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A penguin-chewing louse (Insecta: Phthiraptera) phylogeny derived from morphology

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Abstract. Penguins are parasitised by 15 species of lice in the genera *Austrogoniodes* and *Nesiotinus* and present an opportunity to analyse phylogenetic relationships of two complete genera of chewing lice parasitising a monophyletic group of hosts. Taxonomy of penguin lice has been revised several times, including the erection of the genus *Cesareus* to contain some of the penguin-chewing louse species. Additionally, other groups of species within *Austrogoniodes* have been proposed. We constructed a phylogeny for all the chewing lice parasitising penguins from 46 parsimony-informative morphological characters and found support for two groups within *Austrogoniodes*, but little support for the *Cesareus* genus. *Austrogoniodes metoecus*, the only *Austrogoniodes* species parasitising a bird other than a penguin, was basal in the phylogeny, which suggests that if *A. metoecus* did originate from a louse species parasitising penguins, the host-switching event was unlikely to have been recent. A superficial comparison of louse and penguin phylogenies identified some potential instances of co-speciation. However, a full analysis of co-phylogenetic relationships between penguins and their lice awaits the publication of a better-resolved penguin phylogeny.

Additional keywords: *Austrogoniodes*, *Cesareus*, cladistic, co-evolution, co-phylogeny, lice, *Nesiotinus*, Sphenisciformes.

Introduction

Penguins, order Sphenisciformes, are parasitised by 15 species of chewing lice (Phthiraptera: Philopteridae) from two genera, *Austrogoniodes* Harrison, 1915 (14 species) and *Nesiotinus* Kellogg, 1903 (one species) (Clay 1967; Pilgrim and Palma 1982; Palma 1999; Banks and Palma 2003). The penguin lice present a relatively rare opportunity to analyse the phylogenetic relationships between all the species of two genera of chewing lice parasitising a distinctive monophyletic host order.

Penguin louse systematics has been revised several times. The first penguin-chewing louse described was *Goniodes brevipes* (Giebel, 1876) parasitising king penguins, *Aptenodytes patagonicus* J. F. Miller, 1778. Subsequently, species of penguin-chewing lice, with the exception of *Nesiotinus demersus* Kellogg, 1903, were classified in *Goniocotes* Burmeister, 1838 until Harrison (1915) erected *Austrogoniodes* to contain all species of penguin lice except *N. demersus*. Harrison (1937) noted in the species descriptions of *A. hamiltoni* Harrison, 1937 and *A. mawsoni*

Harrison, 1937 that the two species differed morphologically from the rest of the *Austrogoniodes* species and von K  ler (1952) later erected the genus *Cesareus* to contain these two species along with *A. waterstoni* (Cummings, 1914) and the type species for the genus, *C. concii* (von K  ler, 1952). Hopkins and Clay (1953) considered all *Cesareus* belonged in *Austrogoniodes*, but von K  ler (1954) described *C. bicornutus* (von K  ler 1954) parasitising *Eudyptes chrysophilus* (Brandt, 1837) and transferred *A. macquariensis* Harrison, 1937 to *Cesareus*. Although *Cesareus* is still used occasionally, for example Mey *et al.* (2002), most authors consider all *Cesareus* species to belong in *Austrogoniodes*.

The genus *Austrogoniodes* has also been subdivided informally. Clay (1967) noted that there were two morphologically distinct groups within *Austrogoniodes*, with *A. bicornutus*, *A. concii*, *A. hamiltoni*, *A. keleri* Clay, 1967 and *A. macquariensis* comprising one group and *A. bifasciatus* (Piaget, 1885), *A. cristati* von K  ler, 1952 and *A. demersus* (von K  ler, 1952) in a second group.

Austrogoniodes metoecus Clay, 1971 is unusual within the genus because it parasitises the musk duck, *Biziura*

lobata (Shaw, 1796) of Australia. It is the only species of *Austrogoniodes* that parasitises a species outside the penguin order and it has been speculated that the establishment of *A. metoecus* on the musk duck has been a relatively recent switch to a new host species (Clay 1971). If the switch has been recent, the present geographical distribution of the musk duck suggests blue penguins, *Eudyptula minor* (J. R. Forster, 1781), as the most likely source of the musk duck louse.

Other studies have used morphological characters to examine relationships within and between chewing louse genera to support taxonomic classifications. For example, a study using 58 morphological characters of 122 species of *Geomydoecus* Ewing, 1929 and *Thomomydoecus* Price & Emerson, 1972 parasitising pocket gophers found a moderately resolved phylogeny that supported the existing taxonomy (Page *et al.* 1995). Another study that used morphological characters to investigate relationships within *Dennyus* Neumann, 1906 lice parasitising swiftlets found robust support for earlier subdivisions within *Dennyus* (Clayton *et al.* 1996). Cladistic analysis of morphological characters has also been used to examine relationships between phthirapteran genera and found well-resolved phylogenies that broadly agreed with previous classification schemes (Smith 2000, 2001).

Although the penguin-chewing lice are well described and a taxonomic key has been produced and updated (Clay 1967, 1971; Banks and Palma 2003), phylogenetic relationships within the penguin lice have not been analysed quantitatively. This study presents a cladistic analysis of louse morphological characters to investigate phylogenetic relationships within *Austrogoniodes*, including whether a cladistic analysis would support *Cesareus* or the informal groups of Clay (1967), and examines the origin of *A. metoecus* parasitising the musk duck. We superficially compare the louse phylogeny to a penguin phylogeny, but a more detailed comparison awaits a better-resolved penguin phylogeny.

Materials and methods

Morphological characters (Table 1) were identified, using a compound microscope (Alphabot 2; Nikon, Tokyo, Japan), from 118 male and 115 female slide-mounted specimens of *Austrogoniodes* and *Nesiotinus* borrowed from various museum collections (Appendix 1). The specimens included both sexes except for *A. keleri*, because no females of *A. keleri* have been identified. A single female of *A. brevipes* was examined because it was the only specimen known and no males have been collected (R. Palma, personal communication).

It should be noted that we obtained several specimens of *N. demersus* from king penguins on Macquarie Island (part of the Australian sub-antarctic region) and there are also several individuals of *N. demersus* that were collected from king penguins on Macquarie Island in the collection of the Museum of New Zealand. The suggestion in Harrison (1937) that *N. demersus* may not occur in the Antarctic or Australian sub-antarctic regions because the Australasian Antarctic Expedition 1911–1912 failed to collect *N. demersus* from king penguins is not correct.

Louse taxonomy followed Hopkins and Clay (1953), Clay (1967) and Banks and Palma (2003). We considered the louse species *A. struthus* Harrison, 1915 as *nom. dub.* following the discussion in Clay (1967). Morphological terminology follows Clay (1967) and many of the morphological characters (Table 1) are illustrated in Figs 1–8.

In general, characters chosen were easily categorised; although, for characters relying on continuous data, such as head shape, we carried out a cluster analysis using the k-means clustering function with Euclidean distances of Systat 9 (Systat Software Inc., Point Richmond, CA, USA) to confirm that the categories chosen were not a result of observer biases. Character states were assigned relative to the putative outgroup, *N. demersus*.

Characters 46 and 47, male and female abdominal shape, varied within a species and thus could not always be clearly assigned to a character state using the k-means analysis. We coded characters 46 and 47 as 0/1 for those species that could not be assigned clearly to a character state (Table 2). Seven male characters were pooled with female characters because the character states did not vary between the sexes. Although we did not have female specimens of *A. keleri* or male specimens of *A. brevipes*, we considered it unlikely that they would show variation between the sexes when males and females of the other species of lice did not vary.

Phylogenetic analyses were conducted using PAUP*4.0b10 (Swofford 2002). The branch and bound search option was used and all characters were unordered. Jackknife support was calculated from 100 replicates using PAUP*. Bremer support was calculated using AutoDecay (Eriksson 1998).

The louse phylogeny was then compared visually to a phylogeny estimated for the penguins from a maximum-parsimony analysis of 985 base pairs from the mitochondrial small and large ribosomal subunits (Ritchie 2001).

Results

Examination of adult morphology found 46 parsimony-informative characters, six constant characters (characters 3, 6, 26, 28, 34 and 39) and three autapomorphic characters (characters 4, 30 and 47) (Table 2).

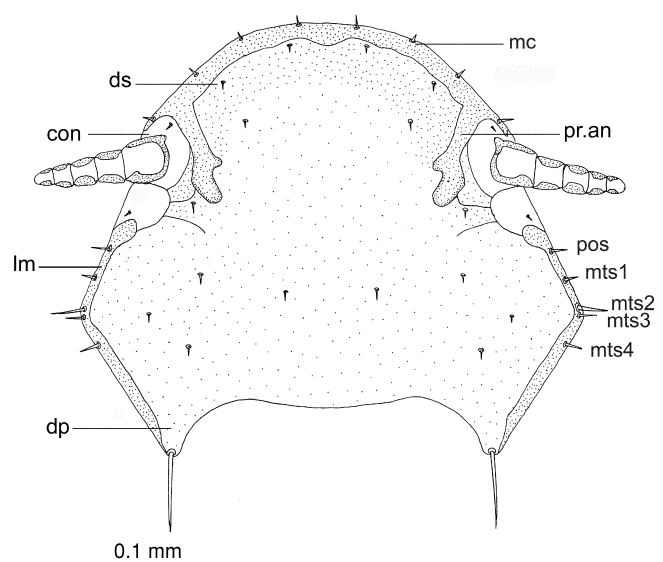


Fig. 1. Female *Austrogoniodes vanalphenae* head. Head characters used in the phylogenetic analysis: *con*, conus; *dp*, dorsal projection; *ds*, dorsal seta; *lm*, lateral margin; *mc*, marginal carina; *mts*, marginal temple seta; *pos*, post ocular seta; *pr.an*, pre-antennal node.

Table 1. Characters and observations

-
- (1) *Males – first antennal segment*: (0) large (first segment > half of entire antenna length); (1) small (first segment < one-third of entire antenna length).
- (2) *Abdominal segment II curved around base of leg 3*: (0) no; (1) yes.
- (3) *Males – rearward projection on first antennal segment*: (0) yes; (1) no.
- (4) *Females – rearward projection on first antennal segment*: (0) no; (1) yes.
- (5) *Males – conus attenuated*: (0) no; (1) yes (Fig. 1).
- (6) *Females – conus attenuated*: (0) no; (1) yes (Fig. 1).
- (7) *Females – setae on vulval margin*: (0) all short (longest seta < 60 µm); (1) mixture of short and long (longest seta > 85 µm).
- (8) *Females – hyaline outgrowth from head*: (0) absent; (1) present.
- (9) *Hyaline margin of pre-antennal region*: (0) <2 µm; (1) ≥2 µm (Fig. 1).
- (10) *Females – vulval margin*: (0) flattened; (1) curved.
- (11) *Males – hyaline margin of terminal segment*: (0) <1 µm thick; (1) >1 µm thick.
- (12) *Males – number of setae on posterior margin of terminal segment*: (0) 13–20; (1) 8–12; (2) >20.
- (13) *Females – marginal temple seta 4*: (0) > 90 µm; (1) < 45 µm (Fig. 1).
- (14) *Males – marginal temple seta 4*: (0) >90 µm; (1) <70 µm (Fig. 1).
- (15) *Marginal temple seta 2*: (0) shorter than marginal temple seta 3; (1) marginal temple seta 2 longer than marginal temple seta 3 (< 50 µm: <20 µm); (2) marginal temple seta 2 much longer than temple seta 3 (≥ 60 µm: ≤10 µm) (Fig. 1).
- (16) *Females – lateral setae on terga II–VII*: (0) all short and spine-like; (1) mixture of long and short (at least one seta is ~10 times the length of the short setae).
- (17) *Males – lateral setae on terga II–VII*: (0) all short and spine-like; (1) mixture of long and short (at least one seta is ~10 times the length of the short setae).
- (18) *Males – internal abdominal thickening*: (0) absent; (1) not bifurcated; (2) bifurcated.
- (19) *Females – projection on anterior side of pteronotum*: (0) no (Fig. 4b); (1) yes (Fig. 4a).
- (20) *Males – parameres*: (0) tip of paramere blunt (Fig. 6); (1) tip of paramere bifurcate (Fig. 8a); (2) paramere bifurcate with one arm turned out (Fig. 8b).
- (21) *Males – setae on posterior margin*: (0) all long (shortest setae > 24 µm); (1) mixture of short and long (shortest setae < 17 µm).
- (22) *Males – genitalia with two medianly fused bladder-like lobes anterior to penis*: (0) no; (1) yes (Fig. 6).
- (23) *Females – setae on posterior margin of tergum VIII*: (0) short and long (shortest < 37 µm; character state); (1) medium and long (shortest > 61 µm).
- (24) *Males – lateral margin of head deeply indented posterior to lens*: (0) no (Fig. 1); (1) yes.
- (25) *Males – third antennal segment*: (0) with tooth; (1) without tooth.
- (26) *Females – third antennal segment*: (0) without tooth; (1) with tooth.
- (27) *Males – antennae*: (0) end rounded; (1) end with flattened facet anteriorly.
- (28) *Females – antennae*: (0) end rounded; (1) end with flattened facet anteriorly.
- (29) *Males – posterior margin of pre-antennal node*: (0) symmetrical (Fig. 2); (1) asymmetrical (Fig. 1).
- (30) *Females – posterior margin of pre-antennal node*: (0) symmetrical (Fig. 2); (1) asymmetrical (Fig. 1).
- (31) *Males – anterior margin of head*: (0) convex; (1) strongly convex.
The distance between the temples divided by the distance from the anterior margin of the head to a line between the temples was calculated for each specimen. The ratios were standardised (mean = 0, standard deviation = 1) and grouped using k means clustering with Euclidean distance. Character states were assigned based on the results of the cluster analysis.
- (32) *Females – anterior margin of head*: (0) strongly convex; (1) convex.
Categorised as for character 31.
- (33) *Males – setae on antennal segment II*: (0) long (> 42 µm); (1) absent or short (< 17 µm).
- (34) *Females – setae on antennal segment II*: (0) short; (1) long.
All were <19 µm.
- (35) *Females – spermathecal sclerite*: (0) angular shape, fine dentation present (Fig. 3e); (1) u-shaped (Fig. 3a); (2) u-shaped but with ‘arms’ reduced and base markedly thickened (Fig. 3b); (3) inverted u-shape (Fig. 3c); (4) discrete, angular shape (Fig. 3d); (5) not visible.
- (36) *Females – lateral pouches*: (0) absent; (1) present.
See Figs 31 and 47 of Clay and Moreby (1967) for a description.
- (37) *Dorsal projection on posterior margin of head capsule*: (0) median side orientated obliquely to anterior-posterior axis (Fig. 5); (1) median side parallel to anterior-posterior axis (Fig. 1).
- (38) *Males – length of setae on dorsal surface of head plate*: (0) long (> 17 µm); (1) short (< 12 µm) (Fig. 1).
- (39) *Females – length of setae on dorsal surface of head plate*: (0) short (< 12 µm) (Fig. 1); (1) long (> 24 µm).
- (40) *Males – number of setae on posterior margin of tergum VIII*: (0) >21; (1) 13–20.
- (41) *Males – length of setae on posterior margin of tergum VIII*: (0) all medium and long (shortest seta > 54 µm); (1) some short, medium and long (shortest seta < 32 µm).
- (42) *Males – penis morphology*: (0) mid point is extended laterally (Fig. 7a); (1) long and straight (Fig. 7b); (2) flanges on the side of the penis (Fig. 7c); (3) short (< 39 µm), not pointed (Fig. 7d); (4) short (< 39 µm) and pointed (Fig. 7e).
-

(continued next page)

Table 1. (continued)

- (43) *Length of pre-antennal node*: (0) short (ratio < 0.078); (1) long (ratio > 0.084).
The ratio of pre-antennal node length divided by total louse length was calculated for each specimen. Ratios were standardised (mean = 0, standard deviation = 1) and grouped using k means clustering with Euclidean distances. Character states were assigned based on the results of the cluster analysis.
- (44) *Females – internal abdominal thickening*: (0) absent; (1) not bifurcate; (2) bifurcate.
- (45) *Males – endomeres with curved ends*: (0) yes; (1) no.
- (46) *Males – abdomen*: (0) rounded (ratio of width to length > 1.00); (1) elongated (ratio of width to length < 0.93).
The ratio of maximum length to maximum width of the abdomen was calculated for each specimen. Ratios were standardised (mean = 0, standard deviation = 1) and grouped using k means clustering with Euclidean distances. Character states were assigned based on the results of the cluster analysis.
- (47) *Females – abdomen*: (0) rounded (ratio of width to length > 0.953); (1) elongated (ratio of width to length < 0.872).
Analysed as for character 46.
- (48) *Males – number of setae on abdominal sternum III*: (0) > 11 ; (1) < 10 .
- (49) *Females – spermathecal sclerite*: (0) spermathecal tube opens in sclerite; (1) spermathecal tube opens outside of the sclerite; (2) opening not visible.
- (50) *Females – number of setae on abdominal sternum III*: (0) < 11 ; (1) > 11 .
- (51) *Females – seta on terminal segment*: (0) short ($< 44\ \mu\text{m}$); (1) long ($> 78\ \mu\text{m}$).
- (52) *Length of lateral setae on abdominal segment III*: (0) all short ($< 15\ \mu\text{m}$, males; $< 20\ \mu\text{m}$, females); (1) medium and long (longer than approximately $190\ \mu\text{m}$).
- (53) *Length of lateral setae on abdominal segment II*: (0) short (approx $10\ \mu\text{m}$); (1) long ($\sim 34\ \mu\text{m}$, males; $\sim 26\ \mu\text{m}$, females).
- (54) *Posterior projection on fore coxa of leg I*: (0) absent; (1) rounded; (2) spine-like.
- (55) *Endomeral plate with fine dentation*: (0) no; (1) yes (Fig. 6).

The branch and bound search, with all characters weighted equally, recovered five most parsimonious trees with a length of 109 steps, a consistency index of 0.566 (excluding uninformative characters) and retention index of 0.739 (Fig. 9). The g_i statistic of 1000 random trees was -0.6509 ($P < 0.001$), indicating the data contained strong cladistic signal (Huelsenbeck 1991). The dataset and the five maximum-parsimony trees (Fig. 9) have been deposited in TreeBASE (Accession number S1031; <http://www.treebase.org>).

Within *Austrogoniodes*, there was jackknife support (57%), but little Bremer support (0), for a group consisting of *A. bifasciatus*, *A. cristati*, *A. demersus* and *A. vanalphenae*.

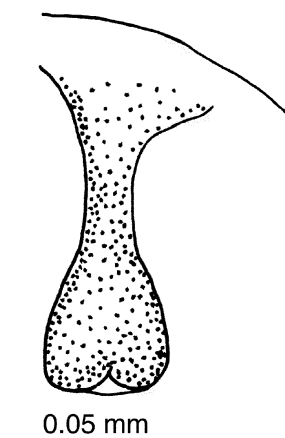


Fig. 2. Pre-antennal node of male *Austrogoniodes keleri* with symmetrical posterior margin (characters 29 and 30). Compare to the asymmetrical posterior margin of *Austrogoniodes vanalphenae* pre-antennal node in Fig. 1.

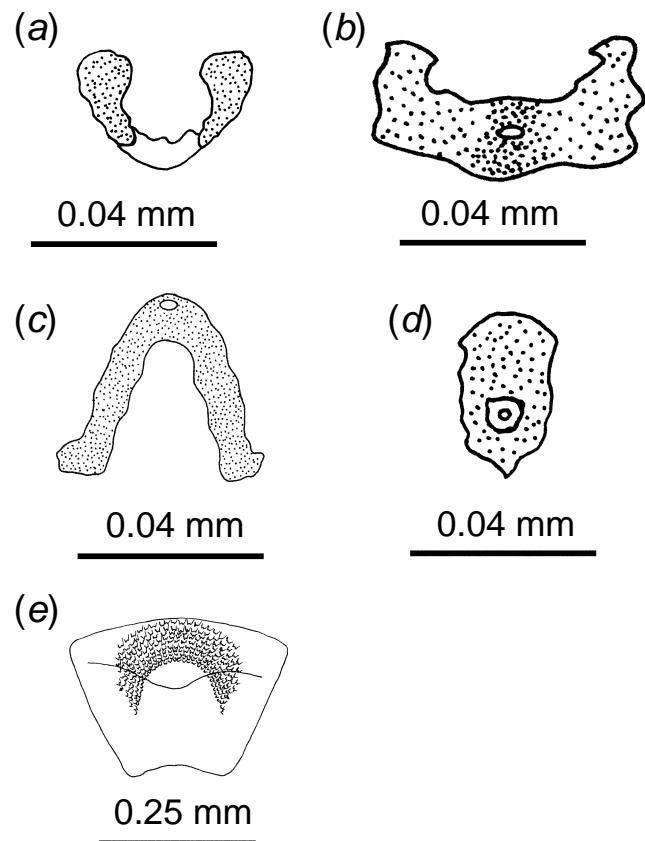


Fig. 3. Spermathecal sclerites (character 35). (a) *Austrogoniodes antarcticus* (character state 1); (b) *Austrogoniodes vanalphenae* (character state 2); (c) *Austrogoniodes macquariensis* (character state 3); (d) *Austrogoniodes mawsoni* (character state 4); (e) *Nesiotinus demersus* (character state 0), note change of scale.

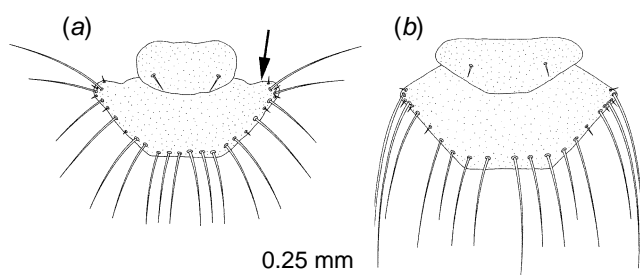


Fig. 4. Thorax types. Arrow highlights the projection on the anterior of the pteronotum (character 19). (a) *Austrogoniodes concii*; (b) *Austrogoniodes vanalphenae*.

Banks & Palma, 2003. The analysis also indicated that *A. bicornutus*, *A. concii*, *A. hamiltoni*, *A. keleri* and *A. macquariensis* formed another morphologically similar group with strong jackknife (82%) and Bremer (5) support. There was also strong jackknife (90%) and Bremer (3) support for placing *A. brevipes* and *A. mawsoni* parasitising the sister-species king penguin, *Aptenodytes patagonicus*, and emperor penguin, *A. forsteri* G. R. Gray, 1844 as sister-taxa. Moderately strong jackknife (63%) and Bremer (3) support was also found for the basal position of *A. metoecus* (Fig. 10).

Discussion

Many previous studies of the systematics of chewing lice have either examined an incomplete selection of lice from closely related groups of hosts, or consisted only of species descriptions (Smith 2000). In this study, we examined all louse species parasitising penguins. The penguin lice presented a rare opportunity to examine the chewing lice of a complete, widely dispersed host order that ranges around the

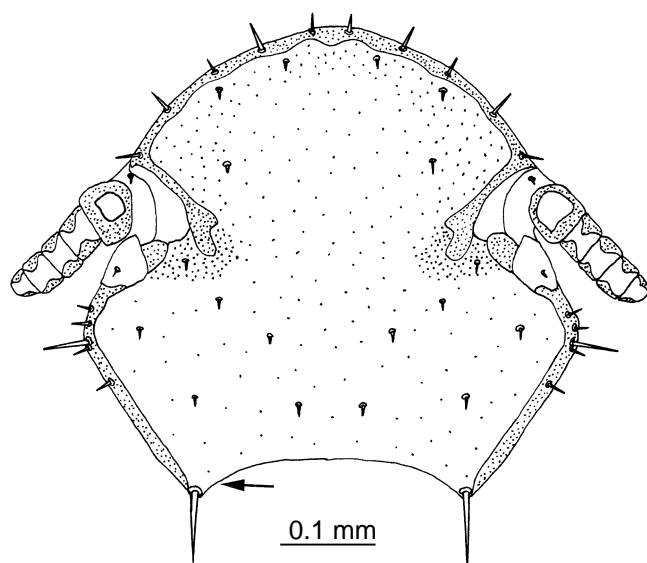


Fig. 5. *Austrogoniodes antarcticus* head showing oblique median margin of the dorsal projection on the posterior edge of the head (character 37; arrow highlights the oblique margin, compare to Fig. 1).

southern hemisphere from the equator to latitude 78°S, below the Antarctic circle (del Hoyo *et al.* 1992).

The louse phylogeny derived from morphological characters was relatively well resolved and whereas support for the recent branches of the phylogeny was strong, the jackknife analysis showed weak support for the deeper nodes in the phylogeny. The absence of strong phylogenetic signal in the deeper branches might be a result of morphological convergence. Morphological convergence may be more likely in the penguin lice than in other groups of bird-chewing lice because penguin louse species share similar habitats and face similar selection pressures owing to similarities in the morphology and marine lifestyle of their host species.

Division of the genus *Austrogoniodes* has been proposed in the past. Harrison (1937) stated that *A. mawsoni* and *A. hamiltoni* differed morphologically from other *Austrogoniodes* species based on their larger size, broad temporal lobes and indistinct demarcation of the antennary articles. Von Kéler (1952, 1954) thought the differences were

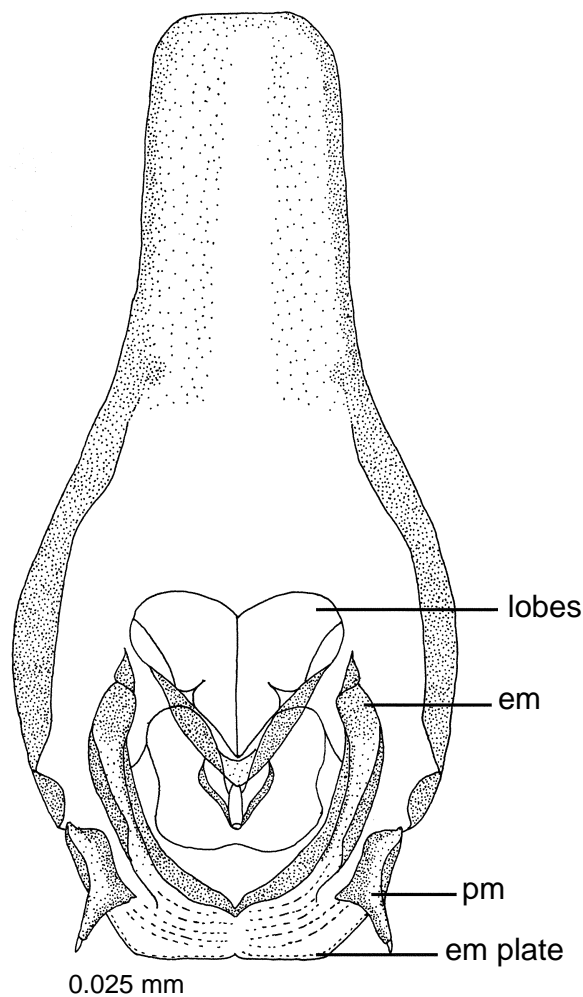


Fig. 6. *Austrogoniodes vanalphenae* male genitalia, dorsal view. em, Endomere; pm, paramere; em plate, endomer plate.

to males in this same species-group. The ‘*concii*-group’ was defined by two morphological characters: marginal temple seta 2 much longer than marginal temple seta 3 (character 15); and the short spine-like lateral setae on terga II–VII (characters 16 and 17). Jackknife (82%) and Bremer values (5) indicated considerable support for the subdivision. Clay (1967) discussed a second group comprising *A. bifasciatus*, *A. cristati* and *A. demersus*, which was also found in the current analysis and included the newly described species *A. vanalphenae* (Banks and Palma 2003). The ‘*cristati*-clade’ was united by similarities in male genitalia, although this group had less jackknife support (57%) than the ‘*concii*-group’ and had little Bremer support (0). It is interesting to note that individual hosts can be parasitised by members of both the ‘*cristati*-’ and ‘*concii*-clades’, for example, the crested penguins, *Eudyptes* Vieillot, 1816 spp., and it seems possible that the two clades occupy different niches on the hosts.

Our analysis found that *A. metoecus*, parasitic on the musk duck, *Biziura lobata*, was basal in the phylogeny. Clay (1971) suggested that *A. metoecus* might have affinities with the ‘*cristati*-group’, but this was not supported in our analysis.

Clay (1971) speculated that the establishment of *A. metoecus* on the musk duck was likely from a relatively recent establishment on the musk duck (i.e. host switching). The present geographical distribution of the musk duck suggested blue penguins, *Eudyptula minor*, as the most likely source of the musk duck louse and thus the louse should be most closely related to *A. waterstoni*. Our analysis did not find a close relationship between *A. metoecus* and *A. waterstoni*. Clay (1971) also noted that a relatively ancient host switch may have established the *A. metoecus* lineage on the musk duck and that adaptation to its new host, combined with extinction of the species ancestral to *A. metoecus* parasitising the penguin, may have obscured the origins of *A. metoecus*. One avenue may have been via the

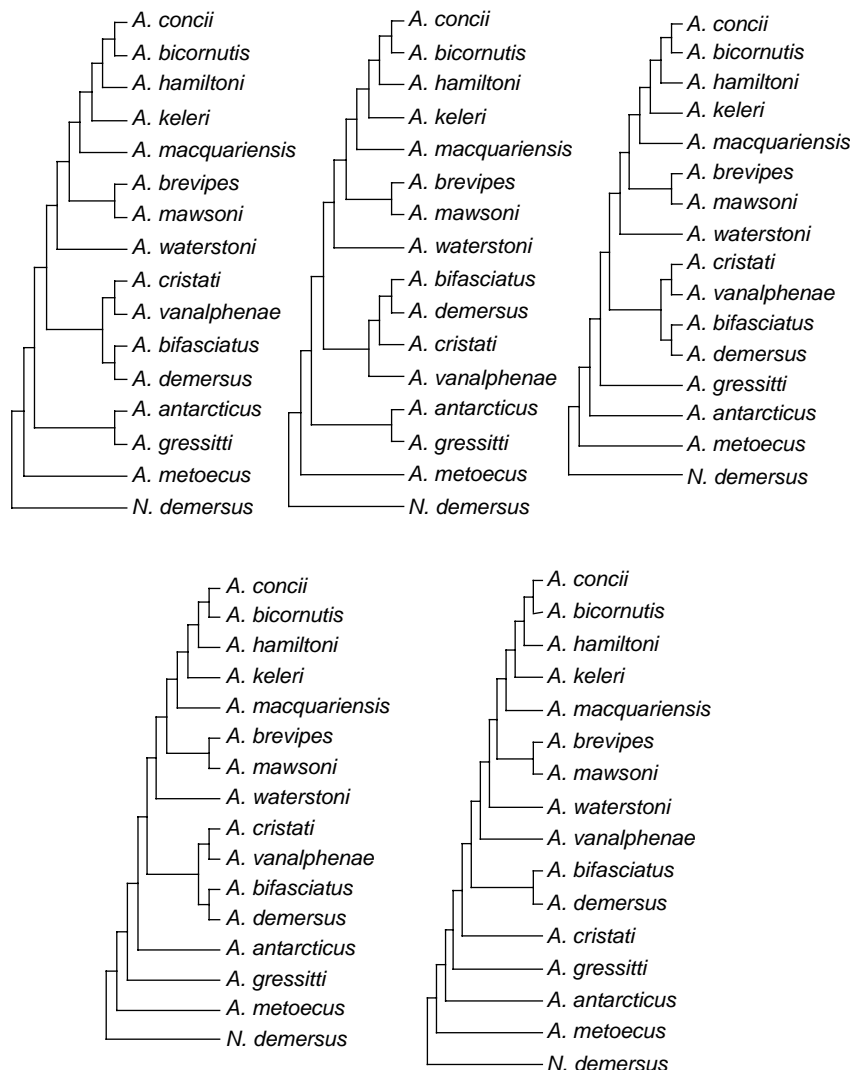


Fig. 9. The five most parsimonious trees obtained from the 46 parsimony-informative characters.

extinct New Zealand musk duck, *Biziura delautouri* Forbes, 1892 (Worthy 2002), and thus *A. metoecus* could have originated from one of several penguin species.

Alternatively, it may be that *A. metoecus* has been incorrectly classified in *Austrogoniodes*. One of the diagnostic features of *Austrogoniodes* is the extension to the fore coxa of leg I (Clay 1967), but in both sexes of *A. metoecus* the extension of the fore coxa is absent. Also, *A. metoecus* does not have tergites with internal thickening, unlike all other *Austrogoniodes*, and the male genitalia are distinctly different from other *Austrogoniodes*. Despite these differences, Clay (1971) included *A. metoecus* in *Austrogoniodes*, but it may be that the morphological similarities between *A. metoecus* and other *Austrogoniodes* lice are a result of similarities in the aquatic lifestyle of musk ducks and penguins. Another possibility may be that rapid adaptation to the relatively novel conditions on musk ducks has resulted in a spuriously basal position for *A. metoecus* in the

phylogeny. Molecular data would be one method to test these possibilities.

A superficial examination of the penguin-lice associations (see Appendix 2) revealed some areas of congruence between the louse and penguin phylogenies (Fig. 11). For example, the closely related *A. brevipes* and *A. mawsoni* exclusively parasitise the sister-species king penguin, *Aptenodytes patagonicus*, and emperor penguin, *A. forsteri*, respectively. Likewise the sister-lice species *A. vanalphenae* and *A. cristati* parasitise the sister-genera *Megadyptes* Milne-Edwards, 1880 and *Eudyptes* and the closely related *A. demersus* and *A. bifasciatus* only parasitise penguin species of the genus *Spheniscus* Brisson, 1760. However, a more rigorous analysis of co-phylogeny is warranted, because host-parasite relationships in the penguin-lice assemblage are complicated (for example, *A. macquariensis* and *A. hamiltoni* are present on some but not all of the crested penguins) and the most complete penguin phylogeny currently available is poorly resolved (Ritchie 2001).

Generally, homologous morphological characters were relatively obvious, despite *N. demersus* being distinctly morphologically different to the *Austrogoniodes* lice. Of the 55 characters used in this study, only character 51, the homologous seta on the terminal segment of female *Austrogoniodes*, could not be found in *N. demersus*. The position of *N. demersus* and *Austrogoniodes* within Ischnocera is beyond the scope of this study; although, given the morphological differences between *Nesiotinus* and *Austrogoniodes*, we are confident the two genera are sufficiently morphologically distinct to retain the present generic classification. Deeper relationships within Ischnocera are problematic (Cruickshank *et al.* 2001), which made the choice of an outgroup difficult. However, it is unlikely that *N. demersus* falls within the *Austrogoniodes* genus given the marked morphological differences between the two genera.

Male and female abdomen shape (characters 46 and 47) was included in the phylogenetic analysis, despite the cluster analysis failing to separate some species clearly into either of two groups. Species with ambiguous character states were assigned the code 0/1. It is possible that the difficulty in separating the character states was caused by distortion of the specimens during mounting of the specimens. Characters that encompass several body segments are more likely to be distorted during treatment of the specimen before mounting and/or by the weight of the cover glass (R. Palma, personal communication). Female characters for *A. keleri* were scored as '?' in our analysis because no female specimens of this species have been described. Use of '?' for unknown character states has been used successfully to analyse hypothetical datasets (Platnick *et al.* 1991; Maddison and Maddison 1992; Maddison 1993). Ordering character 20, paramere morphology, using Dollo ordering, did not alter the groups within *Austrogoniodes*, although it

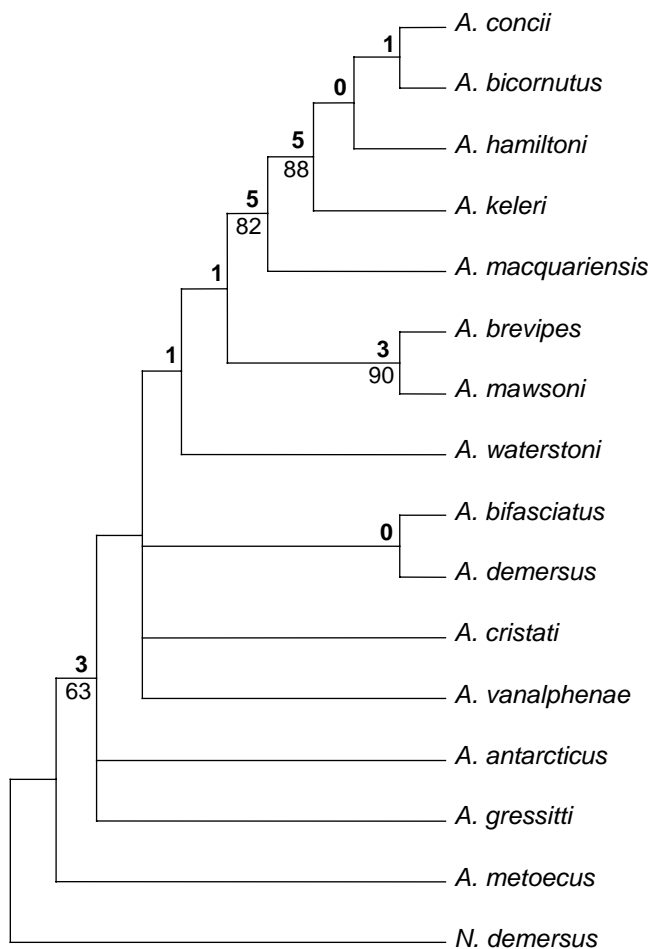


Fig. 10. Strict consensus of the five most parsimonious trees estimated from 46 parsimony-informative morphological characters. Numbers in bold above branches are Bremer support values and numbers below branches are jackknife values >50% (of 100 replicates).

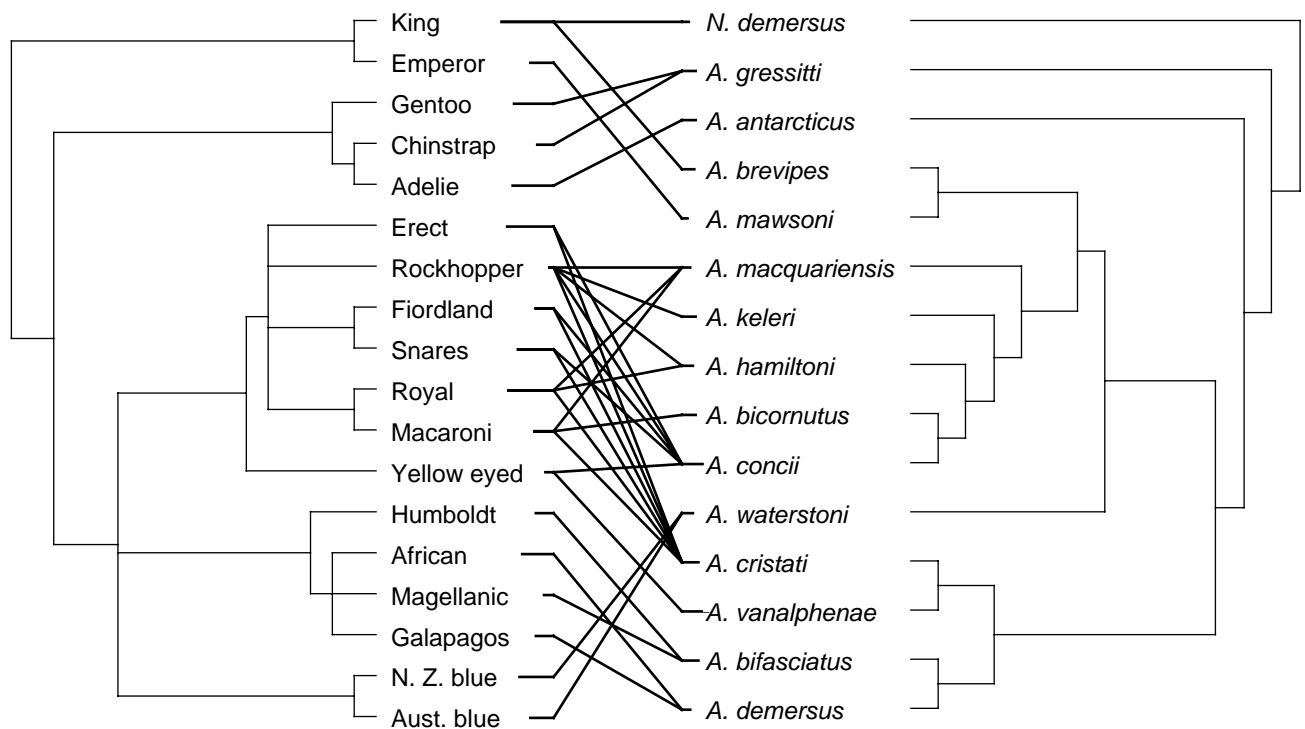


Fig. 11. Tanglegram of louse–penguin associations. The louse phylogeny is one of the five most parsimonious trees generated from morphology (this study); the penguin phylogeny was generated by maximum parsimony from 985 base pairs from the mitochondrial small ribosomal subunit and large ribosomal subunit (branches of the penguin phylogeny with less than 50% bootstrap support have been collapsed) (Ritchie 2001). Blue penguins have been split into the New Zealand and Australian haplotypes following the discussion in Banks *et al.* (2002). Lines connecting hosts and lice indicate associations.

altered the arrangement of the taxa within the ‘*conci*-group’ to (*A. macquariensis* (*A. concii*, *A. keleri* (*A. hamiltoni*, *A. bicornutus*))) in the 50% majority-rule tree.

Although we found some support for the ‘*cristati*-group’ and strong support for the ‘*conci*-group’ and ‘*cristati*-groups’ (Clay 1967) within *Austrogoniodes*, our cladistic analysis of louse morphology found little support for the use of the genus *Cesareus*. The basal position of *A. metoecus* suggests that if a host-switching event between the penguin and musk duck lineages has occurred, the transfer between the hosts was an ancient one. A visual comparison of louse and penguin phylogenies indicated that there might be some instances of co-divergence (Fig. 11) and a quantitative analysis, using molecular and morphological data, will be conducted elsewhere.

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Appendix 1. Material examined

Species	Host	Collection locality	Latitude	Longitude	Lice examined
<i>Austrogoniodes antarcticus</i>	<i>Pygoscelis adeliae</i>	Cape Bird	77.17°S	166.83°W	3 ♂ and 3 ♀ (MONZ)
<i>Austrogoniodes bicornutus</i>	<i>Eudyptes chrysolophus</i>	Heard Is.	53.10°S	73.50°E	2 ♂ and 5 ♀ ^P (BMNH)
<i>Austrogoniodes bifasciatus</i>	<i>Spheniscus magellanicus</i>	Isla Hornos	55.95°S	67.28°W	2 ♂ and 2 ♀ (MONZ)
	<i>Spheniscus sp.</i>	Not recorded			2 ♂ and 2 ♀ (MONZ)
<i>Austrogoniodes brevipes</i>	<i>Aptenodytes patagonicus</i>	Kerguelen Is.	49.25°S	69.17°E	1 ♀ ^l (BMNH)
<i>Austrogoniodes concii</i>	<i>Eudyptes sclateri</i>	Christchurch	43.53°S	172.67°E	1 ♂ and 1 ♀ (MONZ)
		Kaikoura	42.43°S	173.70°E	1 ♂ and 1 ♀ (MONZ)
		Antipodes Is.	49.67°S	178.77°E	1 ♂ and 1 ♀ (MONZ)
	<i>Eudyptes pachyrhynchus</i>	Barrytown	42.25°S	171.33°E	1 ♂ and 1 ♀ (MONZ)
		Thompson Sound	45.15°S	166.95°E	1 ♂ and 1 ♀ (MONZ)
		Jackson Bay	43.97°S	168.70°E	1 ♂ and 1 ♀ (MONZ)
	<i>Eudyptes robustus</i>	Snares Is.	48.04°S	166.56°E	3 ♂ and 3 ♀ (MONZ)
	<i>Megadyptes antipodes</i>	Christchurch	43.53°S	172.67°E	1 ♂ and 1 ♀ (MONZ)
		Kaikoura	42.43°S	173.70°E	1 ♂ and 1 ♀ (MONZ)
		Petone Beach	41.22°S	174.87°E	1 ♂ and 1 ♀ (MONZ)
<i>Austrogoniodes cristati</i>	<i>Eudyptes chrysocome chrysocome</i>	Falkland Is.	51.75°S	59.42°W	5 ♂ and 6 ♀ (MONZ)
	<i>Eudyptes chrysocome filholi</i>	Campbell Is.	52.50°S	169.08°E	3 ♂ and 3 ♀ (MONZ)
	<i>Eudyptes chrysolophus</i>	Marion Is.	46.90°S	37.75°E	1 ♂ and 1 ♀ (MONZ)
	<i>Eudyptes pachyrhynchus</i>	Jackson Bay	43.97°S	168.70°E	3 ♂ and 3 ♀ (MONZ)
	<i>Eudyptes robustus</i>	Snares Is.	48.04°S	166.56°E	3 ♂ and 3 ♀ (MONZ)
	<i>Eudyptes sclateri</i>	Antipodes Is.	49.67°S	178.77°E	1 ♂ and 1 ♀ (MONZ)
		Christchurch	43.53°S	172.67°E	1 ♂ and 1 ♀ (MONZ)
		Napier	39.47°S	176.92°E	1 ♂ and 1 ♀ (MONZ)
<i>Austrogoniodes demersus</i>	<i>Spheniscus demersus</i>	Dassen Is.	33.43°S	18.08°E	2 ♂ and 2 ♀ (MONZ)
		Dyer Is.	34.67°S	19.43°E	2 ♂ and 2 ♀ (MONZ)
	<i>Spheniscus mendiculus</i>	Bahia Elizabeth	0.60°S	91.20°W	3 ♂ and 3 ♀ (MONZ)
<i>Austrogoniodes gressitti</i>	<i>Pygoscelis antarctica</i>	South Georgia Is.	54.25°S	36.75°W	1 ♂ (BMNH)
		Not recorded			1 ♀ ^P (BMNH)
	<i>Pygoscelis papua</i>	Bird Is.	54.00°S	38.06°W	2 ♂ and 1 ♀ (BMNH)
	<i>Pygoscelis sp.</i>	Anvers Is.	64.77°S	64.08°E	1 ♂ and 1 ♀ (BMNH)
<i>Austrogoniodes hamiltoni</i>	<i>Eudyptes chrysocome filholi</i>	Macquarie Is.	54.62°S	158.93°E	4 ♀ and 4 ♂ (BMNH)
		Antipodes Is.	49.67°S	178.77°E	1 ♀ (BMNH)
		Campbell Is.	52.50°S	169.08°E	3 ♂ (MONZ)
	<i>Eudyptes schlegeli</i>	Macquarie Is.	54.62°S	158.93°E	5 ♀ (BMNH)
		Tasmania	41.88°S	148.29°E	1 ♂ and 2 ♀ (MONZ)
<i>Austrogoniodes keleri</i>	<i>Eudyptes chrysocome chrysocome</i>	Falkland Is.	51.75°S	59.42°W	6 ♂ (MONZ)
<i>Austrogoniodes macquariensis</i>	<i>Eudyptes chrysocome chrysocome</i>	Isla Gonzalo	56.53°S	68.73°W	4 ♀ (MONZ)
		Isla Buena Ventura	50.75°S	75.13°W	1 ♀ (MONZ)
		Falkland Is.	51.75°S	59.42°W	6 ♂ and 8 ♀ (MONZ)
	<i>Eudyptes chrysocome filholi</i>	Campbell Is.	52.50°S	169.08°E	6 ♂ (MONZ)
	<i>Eudyptes chrysolophus</i>	Snares Is.	48.04°S	166.55°E	2 ♂ (MONZ)
		Isla Gonzalo	56.53°S	68.73°W	1 ♂ and 2 ♀ (MONZ)
	<i>Eudyptes schlegeli</i>	Green Gorge, Macquarie Is.	54.62°S	158.93°E	2 ♂ (MONZ)
<i>Austrogoniodes mawsoni</i>	<i>Aptenodytes forsteri</i>	Cape Bird	77.17°S	166.83°W	3 ♂ and 3 ♀ (MONZ)
<i>Austrogoniodes metoecus</i>	<i>Biziura lobata</i>	New South Wales	Not recorded		1 ♂ and 1 ♀ (MONZ)
		Perth	31.95°S	115.97°E	1 ♂ and 1 ♀ ^P (KCE)
<i>Austrogoniodes vanalphenae</i>	<i>Megadyptes antipodes</i>	Kaikoura	42.43°S	173.70°E	2 ♂ and 1 ♀ (MONZ)
		Otaki Beach	40.75°S	175.12°E	3 ♂ and 3 ♀ (MONZ)
		St Clair Beach	45.92°S	170.48°E	1 ♂ and 1 ♀ (MONZ)
<i>Austrogoniodes waterstoni</i>	<i>Eudyptula minor albosignata</i>	Kaikoura	42.43°S	173.70°E	1 ♂ and 1 ♀ (MONZ)
		Banks Peninsula	43.75°S	173.00°E	1 ♂ and 1 ♀ (MONZ)
		Waimakariri	43.38°S	172.67°E	1 ♂ and 1 ♀ (MONZ)
	<i>E. m. chathamensis</i>	Long Beach, Chatham Is.	44.00°S	176.50°W	2 ♂ and 2 ♀ (MONZ)
		Rangatira, Chatham Is.	44.35°S	176.17°W	1 ♂ and 1 ♀ (MONZ)
	<i>E. m. iredalei</i>	Ohope Beach	37.96°S	177.03°E	3 ♂ and 3 ♀ (MONZ)
	<i>E. m. minor</i>	Snares Is.	48.04°S	166.55°E	2 ♂ and 2 ♀ (MONZ)
		Stewart Is.	47.00°S	168.25°E	1 ♂ and 1 ♀ (MONZ)
	<i>E. m. novaehollandiae</i>	Phillip Is.	38.48°S	145.23°E	1 ♂ and 1 ♀ (MONZ)
		Millicent	37.60°S	140.35°E	1 ♂ and 2 ♀ (MONZ)
		King Is., Tasmania	39.92°S	144.00°E	1 ♂ and 1 ♀ (MONZ)
	<i>E. m. variabilis</i>	Eastbourne	41.28°S	174.90°E	1 ♂ and 1 ♀ (MONZ)
		Kaikoura	42.43°S	173.70°E	1 ♂ and 1 ♀ (MONZ)
		New Plymouth	39.07°S	174.08°E	1 ♂ and 1 ♀ (MONZ)
<i>Nesiotinus demersus</i>	<i>Aptenodytes patagonicus</i>	St Andrew Bay, Sth Georgia Is.	54.43°S	36.17°W	3 ♂ and 2 ♀ (MONZ)
		Lusitana Bay, Macquarie Is.	54.62°S	158.93°E	2 ♀ (MONZ)
		Green Gorge, Macquarie Is.	54.62°S	158.93°E	1 ♂ and 1 ♀ (MONZ)

MONZ = Museum of New Zealand/Te Papa Tongarewa collection, BMNH = British Museum of Natural History, KCE = K. C. Emerson Collection, ^l = lectotype, ^P = paratype.

Appendix 2. Louse–penguin associations

Austrogoniodes struthius is regarded as *nomen dubium* following the discussion in Clay (1967). Louse–host associations that are likely due to straggling are enclosed in brackets

Louse species	Host species
<i>Austrogoniodes antarcticus</i> Harrison, 1937	<i>Pygoscelis adeliae</i> Adelie penguin ^{1,2}
<i>Austrogoniodes bicornutus</i> (von Kéler, 1954)	<i>Eudyptes chrysolophus</i> macaroni penguin ¹
<i>Austrogoniodes bifasciatus</i> (Piaget, 1885)	<i>Spheniscus magellanicus</i> Magellanic penguin ¹
	<i>Spheniscus humboldti</i> Humboldt penguin ¹¹
	(<i>Pygoscelis adeliae</i> Adelie penguin ^{1,13})
<i>Austrogoniodes brevipes</i> (Giebel, 1876)	<i>Aptenodytes patagonicus</i> king penguin ¹
<i>Austrogoniodes concii</i> (von Kéler, 1952)	<i>Eudyptes chrysocome moseleyi</i> Moseley's rockhopper penguin ¹
	<i>Eudyptes pachyrhynchus</i> Fiordland crested penguin ^{1,2}
	<i>Eudyptes robustus</i> Snares crested penguin ²
	<i>Eudyptes sclateri</i> erect-crested penguin ^{1,2}
	<i>Megadyptes antipodes</i> yellow eyed penguin ²
	(<i>Eudyptes chrysolophus</i> macaroni penguin ^{1,4})
<i>Austrogoniodes cristati</i> von Kéler, 1952	<i>Eudyptes chrysocome chrysocome</i> western rockhopper penguin ⁷
	<i>Eudyptes chrysocome filholi</i> eastern rockhopper penguin ²
	<i>Eudyptes chrysocome moseleyi</i> Moseley's rockhopper penguin ⁷
	<i>Eudyptes chrysolophus</i> macaroni penguin ^{1,2}
	<i>Eudyptes pachyrhynchus</i> Fiordland crested penguin ²
	<i>Eudyptes robustus</i> Snares crested penguin ²
	<i>Eudyptes sclateri</i> erect-crested penguin ^{1,2}
	<i>Eudyptes schlegeli</i> royal penguin ^{1,2}
<i>Austrogoniodes demersus</i> (von Kéler, 1952)	<i>Spheniscus demersus</i> African penguin ¹
	<i>Spheniscus mendiculus</i> Galapagos penguin ¹¹
	(<i>Eudyptes chrysocome</i> rockhopper penguin ^{1,4,5})
	(<i>Eudyptes chrysolophus</i> macaroni penguin ^{1,4,5})
	(<i>Spheniscus magellanicus</i> magellanic penguin ^{1,5,13})
<i>Austrogoniodes gressitti</i> Clay, 1967	<i>Pygoscelis antarctica</i> chinstrap penguin ¹
	<i>Pygoscelis papua</i> gentoo penguin ¹
	(<i>Eudyptes chrysolophus</i> macaroni penguin ⁴)
<i>Austrogoniodes hamiltoni</i> Harrison, 1937	<i>Eudyptes chrysocome filholi</i> eastern rockhopper penguin ⁷
	<i>Eudyptes schlegeli</i> royal penguin ²
	(<i>Eudyptes pachyrhynchus</i> Fiordland crested penguin ^{1,6})
	(<i>Eudyptes robustus</i> Snares crested penguin ^{9,6})
	(<i>Eudyptes sclateri</i> erect-crested penguin (one female louse) ^{1,8})
<i>Austrogoniodes keleri</i> Clay, 1967	<i>Eudyptes chrysocome chrysocome</i> western rockhopper penguin ¹
	(<i>Eudyptes chrysolophus</i> macaroni penguin one male louse) ¹
	(<i>Pygoscelis papua</i> gentoo penguin ^{1,5,13})
<i>Austrogoniodes macquariensis</i> Harrison, 1937	<i>Eudyptes chrysocome chrysocome</i> western rockhopper penguin ⁷
	<i>Eudyptes chrysocome filholi</i> eastern rockhopper penguin ⁷
	<i>Eudyptes chrysolophus</i> macaroni penguin ^{1,2}
	<i>Eudyptes schlegeli</i> royal penguin ²
	(<i>Eudyptes pachyrhynchus</i> Fiordland crested penguin ^{1,6})
	(<i>Eudyptes robustus</i> Snares crested penguin ^{9,6})
	(<i>Pygoscelis antarctica</i> chinstrap penguin ^{1,5,13})
	(<i>Pygoscelis papua</i> gentoo penguin ^{1,5,13})
<i>Austrogoniodes mawsoni</i> Harrison, 1937	<i>Aptenodytes forsteri</i> emperor penguin ^{1,2}
<i>Austrogoniodes metoecus</i> Clay, 1971	<i>Biziura lobata</i> musk duck ¹⁰
(<i>Austrogoniodes struthius</i> nom. dub.)	<i>Eudyptes schlegeli</i> royal penguin ^{1,2}
	<i>Eudyptes sclateri</i> erect-crested penguin ¹
<i>Austrogoniodes vanalphenae</i> Banks & Palma, 2003	<i>Megadyptes antipodes</i> yellow eyed penguin ¹¹
<i>Austrogoniodes waterstoni</i> (Cummings, 1914)	<i>Eudyptula minor albosignata</i> white flippered penguin ^{1,2}
	<i>Eudyptula minor chathamensis</i> Chatham Is. blue penguin ²
	<i>Eudyptula minor iredalei</i> northern blue penguin ²
	<i>Eudyptula minor minor</i> southern blue penguin ²
	<i>Eudyptula minor novaehollandiae</i> fairy penguin ¹²
	<i>Eudyptula minor variabilis</i> Cook Strait blue penguin ²
<i>Nesiotinus demersus</i> Kellogg, 1903	<i>Aptenodytes patagonicus</i> king penguin ²

¹Clay (1967); ²Pilgrim and Palma (1982); ³Palma (1999); ⁴Possibly present due to straggling or contamination (Clay 1967); ⁵Specimens obtained only from zoo penguins (Clay 1967); ⁶Possibly a straggler, contamination or misidentified (Pilgrim and Palma 1982); ⁷R. Palma, personal communication; ⁸Possibly a straggler or contamination (Palma 1999); ⁹Watson (1967); ¹⁰Clay (1971); ¹¹Banks and Palma (2003); ¹²Palma (1996); ¹³Probably a straggler or contamination, R. Palma, personal communication.