965 (USNM); 2 ♂, 3 ♀, Pacific Ocean (11°14′N, 165°29′W), 14 Jun 1965 (KCEM; USNM); 2 ♂, Pacific Ocean (11°50′N, 166°28′W), same date (USNM); 1 ♂, 2 ♀, Pacific Ocean (15°32′N, 170°04′W), 17 Jun 1965 (USNM); 2 ♂, 1 ♀, Meyer I., Kermadec Is, NZ, 30 Dec 1966 (MONZ); 2 ♂, 2 ♀, same locality, 31 Dec 1966 (BMNH; NZAC); 4 ♀, Perth, Western Australia, May 1969 (BMNH; SAIMR); 1 ♀, Ono I., Fiji Is, 17 May 1975 (MONZ); 1 ♀, Noumea, New Caledonia, 25 May 1982 (MONZ); 1 ♀, Ninety Mile Beach, Northland, NZ, 17 Sep 1983 (MONZ); 1 ♂, Curtis I., Kermadec Is, NZ, 10 Nov 1989 (MONZ); 1 ♂, 2 ♀, Masthead I., Capricorn Group, Queensland, Australia, no date (BMNH; SAMA); 1 ♀, Fiji Is, no date (BMNH).

Ex *Puffinus bulleri*: 1 ♂, Himatangi, NZ, 29 Oct 1959 (MONZ); 1 ♂, Long Bay, Auckland, NZ, 26 Jan 1970 (AMNZ); 3 ♂, 2 ♀, Ohiwa Beach, NZ, 26 Oct 1974 (MONZ); 1 ♂, Poor Knights Is, NZ, 27 Oct 1975 (RLCP); 1 ♂, Chatham Is, NZ, 15 May 1976 (MONZ); 2 ♂, 1 ♀, Upper Hutt, NZ, 28 Apr 1977 (MONZ); 3 ♂, 3 ♀, Muriwai Beach, Auckland, NZ, 8 Oct 1978 (MONZ); 3 ♂, Tawhiti Rahi, Poor Knights Is, NZ, 7 Dec 1980 (NZAC); 1 ♀, Eaglehawk Neck, South Tasmania, Australia, 26 Dec 1992 (TMTA); 1 ♂, Akaroa, NZ, no date (CMNZ).

Ex *Puffinus carneipes*: 1 ♂, 1 ♀, Karewa I., Bay of Plenty, NZ, 5 Jan 1959 (MONZ); 1 ♂, 2 ♀, Middle Beach, Lord Howe I., Australia, 21 Nov 1962 (ANIC; BMNH); 1 ♀, Lord Howe I., 11 Sep 1963 (BMNH); 3 ♂, 2 ♀, Coppermine I., Chickens Is, NZ, 30 Aug 1968 (BMNH); 8 ♂, 8 ♀, same locality, 30 Oct 1968 (MONZ; NZAC); 9 ♂, 5 ♀, Whakatane, NZ, 29 Mar 1972 (MONZ; RLCP); 4 ♂, 1 ♀, Karewa I., Bay of Plenty, NZ, 9 Nov 1972 (MONZ; NZAC; RLCP); 2 ♀, Wellington west coast, NZ, 10 Mar 1979 (MONZ); 1 ♂, 3 ♀, Lady Alice I., Hen & Chickens Is, NZ, Mar 1981 (MONZ); 1 ♀, Matarangi Beach, Coromandel, NZ, 23 Dec 1987 (MONZ); 1 ♂, Kauwahaia I., Auckland west coast, NZ, 31 Jan 1990 (MONZ); 1 ♂, 1 ♀, California, USA, no date (BMNH).

Ex *Puffinus creatopus*: 2 ♂, 2 ♀, Monterey Bay, California, USA, Apr 1907 (MONZ); 1 ♂, California, USA, no date (BMNH).

Ex *Puffinus tenuirostris*: 1 ♀, no locality, no date (BMNH).

Ex *Puffinus nativitatis*: 2 ♂, 1 ♀, Eastern I., Midway Atoll, 26 Jul 1962 (MONZ; USNM); 1 ♂, 1 ♀, Wake I., Pacific Ocean, 20 May 1965 (USNM); 8 ♂, 8 ♀, Ducie I., Pitcairn Group, Pacific Ocean, 2 Jul 1991 (MONZ); 5 ♂, 3 ♀, same locality, 2 Aug 1991 (MONZ); 3 ♂, 2 ♀, Hatutu I., Marquesas Is, Pacific Ocean, no date (BMNH).

Ex *Puffinus pinnatus pinnatus*: 1 ♂, Île de Ouessant, France, Apr 1935 (BMNH); 1 ♀, Rhum I., Hebrides Is, Scotland, 20 Apr 1984 (MONZ); 3 ♀ same locality, Sep 1985 (MONZ); 1 ♂, same locality, Aug 1986 (MONZ); 2 ♂, 2 ♀, Bardsey I., Wales, Aug 1987 (MONZ).

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**Fig. 31–33** Male terminalia, ventral views. **Fig. 31** *Naubates (N.) fuliginosus*; **Fig. 32** *Naubates (N.) harrisoni*; **Fig. 33** *Naubates (N.) thieli*. 
Palma & Pilgrim—Revision of genus *Naubates*
Ex Puffinus puffinus opisthomelas: 2 ♂, 1 ♀ (paralecotypes of Lipeurus fuliginosus major) and 2 ♂, 1 ♀, Pacific Grove, California, USA, Oct 1896 (CISC; USNM); 1 ♀, 1 ♂ (lectotype and paralectotype, respectively, of Lipeurus fuliginosus major), Bay of Monterey, California, USA, 1897 (CISC); 1 ♂, Santa Barbara, California, USA, 11 Feb 1903 (MONZ); 6 ♂, 1 ♀, California, USA, no date (BMNH; MONZ).

Ex Puffinus huttoni: 1 ♂, 1 ♀, Spencerville, Canterbury, NZ, 2 Nov 1964 (RLCP); 1 ♂, Kaikoura, NZ, 20 Nov 1966 (RLCP); 2 ♂, 1 ♀, Kaikouras, NZ, 24 Sep 1967 (BMNH; NZAC); 3 ♀, Kowhai River, Kaikoura, NZ, 8 Mar 1970 (RLCP); 1 ♂, 1 ♀, Kaikoura, NZ, 4 Dec 1970 (MONZ); 1 ♀, Akaroa, NZ, 11 Oct 1971 (RLCP); 1 ♂, 3 ♀, Taumutu, Canterbury, NZ, 10 Nov 1973 (RLCP); 2 ♀, Kaikoura, NZ, 23 Mar 1974 (RLCP); 2 ♀, same locality, 5 Jul 1974 (RLCP); 2 ♂, 1 ♀, Waimairi Beach, Canterbury, NZ, 8 Sep 1975 (RLCP); 2 ♀, Lyall Bay, Wellington, NZ, 22 Apr 1977 (MONZ); 1 ♀, Muriwai, Auckland, NZ, 9 Nov 1979 (MONZ); 1 ♂, Waimairi Beach, Canterbury, NZ, 3 Jan 1980 (MONZ); 2 ♂, 1 ♀, North Beach, Christchurch, NZ, 17 Jan 1981 (RLCP); 3 ♂, 1 ♀, Kaikoura, NZ, 20 Oct 1984 (MONZ).

Ex Puffinus lherminieri lherminieri: 1 ♀, Elbow Key, Cay Sol Bank, Bahamas Is, 19 Jun 1930 (KCEM); 1 ♂, 2 ♀, off Miami, Florida, USA, 9 May 1980 (KCEM); 1 ♀, Barbados I., no date (BMNH).

Ex Puffinus lherminieri boydi: 1 ♀, Rombos I., Cape Verde Is, Atlantic Ocean, 25 Nov 1897 (MONZ).

Ex Puffinus assimilis baroli: 5 ♂, 3 ♀, Grande I., Selvagens Is, North Atlantic Ocean, Jul 1987 (MONZ); 1 ♀, Porto Santo I., Madeira Is, no date (BMNH).

Ex Puffinus assimilis (?)tunneyi): 2 ♂, Becher Pt, Western Australia, 1970 (BMNH).

STRAGGLERS AND CONTAMINANTS: Ex Pterodroma externa cervicalis: 1 ♂, Kermadec Is, NZ, no date (BMNH).

Ex Oceanodroma castro: 1 ♀, Cape Verde Is, Atlantic Ocean, no date (BMNH).

Ex Morus capensis: 1 ♂, Table Bay, South Africa, no date (ZMHU).

Ex Sula sula websteri: 1 ♀, Clarion I., East Pacific Ocean, 1901 (CISC).

DISCUSSION: No significant qualitative differences were found among populations of Naubates (N.) harrisoni (173 ♂, 193 ♀) from the 14 species/subspecies of regular hosts, (i.e., excluding stragglers and contaminants). Timmermann (1961, 1965) noted that populations taken from a number (five) of host species tended to show size differences paralleling those of the hosts, i.e., that they conformed to Harrison’s rule, but, having only 15 specimens, he declined to split the species into subspecies without more adequate material. Our findings agree with Timmermann’s (1961) in respect of overall body size and lengths of male genitalia and parameres (see Table 3), though in Pilgrim & Palma (1982, p. 12) we were uncertain about the status of material from P. huttoni because of the lack of samples from a wide range of hosts. Also, Timmermann (1961) considered that, in particular, his two male specimens from Puffinus pacificus were the most different among his material in that the parameres were relatively very short, but even in this case he did not see sufficient reason for establishing a new taxon. Our material (46 males) from Puffinus pacificus is much more extensive than Timmermann’s (1961), and measurements of our specimens fall within the overall range for N. (N.) harrisoni (Table 3). We conclude that there is no case for considering the populations of Naubates from Puffinus hosts as more than one taxon.

Kellogg (1896, p. 130) identified “With some doubt...” as Lipeurus testaceous [sic] five specimens from Puffinus opisthomelas. We have examined these lice, which are mounted on one slide (CISC collection No. 142b), and have identified them as nymphs of
Fig. 34  *Naubates (N.) thieli* dorsal/ventral views of male.
Table 3  Measurements (in mm) of *Naubates (Naubates) harrisoni* (means; ranges in parentheses). Head width at temples. Head length is maximum, from hyaline margin to posterior limit of temple.

<table>
<thead>
<tr>
<th>Host species</th>
<th>Head width</th>
<th>Head length</th>
<th>Total length</th>
<th>Male genitalia length</th>
<th>Paramere length</th>
</tr>
</thead>
<tbody>
<tr>
<td>ex <em>Puffinus gravis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 ♂</td>
<td>0.679 (0.65–0.72)</td>
<td>1.041 (1.01–1.07)</td>
<td>4.101 (3.98–4.32)</td>
<td>1.465 (1.38–1.55)</td>
<td>0.438 (0.40–0.46)</td>
</tr>
<tr>
<td>15 ♀</td>
<td>0.694 (0.66–0.74)</td>
<td>1.071 (1.01–1.12)</td>
<td>4.033 (3.86–4.20)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus pacificus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18 ♂</td>
<td>0.659 (0.64–0.70)</td>
<td>1.007 (0.98–1.03)</td>
<td>3.846 (3.68–4.05)</td>
<td>1.390 (1.34–1.46)</td>
<td>0.394 (0.38–0.41)</td>
</tr>
<tr>
<td>18 ♀</td>
<td>0.675 (0.63–0.73)</td>
<td>1.049 (1.00–1.11)</td>
<td>3.858 (3.63–4.10)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus bulleri</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9 ♂</td>
<td>0.650 (0.62–0.67)</td>
<td>0.997 (0.94–1.03)</td>
<td>3.819 (3.67–3.95)</td>
<td>1.393 (1.30–1.45)</td>
<td>0.403 (0.39–0.42)</td>
</tr>
<tr>
<td>7 ♀</td>
<td>0.666 (0.64–0.68)</td>
<td>1.049 (1.03–1.06)</td>
<td>3.859 (3.82–3.93)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus carneipes</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 ♂</td>
<td>0.695 (0.66–0.73)</td>
<td>1.049 (0.99–1.10)</td>
<td>4.143 (3.82–4.38)</td>
<td>1.489 (1.39–1.60)</td>
<td>0.438 (0.42–0.46)</td>
</tr>
<tr>
<td>15 ♀</td>
<td>0.695 (0.67–0.73)</td>
<td>1.079 (1.04–1.13)</td>
<td>4.033 (3.91–4.15)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus nativitatis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 ♂</td>
<td>0.635 (0.61–0.67)</td>
<td>0.921 (0.87–0.95)</td>
<td>3.577 (3.40–3.80)</td>
<td>1.314 (1.25–1.36)</td>
<td>0.394 (0.38–0.41)</td>
</tr>
<tr>
<td>10 ♀</td>
<td>0.636 (0.62–0.66)</td>
<td>0.948 (0.93–0.97)</td>
<td>3.494 (3.34–3.62)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus p. puffinus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 ♂</td>
<td>0.658 (0.62–0.67)</td>
<td>1.010 (0.91–1.05)</td>
<td>3.880 (3.52–4.03)</td>
<td>1.450 (1.34–1.51)</td>
<td>0.420 (0.38–0.44)</td>
</tr>
<tr>
<td>5 ♀</td>
<td>0.674 (0.65–0.70)</td>
<td>1.036 (0.96–1.11)</td>
<td>3.890 (3.69–4.15)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus p. opisthomelas</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10 ♂</td>
<td>0.652 (0.63–0.67)</td>
<td>0.991 (0.94–1.03)</td>
<td>3.811 (3.47–4.10)</td>
<td>1.453 (1.39–1.52)</td>
<td>0.428 (0.41–0.44)</td>
</tr>
<tr>
<td>3 ♀</td>
<td>0.683 (0.67–0.70)</td>
<td>1.053 (1.04–1.07)</td>
<td>3.877 (3.85–3.91)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus huttoni</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 ♂</td>
<td>0.630 (0.60–0.66)</td>
<td>0.948 (0.90–1.00)</td>
<td>3.741 (3.57–3.92)</td>
<td>1.383 (1.35–1.45)</td>
<td>0.408 (0.40–0.43)</td>
</tr>
<tr>
<td>18 ♀</td>
<td>0.646 (0.61–0.67)</td>
<td>0.987 (0.95–1.02)</td>
<td>3.728 (3.58–3.95)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>ex <em>Puffinus assimilis</em> sspp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 ♂</td>
<td>0.622 (0.61–0.63)</td>
<td>0.938 (0.92–0.96)</td>
<td>3.642 (3.40–3.78)</td>
<td>1.433 (1.34–1.51)</td>
<td>0.413 (0.40–0.52)</td>
</tr>
<tr>
<td>4 ♀</td>
<td>0.630 (0.61–0.64)</td>
<td>0.950 (0.93–0.97)</td>
<td>3.633 (3.52–3.73)</td>
<td>––</td>
<td>––</td>
</tr>
<tr>
<td>All hosts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>99 ♂</td>
<td>0.653 (0.60–0.73)</td>
<td>0.989 (0.87–1.10)</td>
<td>3.840 (3.40–4.38)</td>
<td>1.419 (1.25–1.60)</td>
<td>0.415 (0.38–0.46)</td>
</tr>
<tr>
<td>95 ♀</td>
<td>0.667 (0.61–0.74)</td>
<td>1.025 (0.93–1.13)</td>
<td>3.823 (3.34–4.20)</td>
<td>––</td>
<td>––</td>
</tr>
</tbody>
</table>
Naubates (N.) harrisoni. Kellogg regarded them as including three adult females. In fact, they are one third instar nymph (figured by Kellogg in pl. X, fig. 4 as a female), two second instar nymphs, and two first instar nymphs (one of which is figured by Kellogg in pl. X, fig. 2 as “... a very young.”). Kellogg & Chapman (1899, p. 100) recorded further specimens from Puffinus opisthomelas and P. creatopus as Lipeurus testaceous [sic]. Our examination of the only one of these specimens available (CISC collection No. 514[c?]) shows that it, too, is a (third instar) nymph of N. (N.) harrisoni.

Kellogg (1906, p. 319) recorded “L. fuliginosus Tasch.” from Sula sula websteri, Clarion Island; we have examined one female with identical data (CISC slide No. 1491 (Beck 27)), and have identified it as N. (N.) harrisoni. We regard this host record as the result of straggling or contamination from a Puffinus sp.; the record was repeated by Thompson (1939a, p. 211, entry 102). Kellogg & Mann (1912, pp. 62–63) listed Lipeurus fuliginosus and L. testaceus from Puffinus opisthomelas, Natividad Island. Although we have not been able to locate any of the five specimens referred to in the two entries, we suggest that they may be Naubates (N.) harrisoni, perhaps adults and nymphs, respectively.

Thompson (1938, p. 486, entry 27) listed “fuliginosus major (Lipeurus)” as “probably a synonym of Naubates fuliginosus (Taschenberg).” He appears not to have examined the type specimens of L. f. major or any other material from its type hosts to substantiate his remark.

Timmermann (1961, p. 182) effectively synonymised L. f. major with N. (N.) harrisoni, and our examination of the lectotype and four paralectotypes of L. f. major confirms this synonymy.

Naubates (Naubates) thieli Timmermann, 1965
(Fig. 9, 28, 33–34, 37, 39)

Naubates thieli Timmermann, 1965: 121 (Type host: Pterodroma solandri (Gould, 1844)). Holotype ♂ in ANIC.

Naubates thieli; Palma 1999, p. 378. Listed only.

DIAGNOSIS. Male as in Fig. 34. Head with three long and three short temporal setae on each side; ocular seta approximately ½ length of the long temporal setae. Abdomen: terminalia roughly trapezoidal, its ventral aspect as in Fig. 33, with two longitudinal para-median rows, each of five setae of various lengths, on the subgenital plate. Genitalia as in Fig. 28; parameres massive, markedly asymmetrical, occupying approximately ¼ total length, with short, forwardly projecting processes at their proximal ends; genital sac with a close network of thin thread-like structures and a weakly pigmented, club-shaped sclerite; basal plate tapering gradually towards the proximal end, without a median stripe.

Female head as in Fig. 9; trabeculae not prominent, less than half the length of first antennal segment (Fig. 39). Abdomen: terminalia as in N. harrisoni (see Fig. 30), with total length of last two abdominal segments (8th + 9th visible) less than maximum width of 8th visible segment; subgenital plate as in Fig. 37.

MATERIAL EXAMINED: Ex Pterodroma solandri: 2 ♀, Lord Howe I., Australia, 24 Oct 1913 (RLCP); 2 ♂, same locality, 24 Mar 1914 (MONZ); 1 ♂, Mt Lidgebird, Lord Howe I., Australia, 22 Mar 1921 (BMNH); Paratype ♂, Lagoon, Lord Howe I., Australia, 23 Nov 1962 (ANIC); Holotype ♂, paratype ♂, 1 ♂, Mt Gower, Lord Howe I., Australia, 9 Sep 1963 (ANIC; BMNH); 1 ♂, 7 ♀, Lord Howe I., Australia 22 Aug 1980 (MONZ); 3 ♂, 4 ♀, Dargaville Beach, Northland, NZ, Sep 1984 (MONZ); 1 ♀, no locality, no date (BMNH).

DISCUSSION: The specimens examined (11 ♂, 14 ♀) show that Naubates (N.) thieli is a uniform species, as may be expected in the case of a louse population from a single host species.
Fig. 35–37 Female subgenital plates. **Fig. 35** *Naubates* (*N.*) *fuliginosus*; **Fig. 36** *Naubates* (*N.*) *harrisoni*; **Fig. 37** *Naubates* (*N.*) *thieli*.

Timmermann’s (1965) description of *N. (N.) thieli* is brief and lacks illustrations. He wrote that the presence of a *Naubates* species closely related to *N. (N.) harrisoni*, but on a *Pterodroma* host, was both striking and in need of confirmation. Our examination of material derived from eight individual host birds confirms *Pt. solandri* as a regular host for *N. (N.) thieli* (see material examined). We agree with Timmermann that *N. (N.) thieli* is closely related to *N. (N.) harrisoni*; also, that the occurrence of *N. (N.) thieli* on a *Pterodroma* host is at variance with the distribution of all the other species of the genus *Naubates* parasitic on other species of *Pterodroma*: *N. (N.) thieli* belongs to the subgenus *Naubates* and is morphologically similar to *N. (N.) harrisoni*, a species exclusively parasitic on members of the genus *Puffinus* (see above). Other species of *Pterodroma* are parasitised exclusively, within the genus *Naubates*, by species of the new subgenus *Guenterion* (see below).

From the foregoing, and considering that *N. (N.) harrisoni* occurs on at least 14 different host species/subspecies of the same genus (*Puffinus*) distributed over a wide geographical
range whereas \(N. (N.) \text{thiei}\) is confined to a single host species of a different genus \((Pterodroma)\) with a limited geographical distribution (see Jouanin & Mougin 1979), we suggest that \(Pt. \text{solandri}\) or its ancestor acquired its ancestral infestation of \(N. (N.) \text{thiei}\) from \(Puffinus\) host(s). Warham (1996, p. 489) stated that “winter-breeding \(P. \text{solandri}\) may share burrows with summer-breeding \(Puffinus \text{pacificus}\)”; such a situation could have been responsible for the host switch of the ancestors of \(N. \text{thiei}\) from \(Puffinus \text{pacificus}\) (host of \(N. \text{harrisoni}\)) to \(P. \text{solandri}\).

Timmermann (1965) stated that the holotype and the two paratype males of \(N. (N.) \text{thiei}\) were held in the collection of the BMNH; Spratt (1983, p. 58) listed the holotype and one paratype as deposited in the ANIC. We confirm that Spratt’s allocation is correct.

**Subgenus Guenterion** new subgenus

Type species: \(Lipeurus \text{clypeatus}\) Giebel, 1874.

\(Naubates\) Harrison, 1937: 30 (not \(Naubates\) Bedford, 1930). Type species: \(N. \text{heteroproctus}\) Harrison, 1937 (by original designation).


\(Naubates\) Bedford, 1930; Timmermann 1961, p. 182 (as \(clypeatus\)-group).

\(Naubates\) Bedford, 1930; Timmermann 1965, p. 121 (as \(clypeatus\)-group).

**ETYMOLOGY:** This subgenus is dedicated to the late Günter Timmermann in recognition of his outstanding contributions to petrel lice taxonomy. The gender of \(Guenterion\) is neuter.

**DIAGNOSIS:** Post-marginal carinae with pronounced emargination near the anterior end of the inner margin; posterior prolongations of dorsal carinae not reaching level of mandibles; ventral carinae irregularly curved, narrowing at posterior end (Fig. 3–6); clypeal signature with sharply-defined \(\bigcirc\) or \(\bigcirc\) shaped ventral depression (Fig. 3–6, 10–13). Prosternal plate not oval (Fig. 14–18, 21–25).
REMARKS: The posterior prolongations of the dorsal carinae vary, among species and between sexes, in thickness and in their degree of approximation; the ventral carinae vary between species in thickness and in the extent of their curvature; the ventral depression ("Kernzone" of Timmermann 1961, p. 182, fig. 2) of the clypeal signature is less pigmented between its sharply defined outlines but posteriorly it grades imperceptibly into the remainder of the signature, and its size varies between species, both absolutely and relative to the signature as a whole.
KEY TO SPECIES OF SUBGENUS GUENTERION

(Adults only)
1 First antennal segment swollen, and at least as long as segments II-V together (Fig. 3–5). Genitalia as in Fig. 40–44. MALES
First antennal segment not swollen, much shorter than segments II-V together (6, 69, 71, 73). Terminalia as in Fig. 45–50. FEMALES
2 Posterolateral pteronotal setae on each side arranged in a row of four near the posterior margin, plus a pair situated anteromedially. Length of the two anterior pteronotal setae each greater than half the width of the prothorax (Fig. 51). Ventral terminalia as in Fig. 64. Genitalia as in Fig. 41. N. (G.) prioni
All six posterolateral pteronotal setae on each side situated near the margin (Fig. 52–54). Length of the two anterior pteronotal setae each very much less than half the width of the prothorax (Fig. 52–53). Ventral terminalia and genitalia not as above
3 Genitalia broad and massive; aedeagal sac with a pigmented sclerite (Fig. 43–44, 55–56)
Genitalia slender and weak; aedeagal sac without such sclerite (Fig. 40, 42)
4 Terminalia slightly asymmetrical (Fig. 57–58). [May appear symmetrical if terminal projections are not clearly extended] 5
Terminalia grossly asymmetrical (Fig. 59–61)
6 Terminalia as in Fig. 59. Sclerite of aedeagal sac as in Fig. 55. N. (G.) heteroproctus
Terminalia as in Fig. 60–61. Sclerite of aedeagal sac as in Fig. 56. N. (G.) ultimae
7 Posterolateral pteronotal setae almost contiguous in a smoothly curved row (Fig. 53). Terminalia symmetrical, with a darkly pigmented linear thickening within and parallel to the posterolateral margin of the last sternite (corresponding to 8th + 9th visible segments) (Fig. 62). Clypeal signature as in Fig. 11. N. (G.) damma
Posterolateral pteronotal setae well spaced in a zig-zag arrangement (Fig. 52). Terminalia slightly asymmetrical, without such thickening within the margin of the last sternite. (Fig. 63). Clypeal signature as in Fig. 10. N. (G.) clypeatus
8 Subgenital plate with conspicuous, heavily-pigmented curved stripes within the lateral margins (Fig. 65):
...................................................... on Pterodroma macroptera. N. (G.) heteroproctus
...................................................... on Pterodroma lessonii. N. (G.) lessonii
...................................................... on other Pterodroma species. N. (G.) pterodromi
Subgenital plate without such heavily-pigmented stripes (Fig. 45–48, 66–67)
9 Width:length ratio of 4th visible abdominal segment less than 2.6
Width:length ratio of 4th visible abdominal segment more than 2.6
10 Length: width ratio of prosternal plate more than 2 (Fig. 23). Ventral terminalia and subgenital plate as in Fig. 46. N. (G.) prioni
Length: width ratio of prosternal plate less than 2 (Fig. 24). Ventral terminalia and subgenital plate as in Fig. 45. N. (G.) clypeatus
11 Terminalia as in Fig. 47; subgenital plate as in Fig. 66. N. (G.) damma
Terminalia as in Fig. 48; subgenital plate as in Fig. 67. N. (G.) ultimae

Naubates (Guenterion) clypeatus (Giebel, 1874)
(Fig. 5–6, 10, 17, 24, 40, 45, 52, 63)
Lipeurus clypeatus Giebel, 1874: 236 (Type host: Halobaena caerulea (Gmelin, 1789)).
Syntypes ♀♂ presumed lost.
**Fig. 45–48** Female terminalia, ventral views. **Fig. 45** *Naubates* (*G.*) *clypeatus*; **Fig. 46** *Naubates* (*G.*) *prioni*; **Fig. 47** *Naubates* (*G.*) *damma*; **Fig. 48** *Naubates* (*G.*) *ultimae*.

*Esthiopterum clypeatum* (Giebel, 1874); Harrison 1916, p. 132. Listed only.

*Naubates clypeatus* (Giebel, 1874); Thompson 1935, p. 487.

*Naubates clypeatus*; Timmermann 1961, p. 187, fig. 7.

*Naubates clypeatus*; Timmermann 1965, p. 123, fig. 61.

*Naubates clypeatus*; Pilgrim & Palma 1982, p. 9. Listed only.

**Diagnosis:** Male head as in Fig. 5; first anterior marginal setae (a.m.s. 1) very long, at least three times as long as second anterior marginal setae (a.m.s. 2); four short and one long temporal setae on each side; ocular seta as long as the short temporal setae; clypeal signature with a bluntly rounded posterior projection (Fig. 10). Thorax: prosternal plate as in Fig. 17; anterior pteronotal setae very short; all six posterolateral pteronotal setae of each side well spaced in a zig-zag arrangement (Fig. 52). Abdomen: 4th and 5th visible segments each shorter than adjacent segments; terminalia slightly asymmetrical (Fig. 63); genitalia as in Fig. 40.
Fig. 49–50 Female terminalia, dorsal views. Fig. 49 *Naubates (G.) pterodromi*; Fig. 50 *Naubates (G.) ultimae*.

Female head as in Fig. 6; first anterior marginal setae (a.m.s. 1) approximately as long as a.m.s. 2; two short and one long temporal setae on each side; ocular seta as long as the short temporal setae; clypeal signature with the posterior projection slightly emarginated. Thorax: prosternal plate truncated oval, length:width ratio less than two (Fig. 24); anterior pteronotal setae as in male; inner four posterolateral pteronotal setae of each side with contiguous alveoli surrounded by a single clear area, outer two more widely spaced. Abdomen: ventral terminalia and subgenital plate as in Fig. 45.

MATERIAL EXAMINED: Ex *Halobaena caerulea*: 3 ♂, 15 ♀, 57°30' S, 5°00'E, 3 Jan 1947 (BMNH); 2 ♂, 2 ♀, Heard I., Indian Ocean, 10 Sep 1950 (BMNH); 1 ♂, 1 ♀, Te Horo, Wellington, NZ, 3 Aug 1954 (MONZ); 2 ♂, Hokio Stream, Wellington, NZ, 4 Sep 1954 (MONZ); 2 ♂, 2 ♀, Macquarie I., Australia, 10 Apr 1956 (ANIC); 1 ♂, 1 ♀, Isthmus, Macquarie I., Australia, 25 Sep 1956 (ANIC); 1 ♂, 2 ♀, Macquarie I., Australia, 25 Oct 1956 (ANIC); 2 ♂, 3 ♀, Waikanae Beach, Wellington, NZ, 5 Jul 1959 (MONZ; RLCP); 1 ♂, 4 ♀, Nile, N Tasmania, Australia, 2 Jul 1962 (ANIC; QVTA); 2 ♀, Marion I., Indian Ocean, 14 Nov 1965 (KCEM; SAIMR); 1 ♂, 1 ♀, Otaki Beach, Wellington, NZ, 9 Sep 1972 (MONZ); 2 ♂, 2 ♀, Ohau Beach, Wellington west coast, NZ, 16 Aug 1973 (MONZ); 23 ♂, 11 ♀, New Brighton, Canterbury, NZ, 15 Sep 1974 (CISC; CMNZ; RLCP); 9 ♂, 7 ♀, N. Taranaki, NZ, 7–20 Sep 1975 (RLCP); 1 ♀, 66°21'S, 69°24'E, 22 Feb 1976 (RLCP); 1 ♂, Kariotahi, Auckland, NZ, 16 Jul 1978 (MONZ); 2 ♂, 2 ♀, Plimmerton, Wellington, NZ, 21 Aug 1978 (MONZ); 1 ♂, 1 ♀, Tangimoana Beach, Manawatu, NZ, 2 Feb 1978 (MONZ); 4 ♂, 4 ♀, Otaki Beach, Wellington, NZ, 12 Sep 1978 (MONZ); 1 ♂, Papamoa Beach Rd., Bay of Plenty, NZ, 25 Jul 1979 (MONZ); 4 ♂, 4 ♀, Muriwai Beach, Auckland, NZ, 12 Aug 1979 (AMNZ; MONZ); 3 ♂, 3 ♀, Petone Beach, Wellington, NZ, 17 Jun 1980 (MONZ); 2 ♀, Isla Gonzalo, Diego Ramirez Is, Chile, 26 Dec 1980 (ZUAC); 6 ♂, 6 ♀, Waikanae Estuary, Wellington, NZ, 25 Sep 1981 (MONZ); 4 ♂, 4 ♀, Makara Beach, Wellington, NZ, 27 Sep 1981 (AMNZ; MONZ); 1 ♂, 1 ♀, Coorong, South Australia, 20 Jul 1983 (KCEM); 1 ♂, 5 ♀, Cape Horn, Chile, 5 Apr 1984 (MONZ); 1 ♀, Isla Hall (55°54'S, 67°24'W), Chile, 21 Apr 1984 (MONZ); 5 ♂, 5 ♀, Peka Peka Beach, Wellington, NZ, 4 Aug 1984 (MONZ); 2 ♂, 1 ♀, Cape Portland, NE Tasmania, Australia, 2 Sep 1984 (MONZ; QVTA); 2 ♂, Badger Head, Tasmania, Australia, 5 Sep 1984 (QVTA); 13 ♂, 12 ♀, Port aux Français, Kerguelen I., Indian Ocean, 10 Feb 1985 (MONZ); 1 ♀, Cape Horn, Chile, no date (BMNH).
STRAGGLERS AND CONTAMINANTS: Ex Pachyptila belcheri: 2 ♂, Makara Beach, Wellington, NZ, 31 Aug 1975 (RLCP).

Ex Pachyptila desolata: 1 ♂, 3 ♀, 1 nymph, Kerguelen I., Indian Ocean, 21–23 Dec 1902 (Deutsche Südpolar-Expedition, ZMHU slides 1331/30 and 1407/5). These five specimens are part of the type series of Lipeurus prioni but they were misidentified by Enderlein (1908) in his original description. Following our designation of a lectotype for L. prioni (see below), these five specimens are now “misidentified” paralectotypes.

Ex Pachyptila desolata desolata: 1 ♀, Green Gorge, Macquarie I., 7 Jan 1978 (MONZ).
Ex *Fulmarus glacialoides*: 1 ♀, 57°30′, 5°0′E, 3 Jan 1947 (BMNH).

Host unknown: 2 ♂, on petrel, Antarctic, 19 Mar 1956 (KCEM; USNM).

**DISCUSSION:** The specimens examined (100 ♂, 106 ♀, from 33 samples) show that *Naubates (G.) clypeatus* is a uniform species, as may be expected in the case of a louse population from a single host species.

Reports of *Lipeurus clypeatus* on *Garrodia nereis* (as *Procellaria nereis*) from Kerguelen Island by Giebel (1876, p. 389; 1879, p. 256) and Enderlein (1908, p. 455) are most unlikely to be correct; we have not seen any of the female specimens reported but we agree with Clay (1940, p. 310) that they may refer to *Philoceanus garrodiae* (Clay, 1940). The single male reported from *Diomedea exulans* by Giebel (1876) & Enderlein (1908) remains undefined.

Paulian (1953, pp. 190–192) reported *N. (G.) prioni* from *Pachyptila desolata* and *P. belcheri* at Kerguelen Island; we also record this louse from the same host species (see material examined) but we regard these specimens as stragglers or contaminants. In our opinion, Paulian’s specimens either are in the same category as ours or, more likely, are *N. (G.) prioni* misdetermined in the belief that the latter was still synonymised with *N. (G.) clypeatus* (see below under material examined and discussion of *N. (G.) prioni*).

**Naubates** (Guentherion) **prioni** (Enderlein, 1908)

(Fig. 16, 23, 41, 46, 51, 64)

*Lipeurus prioni* Enderlein, 1908: 454, fig. 194, 196–199 (Type host: *Pachyptila desolata desolata* (Gmelin, 1789)). Lectotype ♂ in ZMHU, slide No. 1407/3a, designated below.

*Esthiopterum clypeatum*; Harrison 1916, p. 140 (in part *Naubates (G.) prioni* Enderlein, 1908; in part *Naubates (G.) clypeatus* Giebel, 1874). Listed only.


“*Naubates (Micronaubates) clypeatus*” Pessôa & Guimarães 1935: 112, fig. 12 (not *Lipeurus clypeatus* Giebel, 1874).

“*Naubates clypeatus*” Harrison 1937: 31 (not *Lipeurus clypeatus* Giebel, 1874).

*Naubates prioni* (Enderlein, 1908); Thompson 1939b, pp. 244, 247. Listed only.

*Naubates prioni*; Timmermann 1961, p. 187, fig. 8a,b.

*Naubates prioni*; Timmermann 1965, p. 123, fig. 62a,b.


Naubates sp.; Green & Munday 1971, p. 9. Listed only.

Naubates prioni; Pilgrim & Palma 1982, pp. 10, 11. Listed only.

**DIAGNOSIS:** Male head similar to *N. (G.) clypeatus* except a.m.s. 1 approximately as long as a.m.s. 2, and ocular seta longer than the short temporal setae. Thorax: prosternal plate triangular (Fig. 16); length of the two anterior pteronotal setae each greater than half the width of the prothorax; posterolateral pteronotal setae on each side arranged in a row of four near the posterior margin plus a pair, surrounded by a clear area, anteromedially (Fig. 51). Abdomen: 4th and 5th visible segments each shorter than adjacent segments; terminalia symmetrical (Fig. 64); genitalia as in Fig. 41.

Female similar to *N. (G.) clypeatus* except: prosternal plate more elongated, length:width ratio more than two (Fig. 23); ventral terminalia and subgenital plate as in Fig. 46.

**MATERIAL EXAMINED:** Ex *Pachyptila desolata*: 1 ♂, Kerguelen I., Indian Ocean, 13 Dec 1902 (Deutsche Südpolar-Expedition, ZMHU slide 1407/4); 1 ♂, 4 ♀, Kerguelen I., 3 Jan 1903 (Deutsche Südpolar-Expedition, ZMHU slides 1407/3a,b; BMNH slide 304): these six specimens are part of the type series, and the male mounted on slide 1407/3a is herewith designated as the **lectotype** of *L. prioni*. 1 ♂, 1 ♀, New Zealand, 22 Aug 1935 (MONZ); 1 ♀, Retreat, Cape Town, South Africa, 29 Aug 1954 (BMNH); 2 ♀, Marion I., Indian Ocean, 11 Feb 1966 (KCEM; SAIMR); 2 ♂, 2 ♀, King I., Tasmania, Australia, 27 Jul 1960 (ANIC; QVTA); 1 ♂, 1 ♀, Wamboro Sound, Western Australia, 1970 (ANIC); 1 ♂, 1 ♀, Greymouth, NZ, 21 Jan 1972 (RLCP); 2 ♂, 2 ♀, Hokitika, NZ, 27 Jun 1974 (RLCP); 2 ♂, 2 ♀, Ashburton, NZ, Aug 1974 (RLCP); 3 ♂, 3 ♀, Perth, Western Australia, 1974 (BMNH); 5 ♂, 5 ♀, Onehunga, Auckland, NZ, 2 Aug 1986 (MONZ; AMNZ); 4 ♂, 5 ♀, Mid-Canterbury coast, NZ, no date (RLCP); 2 ♂, 2 ♀, Brighton, South Australia, no date (SAMA); 1 ♂, 2 ♀, 55°11’S, 55°51’E, no date (BMNH).

Ex *Pachyptila desolata desolata*: 1 ♀, North Island Harbour, Royal Sound, Kerguelen Is, Indian Ocean, 23 Nov 1929 (SAMA); 8 ♂, 8 ♀, Île de Chat, Golf du Morbihan, Kerguelen I., Indian Ocean, 23 Jan 1985 (MONZ); 1 ♂, 3 ♀, Kerguelen Is, Indian Ocean, no date (BMNH).

Ex *Pachyptila desolata alter*: 1 ♂, 2 ♀, Auckland Is, NZ, Jan 1943 (BASE); 1 ♂, 1 ♀, Carnley Harbour, Auckland Is, NZ, 4 Dec 1943 (BMNH); 2 ♀, Campbell I., NZ, 1944 (BMNH); 1 ♀, Macquarie I., Australia, 8 Feb 1950 (BMNH); 1 ♀, same locality, 10 Nov 1950 (ANIC); 1 ♂, 2 ♀, same locality, 20 Jan 1956 (ANIC); 1 ♂, Auckland Is, NZ, 27 Dec 1962 (BPBM); 1 ♂, same locality, 13 Jan 1963 (BMNH); 1 ♂, 1 ♀, Wellington, NZ, 3 Jul 1965 (MONZ); 2 ♂, 2 ♀, Camp Cove, Auckland Is, NZ, 1–2 Feb 1973 (BMNH; NZAC); 1 ♂, 1 ♀, Spencerville, Canterbury, NZ, 11 Mar 1973 (RLCP); 4 ♀, Laurie Harbour, Auckland Is, NZ, 16 Dec 1973 (MONZ); 5 ♂, 4 ♀, Waikanae, Wellington, NZ, 9 Jul 1974 (RLCP); 1 ♀, Macquarie I., Australia, 6 May 1980 (REEC); 2 ♂, 4 ♀, Auckland Is, NZ, no date (BMNH).

Ex *Pachyptila desolata banksi*: 1 ♀, South Georgia I., South Atlantic Ocean, Jan 1910 (BMNH); 2 ♂, St. W. 5.57 “Discovery Expedition”, 17 Jan 1927 (BMNH); 1 ♂, Atlas Cove, Heard I., Indian Ocean, 22 Dec 1949 (BMNH); 4 ♂, 4 ♀, Waikanae, Wellington, NZ, 24 Jan 1974 (MONZ); 1 ♂, Santos, State of São Paulo, Brazil, no date (BMNH).

Ex *Pachyptila vitatta*: 2 ♀, no locality, 18 Apr 1947 (BMNH); 1 ♂, 1 ♀, Orford, Tasmania, Australia, 14 Jun 1970 (QVTA); 1 ♂, Swan I., NE Tasmania, Australia, 27 Jun 1975 (QVTA); 2 ♂, 2 ♀, Wellington west coast, NZ, 30 Jun 1974 (MONZ); 2 ♂, 2 ♀, Waikawa Beach, NZ, same date (MONZ); 2 ♂, 2 ♀, North Otaki Beach, NZ, same date (MONZ); 4 ♂, 4 ♀, Cooran, South Australia, 29 Aug 1985 (KCEM); 3 ♀, New Zealand, no date (BMNH).
Fig. 57–59  Male terminalia, ventral views. Fig. 57 Naubates (G.) pterodromi; Fig. 58 Naubates (G.) lessonii; Fig. 59 Naubates (G.) heteroproctus.
Ex *Pachyptila vittata vittata*: 1 ♂, North Auckland, NZ, 28 Jun 1935 (CMNZ); 4 ♀, Auckland Harbour, NZ, 7 Jul 1936 (CMNZ; AMNZ); 2 ♀, Tristan da Cunha I., South Atlantic Ocean, 7 Feb 1938 (BMNH); 4 ♂, 2 ♀, Lyall Bay, Wellington, NZ, 22 Jul 1948 (MONZ); 6 ♂, 9 ♀, Tristan da Cunha I., South Atlantic Ocean, 28 Feb 1950 (BMNH); 5 ♂, 4 ♀, Nightingale I., Tristan da Cunha Group, South Atlantic Ocean, 24 Oct 1951 (BMNH); 1 ♂, 1 ♀, Te Horo Beach, Horowhenua, NZ, 10 Jul 1954 (MONZ); 2 ♂, 2 ♀, Gough I., South Atlantic Ocean, 6 Dec 1955 (BMNH); 2 ♂, 2 ♀, Feilding, Manawatu, NZ, 1 Jul 1961 (MONZ); 1 ♂, 1 ♀, Tristan da Cunha I., South Atlantic Ocean, 15 Dec [1967?] (BMNH); 2 ♂, Pohokura, Taranaki, NZ, 23 Aug 1969 (RLCP); 2 ♂, 2 ♀, Lake Ellesmere, Canterbury, NZ, Oct 1969 (RLCP); 2 ♂, 2 ♀, Ohoka, Canterbury, NZ, 1969 (RLCP); 4 ♂, 4 ♀, Puketapu, Hawke’s Bay, NZ, 26 May 1970 (MONZ); 2 ♂, 2 ♀, South Taranaki, NZ, Jun 1974 (RLCP); 3 ♂, 2 ♀, Hokitika, Westland, NZ, 27 Jun 1974 (RLCP); 2 ♂, 1 ♀, South Beach, Greymouth, Westland, NZ, same date (RLCP); 4 ♂, 4 ♀, Waikanae, Wellington, NZ, 7 Jul 1974 (RLCP); 8 ♂, 7 ♀, same locality, 9 Jul 1974 (KCEM; RLCP); 2 ♂, 2 ♀, Paekakariki South, Wellington, NZ, 30 Jul 1974 (RLCP); 4 ♂, 4 ♀, Snares Is, NZ, 23 Nov 1974 (RLCP); 6 ♂, 6 ♀, Rangatira I., Chatham Is, NZ, 29 Dec 1974 (MONZ; NZAC); 6 ♂, 6 ♀, South East I., Chatham Is, NZ, same date (MONZ); 2 ♂, 4 ♀, Rangatira I., Chatham Is, NZ, 1 Jan 1975 (MONZ; NZAC); 6 ♂, 6 ♀, same locality, 2 Jan 1975 (MONZ; NZAC); 4 ♂, 4 ♀, same locality, 3 Jan 1975 (NZAC); 2 ♂, 2 ♀, Paekakariki Beach, Wellington, NZ, 7 Feb 1975 (MONZ); 7 ♂, 7 ♀, Snares Is, NZ, 2 Jan 1977 (RLCP); 3 ♂, 4 ♀, Station Cove, Snares Is, NZ, 18 Jan 1977 (RLCP); 2 ♂, 3 ♀, Daption Rocks, Snares Is, NZ, 19 Feb 1977 (RLCP); 10 ♂, 10 ♀, Houruakopara I., Chatham Is, NZ, 1 Jan 1978, 31 Dec 1978, 1 Jan 1979 (MONZ); 4 ♂, South East I., Chatham Is, NZ, 8 Feb 1980 (MONZ); 10 ♂, 9 ♀, Gough I., South Atlantic Ocean, Nov 1985 (MONZ); 1 ♀, Auckland, NZ, no date (CMNZ); 3 ♂, 2 ♀, New Zealand, no date (RLCP; AMNZ; BMNH); 1 ♀, Otago, NZ, no date (BMNH); 1 ♀, Tristan da Cunha I., South Atlantic Ocean, no date (SAMS).

Ex *Pachyptila vittata salvini*: 2 ♀, Northcote, Auckland, NZ, 2 May 1956 (CMNZ); 1 ♀, Marion I., Indian Ocean, 1 Mar 1952 (ZMHU); 4 ♂, 4 ♀, Days Bay, Wellington, NZ, 13 Jun 1954 (MONZ); 4 ♂, 4 ♀, Waitarere Beach, Horowhenua, NZ, 15 Jun 1959 (MONZ; RLCP); 2 ♂, 2 ♀, Panmure, Auckland, NZ, 24 Jun 1966 (RLCP); 1 ♀, Greens Beach, Tasmania, Australia, 13 Aug 1967 (BMNH); 3 ♂, 3 ♀, Sumner, Christchurch, NZ, 15 Jun 1970 (RLCP);

Fig. 60–61  *Naubates* (*G.*) *ultimae*, male terminalia. Fig. 60 ventral view; Fig. 61 dorsal view.
1 ♂, 4 ♀, Oroua Downs, Manawatu, NZ, 22 Jul 1970 (MONZ; RLCP); 1 ♂, 1 ♀, King I., Tasmania, Australia, 28 Jul 1970 (BMNH); 3 ♂, 3 ♀, South of Mandurah, Western Australia, 1970 (ANIC; BMNH; QVTA); 2 ♂, 2 ♀, South Beach, Greymouth, Westland, NZ, 26 Jun 1974 (RLCP); 6 ♂, 6 ♀, Hokitika, Westland, NZ, 28 Jun 1974 (RLCP); 3 ♂, 2 ♀, Kapiti Coast, NZ, Jun 1974 (MONZ); 4 ♂, 4 ♀, Waikanae, Wellington, NZ, 7 Jul 1974 (RLCP); 2 ♂, 2 ♀, New Brighton, Canterbury, NZ, 24 Jul 1974 (RLCP); 4 ♂, 5 ♀, Ikamaru Bay, Wellington, NZ, 27 Jul 1975 (RLCP); 3 ♂, 3 ♀, Waikanae, Wellington, NZ, 24 Jun 1977 (MONZ); 4 ♂, 4 ♀, King I., Tasmania, Australia, 24 Apr 1984 (MONZ; QVTA); 3 ♂, 3 ♀, Indian Ocean (45°S, 36°E), 13 Jan 1986 (MONZ); 6 ♂, 6 ♀, Mid-Canterbury coast, NZ, no date (AMNZ; RLCP).

Ex Pachyptila belcheri: 3 ♂, 2 ♀, Port Stanley, Falkland Is, South Atlantic Ocean, 20 Mar 1935 (BMNH); 2 ♂, 1 ♀, Kermadec Is, NZ, 27 Jul 1944 (MONZ; BMNH); 4 ♂, 4 ♀, New I., W Falkland Is, South Atlantic Ocean, 21 Oct 1958 (BMNH); 3 ♂, 3 ♀, same locality, 18 Nov 1964 (BMNH); 9 ♂, 6 ♀, South Pacific Ocean, off Chile, 12 Apr 1965 (KCEM; USNM); 1 ♂, 1 ♀, Rinconado, Antofagasta, Chile, 25 Aug 1968 (BMNH); 2 ♂, 2 ♀, Peka Peka Creek, NZ, 11 Aug 1968 (MONZ); 1 ♂, 1 ♀, Mandurah, Western Australia, 1968 (BMNH); 4 ♂, 3 ♀, Perth, Western Australia, 1968 (ANIC; BMNH); 5 ♂, 4 ♀, Canelones, Uruguay, 16 Jul 1969 (KCEM; USNM); 3 ♂, 5 ♀, same locality, 20 Jul 1969 (KCEM, USNM); 1 ♂, 1 ♀, Pekapeka, Northland, NZ, 11 Aug 1969 (MONZ); 2 ♂, 2 ♀, Canelones, Uruguay, 31 Aug 1969 (KCEM); 4 ♂, Freycinet Peninsula, Tasmania, Australia, 17 Feb 1970 (TMTA); 5 ♂, 8 ♀, Ashburton Beach, Canterbury, NZ, 23 Jun 1974 (RLCP); 2 ♂, 2 ♀, South Beach, Greymouth, Westland, NZ, 27 Jun 1974 (RLCP); 2 ♂, 2 ♀, Hokitika, Westland, NZ, same date (RLCP); 2 ♂, 2 ♀, Kapiti Coast, NZ, Jun 1974 (MONZ); 8 ♂, 8 ♀, Te Horo, Horowhenua, NZ, 7 Jul 1974 (KCEM; RLCP); 1 ♂, 3 ♀, Ocean Beach, Strahan, Tasmania, Australia, 8 Nov 1974 (QVTA); 3 ♂, 3 ♀, Waiau Pa, Clarks Beach, Auckland, NZ, 7 Jul 1975 (RLCP); 2 ♂, 2 ♀, Ikamaru Bay, Wellington, NZ, 27 Jul 1975 (RLCP); 3 ♂, 4 ♀, Makara Beach, Wellington, NZ, 31 Aug 1975 (RLCP); 3 ♂, 3 ♀, Hokio Beach, Horowhenua, NZ, 23 Aug 1976 (MONZ); 2 ♂, 1 ♀, Badger Head Beach, Tasmania, Australia, 16 Jul 1978 (KCEM; REEC); 2 ♂, 2 ♀, Muriwai Beach, Auckland, NZ, 12 Jul 1981 (MONZ; AMNZ); 5 ♂, 6 ♀, SE Pacific Ocean (39°03’S, 78°40’W), 25 Jul 1983 (MONZ); 4 ♂, 1 ♀, Isla Noir, Chile, 19 Feb 1984 (MONZ); 4 ♂, 8 ♀, Blakeney I., Golf du Morbihan, Kerguelen Is, Indian Ocean, 25 Jan 1985 (MONZ); 8 ♂, 8 ♀, Mehuin, Valdivia, Chile, Jun 1986 (MONZ); 5 ♂, 6 ♀, Waikanae Beach, Wellington, NZ, 2 Aug 1986 (MONZ); 2 ♂, 2 ♀, South Beach, Greymouth, Westland, NZ, no date (RLCP); 6 ♂, 6 ♀, Mid-Canterbury coast, NZ, no date (RLCP).

Ex Pachyptila turtur: 1 ♂, 1 ♀, NZ, 21 May 1944 (CMNZ); 1 ♂, 3 ♀, Lyall Bay, Wellington NZ, 5 Oct 1948 (MONZ); 2 ♂, 2 ♀, Heard I., Indian Ocean, 18 Oct 1950 (ANIC); 4 ♀, Nelson, NZ, 18–19 Jul 1951 (NZAC); 2 ♂, 3 ♀, same locality, Jul 1951 (BMNH; NZAC); 3 ♂, 3 ♀, The Brothers Is, Cook Strait, NZ, 28 May 1952 (MONZ); 3 ♂, 3 ♀, Waikanae, Wellington, NZ, 15 Jun 1954 (MONZ); 1 ♂, 1 ♀, Petone, Wellington, NZ, 12 Jul 1954 (MONZ); 1 ♂, 1 ♀, Big South Cape I., Stewart Is, NZ, 23 Jan 1955 (MONZ); 1 ♂, 1 ♀, Waitarere Beach, Horowhenua, NZ, 28 Aug 1955 (MONZ); 1 ♂, 1 ♀, Evans Bay, Wellington, NZ, Sep 1955 (MONZ); 4 ♂, 3 ♀, New Brighton, Canterbury, NZ, 4 Aug 1957 (BMNH; CMNZ); 4 ♂, 8 ♀, same locality, Aug 1957 (RLCP); 4 ♂, 4 ♀, Island Bay, Wellington, NZ, 13 Oct 1958 (MONZ); 5 ♂, 1 ♀, The Brothers Is, Cook Strait, NZ, 8 Jun 1962 (MONZ); 4 ♂, 2 ♀, Petone, Wellington, NZ, 9 Aug 1963 (MONZ; RLCP); 1 ♂, 3 ♀, Stephens I., Cook Strait, NZ, 8 Oct 1963 (MONZ); 2 ♂, 2 ♀, Kanuka, Southland, NZ, 26 Oct 1964 (MONZ); 1 ♀, Marion I., Indian Ocean, 27 Nov 1965 (KCEM); 1 ♂, same locality, 11 Feb 1966 (KCEM); 1 ♂, Wellington Harbour, NZ, 27 Jan 1967 (RLCP); 5 ♂, 4 ♀, Snares Is, NZ, 7 Feb 1967 (BMNH;
RLCP); 1  ♂, 1 ♀, Miramar, Wellington, NZ, 11 Apr 1968 (MONZ); 1 ♀, Long I., Stewart Is, NZ, 13 Nov 1968 (NZAC); 2  ♂, 2 ♀, Big South Cape I., Stewart Is, NZ, 17 Feb 1969 (NZAC); 1  ♂, 1 ♀, Greymouth, Westland, NZ, 4 Mar 1969 (RLCP); 4 ♀, Motunau I., Canterbury, NZ, 29 Nov 1969 (RLCP); 6 ♀, 2 ♀, Randwick, New South Wales, Australia, 31 Jul 1970 (MONZ; AMSA); 1  ♂, 1 ♀, Snares Is, NZ, 11 Feb 1971 (RLCP); 2  ♂, 2 ♀, New Brighton, Canterbury, NZ, 4 Jul 1971 (RLCP); 3  ♂, 3 ♀, Canterbury, NZ, 29 Aug 1972 (RLCP); 5  ♂, 2 ♀, Whakatane, Bay of Plenty, NZ, 27 Oct 1972 (MONZ); 2  ♂, 2 ♀, Snares Is, NZ, 8 Dec 1972 (RLCP); 1  ♂, 1 ♀, Spencerville, Canterbury, NZ, 22 Jul 1973 (RLCP); 7  ♂, 15 ♀, Tai Tapu, Mid Canterbury, NZ, 11 Aug 1973 (RLCP); 1  ♂, Stradbroke I., Queensland, Australia, 17 Jun 1974 (UQIC); 2  ♂, 2 ♀, South Beach, Greymouth, Westland, NZ, 27 Jun 1974 (RLCP); 4  ♂, 4 ♀, Hokitika, Westland, NZ, same date (RLCP); 1  ♂, Makara, Wellington, NZ, 25 Jul 1974 (RLCP); 7  ♂, 7 ♀, Lake Ellesmere, Canterbury, NZ, 7 Aug 1974 (RLCP); 3  ♂, 3 ♀, Paekakariki South, Wellington, NZ, 30 Aug 1974 (RLCP); 4  ♂, 2 ♀, Perth, Western Australia, 1974 (BMNH); 2  ♂, 2 ♀, Ikamaru Bay, Wellington, NZ, 6 Jul 1975 (RLCP); 9  ♂, 8 ♀, Muriwai, Auckland, NZ, 17 Sep 1975 (AMNZ; RLCP); 4  ♂, 4 ♀, Poor Knights Is, NZ, 27 Oct 1975 (RLCP); 1  ♂, 1 ♀, Anson’s Bay, Tasmania, Australia, 3 Mar 1976 (QVTA); 4  ♂, 4 ♀, Petone Beach, Wellington, NZ, 26 Jun 1976 (MONZ); 3  ♂, 3 ♀, Palliser Bay, Wairarapa, NZ, 27 Jun 1976 (MONZ); 1 ♀, North Promontory, Snares Is, NZ, 28 Nov 1976 (MONZ); 4  ♂, 8 ♀, Broughton I., Snares Is, NZ, 30 Nov 1976 (MONZ); 1  ♂, 1 ♀, Station Pt, Snares Is, NZ, 29 Jan 1977 (RLCP); 1 ♀, Biology Station, Snares Is, NZ, 10 Feb 1977 (RLCP); 2  ♂, 2 ♀, Porirua, Wellington, NZ, 18 Oct 1977 (MONZ); 1  ♂, 3 ♀, Aorangi I., Poor Knights Is, NZ, 11 Jan 1978 (MONZ); 2  ♂, 4 ♀, Green’s Beach, Tasmania, Australia, 20 Jan 1978 (KCEM); 6  ♂, 6 ♀, Antipodes Is, NZ, 18 Nov 1978 (MONZ); 3  ♂, 3 ♀, Petone Beach, Wellington, NZ, 9 Aug 1980 (MONZ); 3  ♂, 3 ♀, Stephens I., Cook Strait, NZ, 4 Nov 1980 (MONZ); 5  ♂, 6 ♀, Tawhiti Rahi, Poor Knights Is, NZ, 4 Dec 1980 (NZAC); 1 ♀, Asbestos Range Beach, Tasmania, Australia, 26 Jan 1981 (QVTA); 2  ♂, 4 ♀, Murray River Mouth, South Australia, 18 Jun 1981 (KCEM); 4  ♂, 4 ♀, Waikanae Beach, Wellington, NZ, 28 Nov 1982 (MONZ); 6  ♂, 6 ♀, Île Grek, Golf du Morbihan, Kerguelen Is, Indian Ocean, 24 Jan 1985 (MONZ); 3  ♂, 3 ♀, Taranaki, NZ, 1 Aug 1985 (MONZ); 6  ♂, 6 ♀, Snares Is, NZ, Feb 1986 (MONZ); 5  ♂, 5 ♀, Motunau I., Canterbury, NZ, 8 Nov 1991 (RLCP); 8  ♂, 7 ♀, Mid-Canterbury coast, NZ, no date (CISC; RLCP); 1  ♂, 1 ♀, New Zealand, no date (ZFMK); 1  ♂, 2 ♀, Australia, no date (BMNH); 1 ♀, Saint Paul I., Indian Ocean, no date (BMNH); 1  ♂, 1 ♀, Guaruja, State of Sào Paulo, Brazil, no date (BMNH); 2  ♂, 2 ♀, Canterbury, NZ, no date (RLCP); 1  ♂, no locality, no date (BMNH).

Ex *Pachyptila crassirostris*: 7  ♂, 6 ♀, New Brighton, Canterbury, NZ, 4 Jul 1971 (BMNH; RLCP); 2  ♂, 2 ♀, Spencerville, Canterbury, NZ, 27 Jul 1973 (RLCP); 2  ♂, 2 ♀, New Zealand, no date (RLCP).

Ex *Pachyptila crassirostris crassirostris*: 2  ♂, Bounty Is, NZ, Nov 1962 (NZAC); 1  ♂, Wairoa, Hawke’s Bay, NZ, 6 Aug 1965 (MONZ); 8  ♂, 8 ♀, Bounty Is, NZ, 2 Nov 1976 (MONZ); 5  ♂, 5 ♀, at sea, off Bounty Is, NZ, same date (MONZ); 3  ♂, 4 ♀, Rima Islet, Snares Is, NZ, 21 Nov 1976 (MONZ); 1  ♂, 1 ♀, North Promontory, Snares Is, NZ, 11 Dec 1976 (RLCP); 6  ♂, 6 ♀, Bounty Is, NZ, 19 Nov 1978 (MONZ); 4  ♂, 4 ♀, Palliser Bay, Wairarapa, NZ, 14 Sep 1980 (MONZ); 6  ♂, 6 ♀, same locality, 10 Aug 1985 (MONZ); 4  ♂, 6 ♀, Kaiotere Spit, Lake Ellesmere, Canterbury, NZ, 27 Jul 1987 (MONZ); 3  ♂, 4 ♀, Okains Bay, Banks Peninsula, Canterbury, NZ, 9 Aug 1987 (MONZ).

Ex *Pachyptila crassirostris eatoni*: 1 ♀, Auckland I., NZ, Oct 1943 (BMNH); 5  ♂, 5 ♀, Ocean I., Auckland Is, NZ, 23 Jun 1998 (MONZ); 1  ♂, 3 ♀, Ewing I., Auckland Is, NZ, 24 Jun 1998 (MONZ).
Ex *Pachyptila crassirostris pyramidalis*: 9 ♂, 9 ♀, Lyall Bay, Wellington, NZ, 29 Jul 1963 (MONZ; RLC); 4 ♂, 4 ♀, Forty Four I., Chatham Is, NZ, 20 Nov 1974 (MONZ); 3 ♂, 3 ♀, at sea, off Pyramid Rock, Chatham Is, NZ, 31 Oct 1976 (MONZ); 1 ♂, 1 ♀, Waimakariri River mouth, Canterbury, NZ, 26 Jul 1987 (MONZ); 3 ♂, 4 ♀, Pyramid Rock, Chatham Is, NZ, 2 Dec 1987 (MONZ).

**STRAGGLERS AND CONTAMINANTS**: Ex *Diomedea epomophora*: 1 ♀, North of Arahura River mouth, Westland, NZ, 29 Jul 1974 (RLCP).

Ex *Diomedea cauta cauta*: 2 ♂, 1 ♀, Wainuiomata River mouth, Wellington, NZ, 11 Jul 1954 (MONZ); 1 ♀, Spit Beach, Otago, NZ, 26 Sep 1973 (NZAC).

Ex *Diomedea cauta eremita*: 6 ♂, 6 ♀, Pyramid Rock, Chatham Is, NZ, 21 Sep 1974 (NZAC).

Ex *Puffinus griseus*: 3 ♂, 3 ♀, Big South Cape I., Stewart Is, NZ, 25 Jan 1955 (MONZ; RLC); 1 ♀, Macquarie I., Australia, 21 Jan 1956 (ANIC); 2 ♀, Taiaroa Head, Dunedin, NZ, 6 May 1974 (NZAC).

Ex *Pelecanoides urinatrix*: 1 ♂, Waitarere Beach, Horowhenua, NZ, 26 Jun 1965 (MONZ); 1 ♂, Makara, Wellington, NZ, 25 Jul 1974 (RLCP).

Ex *Procellaria parkinsoni*: 1 ♂, Kinleith, Waikato, NZ, 31 May 1965 (MONZ).

Ex *Fulmarus glacialisoides*: 1 ♂, 2 ♀, New Brighton, Canterbury, NZ, 4 Jul 1971 (RLCP).

Ex *Halobaena caerulea*: 1 ♀, Kerguelen Is, Indian Ocean, Jan 1903 (BMNH).

Ex *Pterodroma brevirostris*: 1 ♀, Ocean Beach, Strahan, Tasmania, Australia, 11 Jul 1974 (QVTA).

Ex *Pterodroma inexpectata*: 1 ♂, 2 ♀, Big South Cape I., Stewart I., NZ, 23 Jan 1955 (MONZ).

Ex *Pterodroma lessonii*: 2 ♀, Waitarere, Horowhenua, NZ, 29 Jun 1974 (MONZ).

Ex *Pygoscelis papua*: 1 ♀, First Gully, Macquarie I., Australia, 11 Sep 1956 (ANIC).

Ex *Eudyptula minor*: 1 ♂, Paroa Beach, Greymouth, Westland, NZ, 31 Aug 1971 (RLCP).

Ex *Larus dominicanus*: 2 ♂, 5 ♀, Hassleborough Bay, Macquarie I., Australia, 18 Sep 1956 (ANIC).

Ex *Sterna albostriata*: 1 ♀, Wairarapa, NZ, 22 May 1951 (MONZ).

**DISCUSSION**: Despite the fact that *Naubates (G.) prioni* has been found on 10 taxa of regular host birds, all belonging to the genus *Pachyptila* (i.e., excluding stragglers and contaminants), our examination of 624 ♂ and 690 ♀ specimens shows no consistent morphological or size variations correlated with these hosts. *N. (G.) prioni* is not only very abundant on individuals of these regular hosts, but its infestation rate in the host populations appears to be high. It is for these reasons that we consider the few lice (per host) found on the wide range of other birds to represent non-regular occurrences. Many of these birds nest in the vicinity of *Pachyptila* populations (e.g., *Diomedea cauta eremita* and *Pachyptila crassirostris pyramidalis* on Pyramid Rock, Chatham Islands; see Jouanin & Mougin 1979), a situation which increases the possibility of straggling. Most of the reported occurrences are, however, from storm-wrecked birds in conditions where species/subspecies of *Pachyptila* have been far more numerous as individuals (e.g., Roberts 1975; Veitch 1976); it is highly likely that these are instances of contamination by human agency rather than of straggling.

Following his description of *N. (G.) prioni*, Enderlein (1908, p. 455) listed 19 specimens examined, divided into four different samples, three from *Pachyptila desolata* (as *Prion desolatus*) and one from *Diomedea exulans*, but he did not designate a holotype. At present,
from the original 19 syntypes, only 11 (3 samples) are available and are held in the collections at ZMHU (Göllner-Scheiding 1973, p. 41) and at BMNH. Our examination of these syntypes has revealed that, in fact, they belong to two different species: *N. (G.) prioni* (six specimens in two samples) and *N. (G.) clypeatus* (five specimens in one sample); for details, see Material examined of these species. We have therefore selected a syntype male which agrees in the key characters with the male(s) shown by Enderlein (1908, pl. LXI, fig. 194, 196, 198) and have designated it as the lectotype of *N. (G.) prioni* (see above Material examined). The lectotype is conspecific with the many males identified and listed as *N. (G.) prioni* in this paper, and fits the concept of *N. (G.) prioni* as defined by Timmermann (1961, 1965) and Clay & Moreby (1967).

As shown above, *N. (G.) prioni* was synonymised with *N. (G.) clypeatus* by Harrison (1916), followed by Thompson (1935). Thus, there are literature reports of *Naubates* specimens collected from several *Pachyptila* taxa as *N. (G.) clypeatus* (e.g., Paulian 1953, pp. 190–192; Harrison 1937, p. 31). We have not been able to examine the actual specimens reported by these authors but we believe that they are likely to be *N. (G.) prioni*, because the evidence from our extensive material examined of these two species of *Naubates* shows a clear host-louse correlation. We therefore suggest that reports of *N. (G.) clypeatus* from any *Pachyptila* host be reconsidered.

Our examination of the *Naubates* specimens held in KCEM has revealed one male *N. (G.) prioni* ex *Pachyptila turtur* from Marion Island, labelled “*Halipeurus turtur* Edwards, 1961”. This misidentification is listed in Emerson (1971, p. 360).

**Naubates (Guenterion) damma** Timmermann, 1961

(Fig. 3, 11, 18, 25, 42, 47, 53, 62, 66, 68–69)

“*Naubates pterodromi*” Thompson, 1940: 641 (not *N. pterodromi* Bedford, 1930).

*Naubates damma* Timmermann, 1961: 185, fig. 6, 9 lower (Type host: *Pterodroma leucoptera* (Gould, 1844)). Holotype ♂ in BMNH, slide no. 1956–651.


*Naubates damma*; Timmermann 1965, p. 123, fig. 60.

“*Naubates pterodromi*”Amerson & Emerson, 1971: 3, 24 (not *N. pterodromi* Bedford, 1930). Listed only.


“*Naubates pterodromi*” Emerson, 1972b: 25 (not *N. pterodromi* Bedford, 1930). Listed only.


**DIAGNOSIS:** Male as in Fig. 68. Head as in Fig. 3; a.m.s. 1 approximately twice as long as a.m.s. 2; five long temporal setae on each side; ocular seta shorter than temporal setae; clypeal signature as in Fig. 11. Thorax: prosternal plate triangular (Fig. 18); anterior pteronotal setae very short; posterolateral pteronotal setae on each side with outer lateral and innermost long, inner lateral short, the remaining three very long (Fig. 53). Abdomen: 4th visible segment shorter than adjacent segments (Fig. 68); terminalia symmetrical, with a darkly pigmented linear thickening within and parallel to the posterolateral margin of the last sternite (corresponding to 8th + 9th visible segments) (Fig. 62); genitalia as in Fig. 42.

Female as in Fig. 69. Head with a.m.s. 1 and a.m.s. 2 approximately the same length; one long and four short temporal setae on each side; ocular seta as long as the short temporal
setae; clypeal signature as in male. Thorax: prosternal plate variable (Fig. 25A–D); anterior and posterolateral pteronotal setae as in male. Abdomen: subgenital plate as in Fig. 66, and terminalia as in Fig. 47.

MATERIAL EXAMINED: Ex *Pterodroma leucoptera*: Holotype ♂, Tasman Sea, 19 Apr 1956 (BMNH).

Ex *Pterodroma leucoptera leucoptera*: 4 ♂, 3 ♀, Cabbage Tree I., New South Wales, Australia, 14–15 Feb 1977 (RLCP); 2 ♂, 3 ♀, same locality, no date (BMNH).

Ex *Pterodroma leucoptera caledonica*: 1 ♀, Otaki Beach, NZ, 25 Jun 1961 (MONZ); 1 ♀, New Caledonia, Feb 1994 (MONZ).

Ex *Pterodroma arminjoniana arminjoniana*: 2 ♀, Ilha da Trindade, South Atlantic Ocean, no date (BMNH).

Ex *Pterodroma externa*: 2 ♂, 4 ♀, Pacific Ocean, 22 Jul 1964 (KCEM; USNM); 1 ♂, 1 ♀, Pacific Ocean, 8 Aug 1964 (KCEM).

Ex *Pterodroma externa externa*: 1 ♂, 1 ♀, Isla Masatierra, Juan Fernandez Is, Chile, 26 Jan 1917 (BMNH); 2 ♀, Pacific Ocean, 24 Nov 1964 (USNM); 1 ♂, Pacific Ocean (09°07’N, 150°34’W), 9 Jun 1965 (USNM); 2 ♂, 2 ♀, Pacific Ocean (09°N, 155°W), 5 Jul 1965 (USNM); 6 ♂, 4♀, Central Pacific Ocean, 26 Nov 1965 (MONZ); 3 ♂, 2 ♀, Juan Fernandez Is, Chile, Mar 1966 (KCEM); 2 ♂, 11 ♀, Waimanalo, Oahu I., Hawaiian Is, 27 Jul 1991 (BPBM; MONZ).
Ex *Pterodroma externa cervicalis*: 1 ♂, Kermadec Is, NZ, 1895 (RLCP); 2 ♂, 2 ♀, off Isla Masatierra, Juan Fernandez Is, Chile, no date (AMNH).

Ex *Pterodroma phaeopygia*: 1 ♂, 1 ♀, Pacific Ocean, 12 Nov 1963 (USNM).

Ex *Pterodroma phaeopygia phaeopygia*: 1 ♂, 1 ♀, Kauai I., Hawaiian Is, 25 Apr 1978 (KCEM).

Ex *Pterodroma phaeopygia sandwichensis*: 8 ♂, 4 ♀, Haleakala National Park, Maui I., Hawaiian Is, 20 May 1976 (BPBM; MONZ); 2 ♂, 4 ♀, same locality, 2 Jun 1993 (MONZ).

Ex *Pterodroma hypoleuca*: 2 ♂, 2 ♀, Pacific Ocean, 12 Sep 1964 (KCEM).

Ex *Pterodroma cookii*: 2 ♀, Little Barrier I., NZ, 30 Mar 1966 (AMNZ); 1 ♂, 1 ♀, Codfish I., NZ, 16 Dec 1966 (RLCP); 1 ♂, 1 ♀, Little Barrier I., NZ, 1 Feb 1976 (RLCP); 5 ♂, 6 ♀, same locality, 25 Mar 1977 (MONZ); 5 ♂, 3 ♀, Pakiri Beach, Northland, NZ, 16 Apr 1978 (MONZ); 1 ♂, Little Barrier I., NZ, 1 Jan 1983 (MONZ); 1 ♂, 1 ♀, same locality, Apr 1988 (MONZ); 1 ♀, Devonport, Auckland, NZ, 24 Mar 1989 (MONZ); 1 ♂, at sea (47°S, 175°W), no date (AMNH).

STRAGGLER OR CONTAMINANT: Ex *Sterna bergii cristata*: 1 ♀, Port Stephens, Sydney, New South Wales, Australia, no date (BMNH).

DISCUSSION: No significant qualitative differences were found among populations of *Naubates (G.) damma* (57 ♂, 66 ♀) from nine taxa of regular hosts. There are slight differences in the dimensions of both sexes between populations from different hosts (see Table 4, which includes only those hosts from which we have examined 10 or more lice). The total number of setae in the two patches on the posterior aspect of the male subgenital plate (42 specimens examined) varies from 16 to 28 (M = 23.1) and is frequently asymmetrical (Fig. 62). Likewise, in the males there are usually three setae on each side at the posterior margin of the last abdominal segment, but a few specimens show two or four unilaterally. In the females, the shape of the prosternal plate varies from truncated to rounded posteriorly with a pointed or blunt anterior end (Fig. 25A–D). None of these variations can be correlated with any of the nine hosts, and we do not consider that they justify subdivision of the taxon.

As pointed out by Timmermann (1961, pp. 182–186), his *clypeatus*-group (now subgenus *Guenterion*) can be subdivided into two subgroups according to the following features in the male: overall size, number of long temporal setae, genitalia, and relative lengths of the 3rd, 4th, and 5th abdominal segments. We find this subgrouping also conforms to the distribution of the lice on the different host genera. Timmermann (1961) placed *N. (G.) damma* as morphologically intermediate between the *Pterodroma* parasites (*N. (G.) pterodromi* and *N. (G.) heteroproctus*) and the *Halobaena + Pachyptila* parasites (*N. (G.) clypeatus* and *N. (G.) prioni*). Our examination of *N. (G.) damma* females (not available to Timmermann) and of a greater range of males from numerous host species leads us to agree with his conclusions.

Thompson (1940, p. 641) reported “several specimens” of *N. pterodromi* Bedford from *Pterodroma externa* taken at Masatierra, Juan Fernandez Is, 26 Jan 1917. We have examined one male and one female with the same data and identify them as *N. (G.) damma*.

Amerson & Emerson (1971, p. 3) recorded *N. pterodromi* Bedford from *Pterodroma phaeopygia* “Pacific Ocean, at sea: 09°07′ N x 150°34′ W”. We have not seen any specimens with these data but we have examined 12 males and 10 females from this host species (see Material examined) and identify them as *N. (G.) damma*. We therefore believe that the *Naubates* species regularly parasitising *Pt. phaeopygia* is *N. (G.) damma* and that Amerson & Emerson’s (1971) record is a misidentification.
Naubates (Guenterion) pterodromi Bedford, 1930

(Fig. 4, 13, 15, 22, 49, 54, 57, 65)


*Naubates pterodromi* Bedford, 1930: 170 sensu Kéler 1952, p. 213, fig. 6–10 (Host: *Pterodroma incerta* (Schlegel, 1863)). First description of ♂ (Pragmatype, sensu Disney 1987, p. 251, in SAIMR, slide no. 1290/5-5, designated below).

*Naubates sp.*; Clay 1957, p. 3.


*Naubates pterodromi*; Timmermann 1965, p. 121, fig. 54, 57, 59, pl. IV, fig. 3–4.

“*Naubates sp. (probably pterodromi* Bedford)”; Emerson 1971, p. 360. Listed only.


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**Fig. 65–67** Female subgenital plates. **Fig. 65** *Naubates (G.) pterodromi*; **Fig. 66** *Naubates (G.) damma*; **Fig. 67** *Naubates (G.) ultimae.*


Diagnosis: Male head as in Fig. 4; a.m.s. 1 approximately twice as long as a.m.s.2; four long and one short temporal setae on each side; ocular seta as long as the short temporal setae; clypeal signature with the posterior lobe slightly excavated (Fig. 13). Thorax: prosternal plate triangular (Fig. 15); anterior pteronotal setae short; posterolateral pteronotal setae on each side with innermost and two lateral setae long, the remaining three very long (Fig. 54). Abdomen: 3rd and 4th visible segments each shorter than adjacent segments; terminalia slightly asymmetrical (Fig. 57); genitalia very similar to N. (G.) lessonii (Fig. 43).

Female head with a.m.s. 1 and a.m.s. 2 approximately the same length; one long, one medium length and three short temporal setae on each side; ocular seta as long as the short temporal setae; clypeal signature as in male. Thorax: prosternal plate as in Fig. 22; anterior pteronotal setae as in male; posterolateral pteronotal setae on each side with outer lateral long, inner lateral short, the remaining four very long. Abdomen: subgenital plate with conspicuous, heavily pigmented curved stripes within the lateral margins (Fig. 65); dorsal terminalia as in Fig. 49.

Material Examined: Ex Pterodroma incerta: 1 ♀, Atlantic Ocean (36°46’S, 46°29’W), 9 Nov 1912 (RLCP); 2 ♂, 1 ♀, South Atlantic Ocean, 1912–13 (CISC; USNM); 3 ♂, 3 ♀, Tristan da Cunha I., South Atlantic Ocean, 18 Jul 1949 (SAIMR; ZMHU); 1 ♂, 3 ♀, same locality, 24 Aug 1951 (BMNH); 1 ♂, 3 ♀, same locality, 18 Jul 1952 (BMNH); 5 ♂, 6 ♀, Glen Beach, Gough I., South Atlantic Ocean, 10 Apr 1956 (BMNH); 14 ♂, 40 ♀, Gough I., South Atlantic Ocean, Nov 1985 (MONZ); 1 ♀, 3 ♀, Falkland Is, South Atlantic Ocean, no date (BMNH).

Ex Pterodroma mollis mollis: 2 ♂, 4 ♀, South Atlantic Ocean, 1912–13 (CISC; USNM); 1 ♀, Inaccessible I., Tristan da Cunha Group, South Atlantic Ocean, 20 Jan 1938 (BMNH); 1 ♀, Tristan da Cunha I., South Atlantic Ocean, 3 Aug 1950 (BMNH); 3 ♀, Kerguelen Is, Indian Ocean, Feb 1951 (BMNH); 5 ♂, 4 ♀, Glen Beach, Gough I., South Atlantic Ocean, 5 Apr 1956 (BMNH); 2 ♀, Marion I., Indian Ocean, 26 Nov 1965 (KCEM); 1 ♂, 1 ♀, same locality, 10 Mar 1966 (SAIMR); 1 ♀, East I., Crozet Is, Indian Ocean, 31 Dec 1970 (BMNH); 6 ♂, 6 ♀, Golf du Morbihan, Kerguelen Is, Indian Ocean, 10 Feb 1985 (MONZ); 20 ♂, 20 ♀, Gough I., South Atlantic Ocean, Nov 1985 (MONZ); 3 ♀, Antipodes Island, NZ, 9–12 Nov 1995 (MONZ).

Ex Pterodroma mollis feae: 1 ♀, Funchal, Madeira I., 6 Aug 1891 (MONZ); 1 ♀, Bugio I., Desertas Is, 4 Jul 1987 (MFMP); 1 ♀, same locality, Oct 1989 (MONZ); 1 ♂, same locality, 2 Dec 1995 (MONZ).

Ex Pterodroma inexpectata: 4 ♂, 6 ♀, Big South Cape I., Stewart I., NZ, 23 Jan 1955 (MONZ; RLCP); 4 ♀, Waikanae, Wellington, NZ, 23 May 1955 (MONZ; RLCP); 3 ♂, 2 ♀, Snares Is, NZ, 16 Jan 1967 (MONZ; BMNH); 4 ♂, 4 ♀, same locality, 3 Feb 1967 (MONZ; BMNH); 2 ♂, 2 ♀, Big South Cape I., Stewart I., NZ, 9 Nov 1968 (BMNH; NZAC); 10 ♂, 10 ♀, same locality, 16 Feb 1969 (MONZ; NZAC; RLCP); 2 ♂, 4 ♀, Snares Is, NZ, 17 Jan 1971 (RLCP); 2 ♀, Taumutu, Canterbury, NZ, 10 Nov 1973 (RLCP); 13 ♂, 13 ♀, Snares Is, NZ, 14 Jan 1975 (MONZ; RLCP); 3 ♂, 3 ♀, Mahuta Gap, Northland, NZ, 13 Dec 1975 (MONZ); 4 ♂, 5 ♀, Snares Is, NZ, 21 Dec 1976 (MONZ); 1 ♂, 1 ♀, N Daption Rock, Snares Is, NZ, 8 Feb 1977 (MONZ); 4 ♂, 4 ♀, Muriwai Beach, Auckland, NZ, 9 Dec 1978 (MONZ); 1 ♂, 3 ♀, same locality, 7 Jan 1979 (MONZ); 1 ♀, Codfish I., Stewart Is, NZ, 6 Dec 1981
Fig. 68–69  *Naubates (G.) damma* (ex *Pterodroma cookii*). **Fig. 68** male; **Fig. 69** female.

(RLCP); 18 ♂, 18 ♀, Muriwai Beach, Auckland, NZ, 9 Jan 1983 (MONZ; AMNZ); 3 ♂, 4 ♀, Burnie, Tasmania, Australia, 29 Nov 1983 (MONZ; QVTA); 12 ♂, 12 ♀, Codfish I., Stewart I., NZ, 18 Mar 1984 (MONZ); 8 ♂, 16 ♀, Snares Is, NZ, Feb 1986 (MONZ; AMNZ); 1 ♀, Kermadec Is, NZ, no date (BMNH); 2 ♂, 3 ♀, New Zealand, no date (RLCP; BMNH); 2 ♂, 1 ♀, no locality, no date (BMNH).

**STRAGGLERS:** Ex *Pachyptila crassirostris crassirostris*: 2 ♂ 2 ♀, Snares Is, NZ, 20 Dec 1976 (RLCP).
DISCUSSION: No significant differences were found among populations of *Naubates* (G.) *pterodromi* (158 ♂, 228 ♀) from the four regular hosts listed.

Attention is drawn to the fact that the slight asymmetry of the last abdominal segment of the male may be obscured in some specimens if the lateroterminal projections are not clearly extended (see couplet 4 in key). This asymmetry is clearly shown in Kéler’s (1952) fig. 7, 8 of the first male described as *N. (G.) pterodromi*, taken from *Pterodroma incerta*; Timmermann’s (1961) fig. 9 middle fails to illustrate this feature for a male from the same host, perhaps owing to inadequate slide preparation. We have examined the male illustrated by Timmermann (1961, p. 191, fig. d, BMNH slide 1956-600, no. 68) and find the asymmetry is present.

As summarised by Pilgrim & Palma (1982, p. 29–30), *Naubates* females from several *Pterodroma* hosts are morphologically indistinguishable; thus the concept of *N. (G.) pterodromi* established by Bedford (1930) on females only (from *Pt. macroptera*), was incomplete until Kéler (1952) described the male (from *Pt. incerta*). Subsequent collections show that males from *Pt. macroptera* fit the concept of *N. pterodromi* sensu Kéler, 1952; strict application of the priority rules would lead to placing *N. (G.) heteroproctus* Harrison, 1937; to necessitating a new name for the *Naubates* population from *Pterodroma incerta*. This solution has never been adopted, more recent authors having followed the concept of *N. pterodromi* sensu Kéler, 1952, although some have continued to apply the name *N. pterodromi* to males, from two hosts, which we recognise as clearly distinct, e.g., Clay & Moreby (1970, p. 218), Emerson (1971, p. 360), Crafford et al. (1986, p. 78). These latter papers are faunistic lists without supporting evidence to justify the taxonomy adopted; however, Timmermann’s revision (1961, 1965) embodied the use of *N.

<table>
<thead>
<tr>
<th>Table 4</th>
<th>Measurements (in mm) of <em>Naubates</em> (Guenterion) damma (means; ranges in parentheses). Head width at temples. Head width at temples.</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Host species</td>
<td>ex <em>Pterodroma teres</em></td>
<td>ex <em>Pterodroma cookii</em></td>
<td>ex <em>Pterodroma externa</em></td>
</tr>
<tr>
<td>Head width</td>
<td>0.460 (0.45–0.47)</td>
<td>0.501 (0.49–0.52)</td>
<td>0.514 (0.49–0.53)</td>
</tr>
<tr>
<td>Head length</td>
<td>0.522 (0.50–0.54)</td>
<td>0.501 (0.48–0.52)</td>
<td>0.563 (0.55–0.58)</td>
</tr>
<tr>
<td>Head width at temples</td>
<td>0.481 (0.46–0.49)</td>
<td>0.501 (0.48–0.52)</td>
<td>0.514 (0.49–0.53)</td>
</tr>
<tr>
<td>Head length at temples</td>
<td>0.501 (0.48–0.52)</td>
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</tr>
</tbody>
</table>
Palma & Pilgrim—Revision of genus *Naubates*

**Fig. 70–71** *Naubates* (G.) *lessonii*. **Fig. 70** holotype male; **Fig. 71** allotype female.

*p. terodromi* sensu Kéler for the population from *Pt. incerta* (together with other hosts) and *N. heteroproctus* for the males only from *Pt. macroptera*, but Timmermann (1961, p. 183–185) failed to associate the females from the latter host with the males, and designated them as *N. pterodromi*.

Since females of *Naubates* (G.) *pterodromi* and *N. (G.) heteroproctus* are at present indistinguishable, and for the sake of preserving a stable nomenclature based on males, we
have elected to use *N. (G.) pterodromi* Bedford sensu Kéler, 1952, for lice from the four hosts listed in Material examined above, and to restrict the concept of *N. (G.) heteroproctus* Harrison, 1937 to the *Naubates* population from *Pt. macroptera* only (Palma & Pilgrim 1977, p. 290; Horning et al. 1980, p. 6; Pilgrim & Palma 1982, p. 8; Palma & Barker 1996, p. 192). We regard females taken in association with males as being conspecific with them; females found without males are listed according to the host-lice associations now established.

It follows from the foregoing that a problem arises as to the status of the three female types of *N. (G.) pterodromi*: holotype slide in SAMS, two paratype slides in OCSA; all from *Pterodroma macroptera*, Cape Town, South Africa, 1929. In accordance with our decision, above, we place these specimens together with others from the same host species as *N. (G.) heteroproctus*. Further, the concept of *N. (G.) pterodromi* Bedford, sensu Kéler, 1952, being different from that of *N. (G.) pterodromi* Bedford, 1930, requires that one of the male specimens described by Kéler should become a name-bearing type; for this, we find that the term “pragmatype” (Disney 1987, p. 251) is appropriate and we so designate the male from *Pterodroma incerta*, Tristan da Cunha I., South Atlantic Ocean, 18 Jul 1949 (Slide no. 1290/5-5, in SAIMR).

**Naubates (Guenterion) lessonii** new species

(Fig. 43, 58, 70–71)

Type host: *Pterodroma lessonii* (Garnot, 1826). Holotype ♂ in MONZ.


*Naubates pterodromi* sensu lato; Green & Palma 1991, p. 15. Listed only.

*Naubates pterodromi*; Palma & Barker 1996, p. 193 (in part *N. (G.) lessonii*; in part *N. (G.) pterodromi*).

ETYMOLOGY: The name *lessonii* is a noun in apposition derived from the name of the host.

DIAGNOSIS: Male as in Fig. 70, very similar to *Naubates (G.) pterodromi*, but the terminalia are more asymmetrical (Fig. 58), with the left lateral terminal projection less pointed and the median terminal lobe longer. Genitalia as in Fig. 43.

Female as in Fig. 71, not distinguishable from *N. (G.) pterodromi*.

MATERIAL EXAMINED: Ex *Pterodroma lessonii*: Holotype ♂, allotype ♀ and paratypes 4 ♂, 7 ♀, Waikanae Beach, Wellington, NZ, 30 Sep 1984 (MONZ). Other paratypes: 1 ♀, Auckland Is, NZ, 3 Nov 1943 (RLCP); 4 ♀, Macquarie I., Australia, 25 Sep 1956 (ANIC; BMNH); 3 ♀, Pukerua Bay, Wellington, NZ, 6 Nov 1957 (MONZ); 2 ♀, Macquarie I., Australia, 26 Feb 1968 (ANIC); 1 ♀, Perth, Western Australia, Jun 1970 (BMNH); 5 ♂, 2 ♀, 9 miles E of Conara, Tasmania, Australia, 15 Jun 1970 (BMNH; QVTA); 4 ♂, 16 ♀, Pukerua Bay, Wellington, NZ, 26 Jun 1974 (MONZ); 2 ♀, Blaketown Beach, Westland, NZ, 27 Jun 1974 (RLCP); 2 ♀, Kurnell Beach, New South Wales, Australia, 22 Jun 1975 (AMSA); 2 ♀, Petone
Beach, Wellington, NZ, Jun 1978 (MONZ); 1 ♀, Waitarere Beach, Horowhenua, NZ, 22 Sep 1978 (MONZ); 5♂, 9 ♀, Hokio Beach, Horowhenua, NZ, 15 Oct 1978 (MONZ); 3♂, 3 ♀, Muriwai Beach, Auckland, NZ, 6 Apr 1980 (AMNZ; MONZ); 4♂, 8 ♀, Titahi Bay, Wellington, NZ, 11 Sep 1980 (MONZ); 1♂, 2♀, Tawa, Wellington, NZ, 28 Jun 1983 (MONZ); 1♂, 3♀, Waikanae Beach, Wellington, NZ, Oct 1984 (MONZ); 4♂, 6♀, Collaroy Beach, New South Wales, Australia, 8 Nov 1984 (MONZ; AMSA); 1♂, Carlton Beach, SE Tasmania, Australia, 13 Nov 1984 (TMTA); 1♂, 7♀, Pukekura Park, New Plymouth, NZ, 6 Jun 1985 (MONZ); 4♂, 4♀, Peka Peka Beach, Wellington, NZ, 23 Sep 1995 (MONZ); 2♂, 6♀, New Zealand, no date (RLCP).

CONTAMINANTS: Ex Diomedea exulans: 1♂, 1♀, Macquarie I., Australia, 27 Sep 1956 (ANIC).

DISCUSSION: Like other Naubates species found on a single host species, Naubates (G.) lessonii is morphologically very uniform. In some males, the lateral terminal projections and the median terminal lobe of the last abdominal segment appear to be different from those shown in Fig. 58 because these features are thin and liable to bend during the mounting process.

In addition to the diagnostic characters, males of N. (G.) lessonii are longer (see Table 1) and more robust than those of N. (G.) pterodromi. We have examined 50♂ and 101♀ from 23 host specimens taken from within the Australasian region and find that, although the females are not separable from those of N. (G.) pterodromi, the males are distinct. Timmermann (1961, p. 183) considered that, among Naubates males from various species of Pterodroma, some differences, particularly in the last abdominal segment, could indicate subspecific division of N. (G.) pterodromi populations. We have taken the approach shared by various colleagues that these louse populations should be regarded as full species.

Although Pterodroma lessonii is the type host of Naubates (G.) heteroproctus we show, under the discussion of the latter species, that this bird is not its regular host. The specimen(s) listed by Watson (1967, p. 72) as N. heteroproctus from Pt. lessonii “ANARE, 1949” have not been found in any collection searched, and we are unable to comment on the true taxonomic status of that sample.

**Naubates (Guentherion) heteroproctus** Harrison, 1937

(Fig. 55, 59)

*Naubates heteroproctus* Harrison, 1937: 30, pl. II, fig. 4–7 (Type host: Pterodroma lessonii (Garnot, 1826); in error). Syntypes ♀ presumed lost.


*Naubates heteroproctus*; Timmermann 1961, p. 184, fig. 9 upper.


*Naubates heteroproctus*; Timmermann 1965, p. 122, fig. 63b.


DIAGNOSIS: Male similar to N. (G.) pterodromi but with terminalia grossly asymmetrical (Fig. 59). Sclerite of aedeagal sac as in Fig. 55.

Female as for N. (G.) pterodromi.

MATERIAL EXAMINED: Ex Pterodroma macroptera: 1 ♂, 34°S, 180°W, Nov 1925 (BMNH); 1 ♀, Capetown, South Africa, 1929 (BMNH); 2 ♀, SW Tristan da Cunha I., South Atlantic Ocean, 4 Nov 1951 (BMNH); 1 ♀, Marion I., Indian Ocean, 16 Nov 1952 (ZMHU); 2 ♀, Glen Beach, Gough I., South Atlantic Ocean, 3 May 1956 (BMNH); 1 ♂, 3 ♀, Marion I., Indian Ocean, 1 Nov 1966 (KCEM; SAIMR); 2 ♂, 2 ♀, Flinders I., Tasmania, Australia, 13 Aug 1968 (BMNH); 3 ♂, 3 ♀, Marshall Bay, Flinders I., Tasmania, Australia, 13 Aug 1968 (ANIC; BMNH; QVTA); 1 ♂, 2 ♀, Perth, Western Australia, 1970 (BMNH); 2 ♂, Fitzmaurice Bay, King I., Tasmania, Australia, 24 Aug 1984 (QVTA); 2 ♂, 1 ♀, King I., Tasmania, Australia, 25 Aug 1984 (QVTA); 2 ♂, 2 ♀, Badger Head, N Tasmania, Australia, 25 Aug 1984 (MONZ; QVTA); 1 ♂, 1 ♀, same locality, 2 Sep 1984 (MONZ).

Ex Pterodroma macroptera gouldii: 1 ♂, 2 ♀, Tauranga I., NZ, 10 Jul 1929 (RLCP); 1 ♂, 2 ♀, Bay of Plenty, NZ, Jul 1929 (RLCP); 2 ♀, Auckland, NZ, Apr 1933 (CMNZ); 1 ♀, Little Barrier I., NZ, May 1953 (AMNZ); 1 ♂, 1 ♀, Wainuiomata, Wellington, NZ, 11 Apr 1968 (MONZ); 1 ♂, 1 ♀, Great I., Three Kings Is, NZ, 1 Nov 1970 (NZAC); 1 ♂, Taumarunui, NZ, 14 May 1973 (MONZ); 3 ♀, Whakatane, NZ, 19 Dec 1973 (MONZ); 6 ♂, 16 ♀, Whangamata Is, NZ, 22 Jun 1975 (RLCP); 2 ♂, 8 ♀, Muriwai, Auckland, NZ, 8 Aug 1976 (AMNZ; MONZ); 1 ♂, Oreti Beach, Southland, NZ, 7 May 1978 (MONZ); 2 ♀, Dargaville Beach, Northland, NZ, 24 Feb 1979 (MONZ); 4 ♂, 4 ♀, Petone Beach, Wellington, NZ, 31 Mar 1979 (MONZ); 1 ♂, 2 ♀, same locality, 4 Sep 1979 (MONZ); 4 ♂, 6 ♀, Palliser Spit, NZ, 5 Sep 1979 (MONZ); 4 ♂, 8 ♀, Whale I., Bay of Plenty, NZ, 10 Jul 1980 (AMNZ; MONZ); 1 ♀, North Beach, Christchurch, NZ, 17 Jan 1981 (RLCP); 3 ♂, 3 ♀, Kauwhaia I., Auckland, NZ, Apr 1990 (MONZ); 2 ♂, 2 ♀, same locality, 16 May 1990 (MONZ); 4 ♂, 4 ♀, Saddle I., Te Hapua, NZ, 24 Aug 1990 (MONZ); 1 ♂, 3 ♀, Mt Manganui, Bay of Plenty, NZ, 11 Aug 1991 (MONZ); 4 ♂, 4 ♀, Tiritiri Matangi I., Auckland, NZ, 6 Jul 1995 (MONZ); 1 ♀ Hauraki Gulf, NZ, no date (BMNH).

STRAGGLERS AND CONTAMINANTS: Ex Pachyptila turtur: 1 ♂, Miramar, Wellington, NZ, 11 Apr 1968 (MONZ).

Ex Procellaria aequinoctialis aequinoctialis: 1 ♂, Cape Hen, South Africa, 1901 (BMNH).

Ex Pterodroma leucoptera brevipes: 1 ♂, 1 ♀, Fiji, no date (BMNH).

DISCUSSION: The specimens examined from Pterodroma macroptera (56 ♂, 96 ♀) show that Naubates (G.) heteroproctus is a uniform species, as in the case with other Naubates species from a single host species. From the material examined (26 samples containing males) it is clear that Pterodroma macroptera is the only regular host of this species. Despite the fact that N. (G.) heteroproctus was described by Harrison (1937) from specimens purportedly taken from Pterodroma lessonii (as Aestrelata lessonii), we believe that this was the result of an incorrect louse-host association; this conclusion is supported by the presence on Pt. lessonii of a different species, Naubates (G.) lessonii (see above). Although Harrison (1937, p. 30) listed only “One female and one young...” specimens as his material examined, his diagnosis shows clearly that he had a male in front of him and this is confirmed by his pl. II, fig. 4, 6 and 7. Harrison’s record is repeated in Watson (1967, p. 72) but none of this type material has since been found despite extensive search.

Confusion arising from Bedford’s (1930) incomplete concept of N. (G.) pterodromi (see under that species) led Emerson (1971, p. 360), followed by Crafford et al. (1986, p. 78), to use this name for specimens taken at Marion Island (see Material examined); we have
examined one male and three females from that collection and recognise them as *N. (G.) heteroproctus*. We have also examined the male and female reported by Timmermann (1961, p. 184) from *Pt. leucoptera brevipes* and confirm his identification; however, since two other subspecies of *Pt. leucoptera* are regular hosts of *N. (G.) damma* (see above), we believe Timmermann’s specimens represent an instance of contamination or straggling. We have not seen the specimen(s) reported by Paulian (1953, p. 178) from *Pt. brevirostris* but since this
bird is not a regular host for any species of Naubates (Palma & Pilgrim 1983), we believe this to be an incorrect louse-host association.

**Naubates (Guenterion) ultimae new species**

(Fig. 12, 14, 21, 44, 48, 50, 56, 60–61, 67, 72–73)

Type host: Pterodroma ultima Murphy, 1949. Holotype ♂ in MONZ.

ETYMOLOGY: The name *ultimae* is a noun in apposition derived from the name of the host.

DIAGNOSIS: Male as in Fig. 72. Head with a.m.s. 1 approximately twice as long as a.m.s. 2; three long and two short temporal setae on each side; ocular seta about half the length of the long temporal setae; clypeal signature with the posterior lobe slightly excavated (Fig. 12). Thorax: prosternal plate triangular (Fig. 14); anterior pteronotal setae short; posterolateral pteronotal setae on each side with the two lateral and the innermost equally long, remaining three very long (as in Fig. 54). Abdomen: 4th visible segment shorter than adjacent segments (Fig. 72); terminalia grossly asymmetrical (Fig. 60–61); genitalia as in Fig. 44; sclerite of aedeagal sac as in Fig. 56.

Female as in Fig. 73. Head with a.m.s. 1 and a.m.s. 2 approximately the same length, one long, one medium length and three short temporal setae on each side; ocular seta as long as the short temporal setae; clypeal signature as in male. Thorax: prosternal plate as in Fig. 21; anterior pteronotal setae as in male; posterolateral pteronotal setae on each side with the two lateral setae shortest, the innermost of medium length, the remaining three very long. Abdomen: ventral terminalia as in Fig. 48; subgenital plate as in Fig. 67; dorsal terminalia as in Fig. 50, alveoli of tergal posterolateral setae of 8th visible segment each surrounded by a pigmented area.
MATERIAL EXAMINED: Ex Pterodroma ultima: Holotype ♂, allotype ♀ and paratypes 3 ♂, 4 ♀, Oeno I., Pitcairn Group, South Pacific Ocean, 10 Oct 1956 (MONZ). Other paratypes: 2 ♂, 1 ♀, Bass Rock, Tubuai Is, French Polynesia, 17 Feb 1922 (MONZ); 1 ♀, Ducie I., Pitcairn Group, South Pacific Ocean, 25 Mar 1991 (MONZ); 1 ♂, Oeno I., Pitcairn Group, South Pacific Ocean, 30 May 1991 (MONZ); 28 ♂, 27 ♀, Henderson I., Pitcairn Group, South Pacific Ocean, 22 Jul 1991 (MONZ; BMNH; BPBM; USNM); 11 ♂, 12 ♀, same locality, 23 Jul 1991 (MONZ); 4 ♂, 15 ♀, Ducie I., Pitcairn Group, South Pacific Ocean, 1 Aug 1991 (MONZ); 2 ♂, 2 ♀, Oeno I., Pitcairn Group, South Pacific Ocean, no date (AMNH).

DISCUSSION: No significant morphological differences were found among the 52 males and 63 females taken from four distinct host populations. Males show minor variations in the detailed outline of the strongly sclerotised portions of the last abdominal segment and in the total number of setae (range: from 28 to 34) on the posterior area of the subgenital plate. In some females, the alveoli of the anterolateral setae of the 8th visible abdominal segment are also surrounded by pigmented areas. The length of the anterior median setae of the female subgenital plate is variable (Fig. 48, 67).

Naubates (G.) ultimae is morphologically closest to N. (G.) pterodromi, N. (G.) lessonii, and N. (G.) heteroproctus. However, males of N. (G.) ultimae are easily separated from males of those species by the different shapes of the terminalia (compare Fig. 60 with Fig. 57–59) and the genitalia, including the aedeagal sac + sclerite (compare Fig. 44, 56 with Fig. 43, 55 respectively). Females of N. (G.) ultimae are also readily differentiated from those of N. (G.) pterodromi, N. (G.) lessonii and N. (G.) heteroproctus by characters of the terminalia (compare Fig. 50 with Fig. 49) and of the subgenital plate (compare Fig. 67 with Fig. 65).

MORPHOLOGICAL RELATIONSHIPS OF NAUBATES SPECIES
WITH REMARKS ON THEIR HOST DISTRIBUTION AND CURRENT CLASSIFICATIONS OF THE PROCELLARIDAE

Based on the morphological characters described and figured in this paper, we propose a phylogenetic tree (Fig. 74) for the 10 species we have recognised as valid within the genus Naubates. Although there are no quantitative analyses and the absolute lengths of the branches are arbitrary, they are drawn proportionately to the levels of similarity (or distinctiveness) we have observed among the 10 species. We are confident about the main basal clusters which we now recognise as two different subgenera, i.e., Naubates sensu stricto and Guenterion (see above). Also, within Naubates s.s., we feel confident that N. (N.) fuliginosus has diverged for a considerable length of time from the species pair N. (N.) harrisoni—N. (N.) thieli, which are morphologically close to one another.

Within the subgenus Guenterion, the species pair N. (G.) clypeatus—N. (G.) prioni is also morphologically close but well separated from the N. (G.) ultimae—N. (G.) heteroproctus — N. (G.) pterodromi—N. (G.) lessonii cluster. We are less confident about the position of N. (G.) damma; as discussed earlier in this paper, this species is morphologically intermediate between the two well-defined clusters of species within Guenterion. We have chosen to place N. (G.) damma as a sister species to the N. (G.) ultimae—N. (G.) heteroproctus—N. (G.) pterodromi—N. (G.) lessonii cluster mainly because of its host associations, the lice being all parasites of several Pterodroma species (see Table 5).

A tree based on Kuroda’s (1983) classification of the five genera of petrels which include all the host species for the 10 Naubates species, has been included in Fig. 74. The host switch of Naubates thieli becomes apparent when comparing the two trees (see above under this species). All species of Naubates are regular parasites of birds of the family Procellariidae only. With the exception of Naubates (N.) thieli on Pterodroma solandri, the taxonomy of
the two subgenera of Naubates parallels that of the host birds (Kuroda 1954, 1983; Table 5; Fig. 74): Naubates (Guenterion) is found only on Pterodroma, Halobaena, and Pachyptila (subfamily Fulmarinae), while Naubates (Naubates) is found exclusively on Procellaria and Puffinus (subfamily Procellariinae).

In the morphologically more uniform subgenus Naubates there is good correlation between two species of lice and two genera of hosts: N. (N.) fuliginosus is found only on species of Procellaria, and N. (N.) harrisoni only on species of Puffinus. Species of the subgenus Guenterion are less uniform morphologically. Five species of Guenterion are confined to hosts of the tribe Pterodromini, being found on many species of Pterodroma. The remaining two species of Guenterion are morphologically very similar and stand apart from the rest; they are confined to hosts of the tribe Pachyptilini: N. (G.) clypeatus is host-specific to Halobaena; N. (G.) prioni is found exclusively on species of Pachyptila.

Thus, there is good correlation between the classification of the Naubates taxa and that of the hosts down to the genus level. However, on the basis of the Naubates species distribution, there does not appear to be any support either to the “superspecies” groups of Pterodroma suggested by Jouanin & Mougin (1979), or to the grouping of Pterodroma species into subgenera as proposed by Imber (1985). No specimens of Naubates have been seen as regular parasites from any species/subspecies of the Procellariidae listed by Jouanin & Mougin (1979) which are not included in Table 5, nor are any reported in the literature examined.

We offer this basic analysis and proposed phylogenetic tree to encourage further research on the evolutionary relationships of Naubates taxa based on molecular data or other techniques.

Table 5 List of hosts and their Naubates parasites. Hosts are listed sequentially following Jouanin & Mougin (1979), with one addition*. Suprageneric classification is after Kuroda (1954, 1983). Kuroda’s (1983) designation of Subfamily Procellariinae as Puffiniae is incorrect.

<table>
<thead>
<tr>
<th>Family PROCELLARIIDAE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subfamily FULMARINAe</td>
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<tr>
<td>Tribe Pterodromini</td>
</tr>
<tr>
<td>Genus Pterodroma</td>
</tr>
<tr>
<td>Pt. macroptera gouldi (Hutton, 1869) Naubates (Guenterion) heteroproctus</td>
</tr>
<tr>
<td>Pt. lessonii (Garnot, 1826) Naubates (Guenterion) lessonii</td>
</tr>
<tr>
<td>Pt. incerta (Schlegel, 1863) Naubates (Guenterion) pterodromi</td>
</tr>
<tr>
<td>Pt. solandri (Gould, 1844) Naubates (Naubates) thieli</td>
</tr>
<tr>
<td>Pt. arminjoniana arminjoniana (Giglioli &amp; Salvadori, 1869) Naubates (Guenterion) damma</td>
</tr>
<tr>
<td>Pt. ultima Murphy, 1949 Naubates (Guenterion) ultimae</td>
</tr>
<tr>
<td>Pt. mollis mollis (Gould, 1844) Naubates (Guenterion) pterodromi</td>
</tr>
<tr>
<td>Pt. mollis feae (Salvadori, 1899) Naubates (Guenterion) pterodromi</td>
</tr>
<tr>
<td>Pt. inexpectata (Forster, 1844) Naubates (Guenterion) pterodromi</td>
</tr>
<tr>
<td>Pt. externa externa (Salvin, 1875) Naubates (Guenterion) damma</td>
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<td>Pt. externa cervicalis (Salvin, 1891) Naubates (Guenterion) damma</td>
</tr>
<tr>
<td>Pt. phaeopygia phaeopygia (Salvin, 1876) Naubates (Guenterion) damma</td>
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<td>Pt. phaeopygia sandwichensis (Ridgway, 1884) Naubates (Guenterion) damma</td>
</tr>
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<td>Pt. hypoleuca (Salvin, 1888) Naubates (Guenterion) damma</td>
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<tr>
<td>Pt. cookii (Gray, 1843) Naubates (Guenterion) damma</td>
</tr>
<tr>
<td>Pt. leucoptera leucoptera (Gould, 1844) Naubates (Guenterion) damma</td>
</tr>
<tr>
<td>*Pt. leucoptera caledonica Imber &amp; Jenkins, 1981 Naubates (Guenterion) damma</td>
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</table>

Continued on next page
Table 5  Continued

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Genus</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pachyptiliini</td>
<td>Naubates</td>
<td><em>Naubates</em> (Guenterion) clypeatus</td>
</tr>
</tbody>
</table>

**Genus Halobaena**

*H. caerulea* (Gmelin, 1789) ...................................................  *Naubates* (Guenterion) prioni

**Genus Pachyptila**

*P. assimilis* baroli (Bonaparte, 1857) ...................................................  *Naubates* (Guenterion) prioni
*P. lherminieri* boydi Lesson, 1839 ...............................................  *Naubates* (Guenterion) prioni
*P. lherminieri* lherminieri Mathews, 1912 ...................................................  *Naubates* (Guenterion) prioni
*P. huttoni* ...........................................................................  *Naubates* (Guenterion) prioni
*P. puffinus* puffinus (Brünnich, 1764) ...................................................  *Naubates* (Guenterion) prioni
*P. puffinus* opisthomelas Coues, 1864 ...................................................  *Naubates* (Guenterion) prioni
*P. belcheri* Mathews, 1912 ..................................................................  *Naubates* (Guenterion) prioni
*P. turtur* Kuhl, 1820 ...........................................................................  *Naubates* (Guenterion) prioni
*P. crassirostris* crassirostris (Kuhl, 1820) ...................................................  *Naubates* (Guenterion) prioni
*P. turtur* (Mathews, 1912) ..................................................................  *Naubates* (Guenterion) prioni
*P. turtur* Fleming, 1939 .................................................................  *Naubates* (Guenterion) prioni
*P. turtur* (Mathews, 1912) ..................................................................  *Naubates* (Guenterion) prioni
*P. crassirostris* pyramidalis Fleming, 1939 ...................................................  *Naubates* (Guenterion) prioni
*P. crassirostris* eatoni (Mathews, 1912) ...................................................  *Naubates* (Guenterion) prioni

**Genus Procellaria**

*P. aequinoctialis* aequinoctialis Linnaeus, 1758 ...................................................  *Naubates* (Naubates) fuliginosus
*P. westlandica* Falla, 1946 ................................................................  *Naubates* (Naubates) fuliginosus
*P. parkinsoni* Gray, 1862 ....................................................................  *Naubates* (Naubates) fuliginosus
*P. cinerea* Gmelin, 1789 ....................................................................  *Naubates* (Naubates) fuliginosus

**Genus Puffinus**

*P. pacificus* (Gmelin, 1789) ...................................................  *Naubates* (Naubates) harrisoni
*P. bulleri* Salvini, 1888 ..................................................................  *Naubates* (Naubates) harrisoni
*P. carneipes* Gould, 1844 ..................................................................  *Naubates* (Naubates) harrisoni
*P. creatopus* Coues, 1864 ..................................................................  *Naubates* (Naubates) harrisoni
*P. gravis* O’Reilly, 1818 ................................................................  *Naubates* (Naubates) harrisoni
*P. tenuirostris* (Temminck, 1835) ...................................................  *Naubates* (Naubates) harrisoni
*P. nativitatis* Streets, 1877 ................................................................  *Naubates* (Naubates) harrisoni
*P. puffinus* puffinus (Brünnich, 1764) ...................................................  *Naubates* (Naubates) harrisoni
*P. puffinus* opisthomelas Coues, 1864 ...................................................  *Naubates* (Naubates) harrisoni
*P. huttoni* Mathews, 1912 ................................................................  *Naubates* (Naubates) harrisoni
*P. herminieri* herminieri Lesson, 1839 ...................................................  *Naubates* (Naubates) harrisoni
*P. herminieri* boydi Mathews, 1912 ...................................................  *Naubates* (Naubates) harrisoni
*P. assimilis* baroli (Bonaparte, 1857) ...................................................  *Naubates* (Naubates) harrisoni
*P. assimilis* (?) tunneyi Mathews, 1912 ...................................................  *Naubates* (Naubates) harrisoni

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