



## A review of the taxonomic status of the New Caledonia Wattled Bat *Chalinolobus neocaledonicus* Revilliod, 1914 (Chiroptera: Vespertilionidae) and *Chalinolobus gouldii venatoris* Thomas, 1908 from northern Australia

HARRY E PARNABY<sup>1,2\*</sup>, ANJA DIVLJAN<sup>1,3</sup> & GLENN HOYE<sup>4</sup>

<sup>1</sup>Mammalogy, Australian Museum Research Institute, Australian Museum, 1 William Street, Sydney, New South Wales, 2010, Australia

<sup>2</sup>✉ [parn@ozemail.com.au](mailto:parn@ozemail.com.au); <https://orcid.org/0000-0003-2409-1632>

<sup>3</sup>✉ [Anja.Divljan@austmus.gov.au](mailto:Anja.Divljan@austmus.gov.au); <https://orcid.org/0000-0003-2832-8713>

<sup>4</sup>Fly By Night Bat Surveys Pty Ltd, PO Box 271, Belmont, New South Wales, 2280, Australia

✉ [glenn@flybynightbatsurveys.com.au](mailto:glenn@flybynightbatsurveys.com.au); <https://orcid.org/0000-0002-0939-4064>

\*Corresponding author

### Abstract

The taxonomic status of the New Caledonia Wattled Bat *Chalinolobus neocaledonicus* Revilliod, 1914 has remained uncertain since its synonymy with mainland Australian Gould's Wattled Bat *C. gouldii* (Gray, 1841) in 1971. Although *Chalinolobus neocaledonicus* is now widely accepted as a valid species, this was based on a tentative taxonomic opinion published in 1995. We examined most of the original material used to justify synonymy with *C. gouldii*, which included the type series of *C. gouldii venatoris*, a small northern Australian form that superficially resembles *C. neocaledonicus* but is currently not generally recognised as a valid subspecies. We found consistent differences in key diagnostic external and cranial criteria that support species status for *C. neocaledonicus*. We also review the taxonomic status of *venatoris*. Contrary to previous assessments, our re-interpretation of the taxonomic literature supports subspecific recognition of *venatoris*. Nevertheless, we are unable to conclusively resolve the status of *venatoris* because a more complex pattern of variation than a simple latitudinal size cline is apparent in *C. gouldii*. We argue that recognition of *venatoris* as the northern subspecies of *C. gouldii* has merit, pending a comprehensive analysis of variation in mainland *C. gouldii* to test for the presence of cryptic taxa.

**Key words:** subspecies, morpho-taxonomy, geographic variation, Endangered species, *Chalinolobus nigrogriseus*

### Introduction

The New Caledonia Wattled Bat (*Chalinolobus neocaledonicus* Revilliod, 1914) is one of six endemic bat species, of a total of nine bat species known from New Caledonia (Simmons 2005), a French territory in the southwest Pacific. It has an IUCN Red List status of Endangered (Brescia 2008) and is the only species of *Chalinolobus* recognised from New Caledonia and, along with the New Caledonia Long-eared Bat *Nyctophilus nebulosus* Parnaby, 2002, is the only representative of the family Vespertilionidae recorded from that territory. Kirsch *et al.* (2002) greatly increased distributional knowledge of the species and summarised the limited information that exists for this species. Their work, along with Millon *et al.* (2018) who monitored echolocation calls of the species at two montane wind farms, is the only literature that we have found on the species other than a small number of traditional taxonomic assessments based on morphology (Tate 1942; Koopman 1971), a report of subfossils (Hand & Grant-Mackie 2012) and the summary by Burgin (2019).

The genus *Chalinolobus* was first recorded from New Caledonia based on one specimen reported by Revilliod (1914). To our knowledge there are only 13 voucher specimens of the New Caledonia Wattled Bat in world collections. Kirsch *et al.* (2002) list 11 specimens in addition to the holotype, which is located in Naturhistorisches Museum Basel, Switzerland. Koopman (1971) mentions an additional specimen in the American Museum of Natural History (AMNH 135948), from the mouth of the Huailu River valley on the central northeast coast of the main island. Six females and an adult male were collected from a tree hole at Tiare, on the southern coast of the main

island in 1914 and are in the Natural History Museum, London. Three specimens obtained by Kirsch *et al.* (2002) are in the Natural History Museum, Paris and the remaining specimen in the Zoological Collection of the Australian National University, Canberra is possibly lost (Hand & Grant-Mackie 2012).

The genus *Chalinolobus* is restricted to Australia, Papua New Guinea, New Caledonia and New Zealand (Simmons 2005). Six species are recognised outside New Caledonia: five from mainland Australia and Tasmania (Van Dyck & Strahan 2008), one of which (*C. nigrogriseus* (Gould, 1856)) also occurs in Papua New Guinea (Bonaccorso 1998). The endemic Long-tailed Bat *C. tuberculatus* (Forster, 1844) is the only species of this genus recognised from New Zealand (O'Donnell 2005). A taxon on Norfolk Island appears to be extinct (Hoye 2011) and, although usually assigned to Gould's Wattled Bat *C. gouldii* (Gray, 1841), is possibly a distinct species (Flannery 1995), and its taxonomic status requires clarification.

Intraspecific morphological variation remains poorly defined for all species of *Chalinolobus* and a complete revision of the genus is warranted. Relationships of species within the genus have not been explored using genetic techniques. The most recent taxonomic study of the genus that included all named forms is the morphological review by Tate (1942). Other studies include assessments of morphological variation within *C. nigrogriseus* and *C. picatus* (Gould, 1852) and related forms by Ryan (1966) and Van Deusen & Koopman (1971), and a morphometric study of geographic variation within Australian *C. gouldii* that included New Caledonian material, by Tidemann (1986). Interspecific differences in baculum shape are illustrated for currently recognised species other than *C. dwyeri* Ryan, 1966 and *C. neocaledonicus* by Hill & Harrison (1987: fig. 17), but penile morphology has not been examined in *Chalinolobus* species.

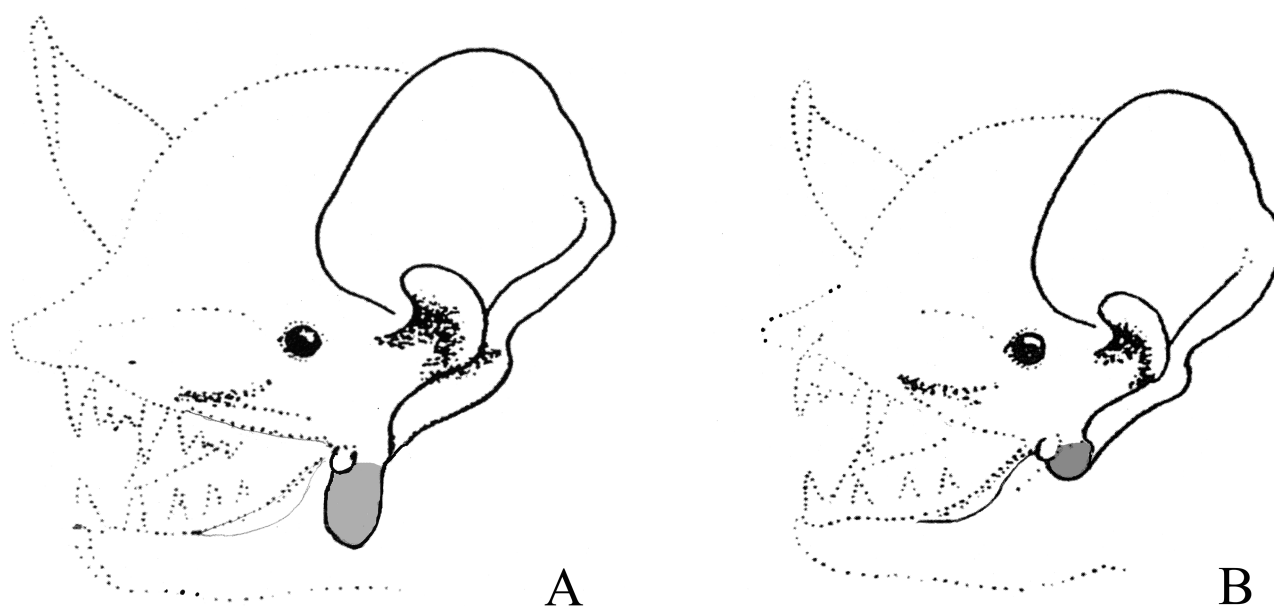
The taxonomic status of *C. neocaledonicus* remains unresolved. Since the original description by Revilliod (1914), all taxonomic authorities prior to Koopman (1971) treated it as a valid species. Koopman (1971) examined specimens of *neocaledonicus* and a small northern Australian form of Gould's Wattled Bat (*C. gouldii*) which Thomas (1908) had named *C. gouldii venatoris*, and concluded that *neocaledonicus* is best regarded as a subspecies of the Australian Gould's Wattled Bat *C. gouldii*. Koopman's view of subspecific status was subsequently adopted. In the only detailed morphometric study of *C. gouldii*, Tidemann (1986) concluded that recognition of the subspecies *venatoris* and *neocaledonicus* was unwarranted, i.e. that *neocaledonicus* was invalid even as a subspecies of *C. gouldii*, a view that is still maintained by some authors (e.g., Chruszcz & Barclay 2002; Dixon & Lumsden 2008). Tidemann (1986) believed that the statistical differences between *Chalinolobus* specimens from Norfolk Island and New Caledonia fell within the range of between-population differences from widely separated localities on mainland Australia. However, his study did not examine non-metric external or cranial characters.

Today, most authors follow the assessment of Flannery (1995) and Simmons (2005), who recognised *C. neocaledonicus* as a species. The only reason Flannery (1995) explicitly gave for his decision is that he regarded the statistical analysis of Tidemann (1986) to be a weak foundation for synonymising *neocaledonicus* with *C. gouldii*. Flannery (pers. comm., 2019) was unable to examine sufficient material of *neocaledonicus*, as reflected by the uncertainty of his statement (Flannery 1995: 363) that *neocaledonicus* might possibly share the downwardly projecting ear flap which is diagnostic for *C. gouldii*. Simmons (2005) was uncertain of the status of *neocaledonicus*, stating that her recognition of species status was tentative, and followed Flannery (1995).

Morphological criteria used to differentiate species of *Chalinolobus* include overall size, fur colour pattern, tragus shape, development of skin lobes on the lower lip, the relative size and shape of the ears, morphology and relative size of the upper incisors, extent of development of an internal cusp on the upper fourth premolars (P<sup>4</sup>), degree of inflation of the infra-orbital swellings, and the ratio of inter-orbital to inter-temporal widths (Dobson 1878; Tate 1942; Ryan 1966). In particular, the morphology of the ear margin where it terminates near the angle of the mouth has been used to distinguish species of the genus. A large, pendant skin flap on the outer margin of the ear has long been recognised as a diagnostic feature for differentiating *C. gouldii* from all other Australian members of the genus (Fig. 1A). In this species, the outer margin of the ear terminates in a clearly visible, enlarged flap of skin that is attached near the margin of the mouth (Fig. 1A). The diagnostic value of this character appears to have been first recognised by Dobson (1878), who provided an illustration. It has since been adopted as a character unique to Australian *C. gouldii* (e.g., Wood Jones 1925; Troughton 1926; Parnaby 1992; Baker 2013) and is not known to be present in any other species of the genus. In all other species of *Chalinolobus*, including *C. neocaledonicus* (Fig. 1B), the ear margin terminates either in a relatively small skin flap (e.g., the Hoary Bat *C. nigrogriseus* of northern Australia) or it is absent.

A further indication that the taxonomic status of *neocaledonicus* requires re-evaluation arises from the inad-

equate treatment of what we consider to be a key diagnostic external feature in previous taxonomic assessments by Koopman (1971), Tidemann (1986) and Flannery (1995). This is the extent of development of the downwardly projecting flap of skin formed by the outer ear margin where it terminates near the angle of the mouth (Fig. 1). Koopman (1971) concluded that this feature was variable based on the small number of alcohol-preserved *C. gouldii* that he examined and concluded, we believe incorrectly, that it had no diagnostic value. Because he did not specify which alcohol specimens he examined, we are unable to resolve his conflicting conclusion. His assessment of the status of *C. neocaledonicus* was also based on an examination of eight specimens of *C. neocaledonicus* and the type series of *C. gouldii venatoris*. Tidemann (1986) does not mention this character and it appears that his conclusions were based largely on multivariate analysis of external and cranial measurements. As noted above, Flannery (1995) was uncertain about the extent of development of the terminal ear flap in *C. neocaledonicus*.



**FIGURE 1.** Diagrammatic illustration of species differences in the degree of development of the terminal lobe or flap (gray shading) in the outer ear margin of: A, *Chalinolobus gouldii gouldii* and *C. gouldii venatoris*, and B, *C. neocaledonicus* and *C. nigrogriseus*. Note that other illustrated features are generalised *Chalinolobus* representations that might not reflect interspecific differences (modified from Parnaby 1992: fig. 15).

A taxonomic assessment of *C. neocaledonicus* requires comparisons with taxa that are morphologically most similar. These are *C. gouldii venatoris* and *C. nigrogriseus nigrogriseus*. Koopman (1971) noted that *venatoris* and *neocaledonicus* were of similar size, overlapping in forearm length and condylo-basal skull length. Overall, he believed that *C. gouldii venatoris* was about equally different from the larger southern *C. gouldii gouldii* as it was from *C. neocaledonicus* and on that basis concluded that *neocaledonicus* should be relegated to a subspecies of *C. gouldii* (Koopman 1971; 1993). Thomas (1908) established *C. gouldii venatoris* as a smaller, darker-furred form of southern Australian *C. gouldii gouldii*. He states that he examined six specimens from Alexandria, Northern Territory and that his new subspecies resembled southern *C. gouldii* but had smaller body and cranial dimensions, was darker, and had a less elevated braincase. Thomas (1908) noted that southern mainland Australian *C. gouldii* were intermediate in size between *venatoris* and what he regarded as “true” *C. gouldii gouldii* from Tasmania. Thomas (1905) had previously selected a lectotype for *C. gouldii gouldii*, thereby fixing the type locality as Launceston, Tasmania. The taxonomic validity of *C. gouldii venatoris* is contentious and we regard its status to be unresolved. Some authors recognise the subspecies (e.g., Menkhorst & Knight 2011; Jackson & Groves 2015), while many do not (e.g., How *et al.* 2001; Simmons 2005; Churchill 2008; Burbidge *et al.* 2014), presumably influenced by the morphometric analysis of Tidemann (1986), who did not recognise subspecies within *C. gouldii*.

An evaluation of the status of *C. neocaledonicus* also requires comparisons with *C. nigrogriseus*. Gould (1856) based his description of *nigrogriseus* (as *Scotophilus nigrogriseus*) on one animal, an adult of unknown sex from Morton Bay (= Brisbane environs, Queensland). In his original description of *C. neocaledonicus*, Revilliod (1914) regarded his new species to be most similar to *C. nigrogriseus*. Revilliod treated the smaller form *rogersi* Thomas, 1909 from north-western Australia as a valid species, as did all authorities prior to Johnson (1964). This form is cur-

rently either treated as a junior synonym of *C. nigrogriseus* (e.g., Burbidge *et al.* 2014) or as a western subspecies of *C. nigrogriseus* which extends from northern Western Australia across northern Northern Territory to western Queensland (Simmons 2005; Kutt *et al.* 2008; Jackson & Groves 2015). We have restricted our comparisons of *C. nigrogriseus* to material from New South Wales or eastern Queensland outside the suspected overlap or intergrade zone with *rogersi* proposed by Van Deusen & Koopman (1971). We have done this as a precaution until the status of *rogersi* is resolved and we use the trinomial *C. nigrogriseus nigrogriseus* as a convenient geographical designation.

This study began when we noticed that the original description of Revilliod (1914) specifically states that the enlarged terminal ear flap was absent in the holotype of *C. neocaledonicus*, the only specimen upon which he founded the species. He states, that “The outer edge [of the ear] extends to the posterior angle of the mouth into a horizontal blade. There is no vertical appendage similar to that of *C. gouldii*”. If all *Chalinolobus* from New Caledonia lacked the “vertical appendage” diagnostic of *C. gouldii*, it would potentially suggest species level differentiation from *C. gouldii*. We had assumed, as had Flannery (1995), that this character must therefore be present in New Caledonian populations given past doubt about the distinction between *C. neocaledonicus* and *C. gouldii*, but we could not resolve this from the published literature. It therefore seemed possible that in addition to *C. neocaledonicus*, another species might occur that resembled *C. gouldii*. It was also important to determine whether the “vertical appendage” was present in the type series of *C. gouldii venatoris* but we could not determine this from the literature because it is not specifically mentioned in the original description by Thomas (1908) or subsequent studies.

In late 2018 an opportunity arose for one of us (Anja Divljan, AD) to visit research collections in Europe to examine most of the material used in Koopman’s study in the Natural History Museum, London and the holotype of *C. neocaledonicus*. Time constraints limited the focus to photographing key diagnostic features of fur colour, ear structure and upper incisor morphology, along with skull measurements. Our primary aim is to review the original basis for Koopman’s decision to synonymise *neocaledonicus* with *C. gouldii*. We therefore focus on the type series of *C. gouldii venatoris* and material of *C. neocaledonicus* and do not address the complex secondary issue of the taxonomic validity of *venatoris* in relation to *C. gouldii*. Consequently, we have not included additional northern Australian *C. gouldii* in our assessment. However, we present a re-interpretation of the taxonomic literature and argue that, contrary to previous assessments, the morphometric study of Tidemann (1986) actually supports recognition of subspecific status of *venatoris*.

## Material and methods

The holotype and ten specimens of *C. neocaledonicus*, the type series of *Chalinolobus gouldii venatoris* Thomas, 1908, and the holotype of *Chalinolobus nigrogriseus* (Gould, 1856) were measured and photographed in November 2018.

Standard cranial and dental measurements and forearm length (FA) were made using digital callipers as follows: **GL**, greatest length of skull; **BASL**, skull basilar length, from the most anterior margin of the foramen magnum to most anterior margin of premaxilla; **CON**, condylo-basal length, from the most posterior point of the condyles to the anterior most point of the premaxilla; **C<sup>1</sup>–C<sup>1</sup>**, from the labial margin of the canine cingula at base; **CM<sup>3</sup>**, from base of the canine to the posterior margin of M<sup>3</sup>; **M<sup>3</sup>–M<sup>3</sup>**, outside breadth of upper third molars taken from the cingula; **ZYG**, breadth of zygomatic arches at widest point; **PAL**, sinu-palatal length, taken from the most anterior of premaxilla to most anterior margin of the pterygoid fossa; **POC**, post-orbital constriction; **MASB**, mastoid breadth; **D3p1**, length of the first phalanx of the third digit, measured from the anterior of the FA to the midpoint of adjoining joints, measured to the nearest mm from scaled, dorsal and ventral images of seven skins of *C. neocaledonicus* from Tiare and the type series of *venatoris*. Additional cranial and external measurements of the holotype of *C. neocaledonicus* are defined in Results below. Wing metacarpal length was measured on a small number of specimens with the wings folded. Two sets of measurements were taken of each metacarpal: one from the anterior of the forearm, the other from the junction of the metacarpal with the wrist from the ventral surface of the wing.

Summary statistics and Principal Components Analyses (PCA) were run using the statistical package PAST version 3.21 (Hammer *et al.* 2001). PCAs were run using both the variance-covariance matrix and the correlation matrix and the spatial arrangement of specimens was compared using each matrix. GL was not included in analyses as a precaution because the rear braincase wall appeared to be incomplete in some specimens of the type series of *venatoris*.

We also included measurements of *C. nigrogriseus* specimens tabulated by Van Deusen & Koopman (1971) in our analysis. We used their measurements for Queensland and New South Wales specimens (localities 29 to 35 in their fig. 2), excluding material from Western Australia, Northern Territory and western Queensland because this fell within the expected geographic range of *C. nigrogriseus rogersi* Thomas, 1909. They used standard, self-explanatory cranial measurements. Several *C. nigrogriseus* skulls used in their study were remeasured and found to be equivalent to ours.

Institutional abbreviations used throughout the text are: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; ANUZ, Zoology collection, Australian National University, Canberra; MNHN, Muséum National d'Histoire Naturelle, Paris; NMB, Naturhistorisches Museum, Basel, Switzerland; NHML, Natural History Museum, London.

### Material examined

The type material of *C. g. venatoris* and *C. nigrogriseus* along with 10 *C. neocaledonicus* listed in Table 1. *C. nigrogriseus* in the AM, bodies in alcohol: **Queensland.** M16101–16103, males, Station Creek, S of Coen, Cape York, 14° 06' S, 143° 12' E. M16104–16405, males, Development Road, 65 km SE Musgrave, Cape York, 15° 12' S, 143° 52' E. M13312, male, Spring Creek on the Mt Molloy–Cooktown Road, 16° 23' S, 144° 44' E. M51095, female, 28 km W of Baralaba, c. 24° 09' S, 149° 32' 30" E. M13314, male, junction of East Normanby River & Cooktown Road, 15° 15' S, 145° 01' E. **New South Wales.** M25437, male, Ramornie State Forest, SW of Grafton, 29° 43' 01" S, 152° 38' 24" E. M29095, male, Sugarloaf State Forest, 28° 56' 20" S, 152° 37' 17" E. M30390, female, Bom Bom State Forest, S of Grafton, 29° 45' 39" S, 152° 56' 57" E. M33489, male, Grange State Forest, 29° 29' 36" S, 152° 33' 23" E. M26598, female, North Bundjalung National Park, 29° 17' S, 153° 17' E. M36022, female, Bundjalung National Park, 29° 19' 55" S, 153° 20' 06" E. M31079, male, Newfoundland State Forest, Newfoundland Road, 29° 56' 28" S, 153° 09' 19" E. M31090, female, Bundjalung National Park, Wendouree Lagoon, 29° 16' 04" S, 153° 20' 39" E. M31093, female, Bundjalung National Park, Bombing Range Road, 29° 23' 48" S, 153° 10' 36" E. M50019 and M50020, females, Bundjalung National Park 29° 10' 13" S, 153° 23' 52" E.

### Adult bats measured and released

*C. gouldii*: **Western Australia.** Mt Bruce Well, 27 km NE of Tom Price, Pilbara, 22° 33' S, 118° 01' E (19 females, 1 male, 29 Sep 1989, Harry Parnaby, HP). Corktree Bore, 20 km SW of Marillana Station, Pilbara, 22° 47' S, 119° 18' E (18 females, 1 male, 27 Sep 1989, HP). Dryandra Woodlands, 32° 47' 28" S, 116° 59' 46" E (3 females, 2 males, 23 Nov 2007, HP). **Northern Territory.** McArthur, 16° 41' S, 135° 44' E (5 females, 1 male, 2 Oct 1988, GH). **Queensland.** Gregory River at Gregory Station, 18° 38' S, 139° 14' E (1 female, 22 Sep 1988, GH). Georgetown, 18° 17' S, 143° 33' E (5 females, 1 male, 20 Sep 1988, GH). **New South Wales.** Andersens Tank, Windbar, 30° 51' 17" S, 144° 52' 04" E (30 females, 27 males, 19 Apr 1995, Harry Hines). **Victoria.** Otway Ranges, 38° 41' S, 143° 35' E (35 females, 21 males, Feb and Mar, 1988, HP).

*C. nigrogriseus* **Queensland.** Petford, Chillago Road, 17° 20' S, 144° 57' E (10 males, 4 Sep 1983, HP). Mt Garnett, 34 km S, c. 17° 41' S, 145° 07' E (1 female, 1 male, 16 Jul 1982, Terry Reardon, TR). Laura, 20 km S, 15° 43' S, 144° 32' E (1 male, 1 female, 19 Jul 1982, TR). Archer River, 5 km S, c. 13° 30' S, 142° 32' E (1 male, 26 Jul 1982, TR). Strathburn Station, Cape York, 14° 26' 58" S, 142° 44' 34" E (2 males, 4 Sep 2009, TR). Norman Creek, Cape York, 13° 02' 07" S, 141° 38' 44" E (1 male, 31 Aug 2009, TR). Morehead River, S of Musgrave, Cape York, 15° 01' 22" S, 143° 39' 52" E (1 female, 13 Sep 2009, TR). Batavia, Cape York, 12° 10' 38" S, 141° 53' 47" E (1 male, 27 Aug 2009, TR). Bertiehaugh Station, Cape York, 12° 11' 04" S, 142° 29' 27" E (1 female, 25 Aug 2009, TR). Piccaninny Plains, Cape York, c. 13° 09' S, c. 142° 46' E (11 males, 24 Sep 2012, TR). King Junction, Cape York, 15° 53' 07" S, 143° 33' 49" E (11 males, 5 females, 8 Sep 2008, TR). Horseshoe Lagoon, Lakefield, 15° 17' 03" S, 144° 36' 36" E (2 males, 9 Sep 2009, TR). Burdekin River, 18 km E Charters Towers, 20° 06' S, 146° 26' E (1 female, 1 Oct 1983, HP). Musgrave, 54 km N, 14° 41' S, 143° 50' E (2 males, 25 Apr 1981, HP). **New South Wales.** Bundjalung National Park, 29° 15' S, 153° 20' E (2 females, 28 Jan 1994, GH). Bundjalung National Park, 29° 10' S, 153° 23' E (4 females, Oct 1991, Dave Milledge).

*C. neocaledonicus* Tendo, 20° 42' 46" S, 164° 47' 00" E, Grande Terre, New Caledonia (41 females, 11 Oct 2017, GH).

## Results

### The holotype of *C. neocaledonicus*

As the original account by Revilliod (1914) remains the only published description of the holotype, we provide additional observations here. The holotype is NMB 1751, body in alcohol, tongue preserved separately in alcohol; the extracted skull is NMB number Ost.5176, an intact cranium and dentaries, missing right zygomatic arch. Collected from a house in Canala, Noumea by F. Sarasin and J. Roux in 1913, exact date not cited.

An accurate determining of body fur colour of the holotype is difficult because it is an alcohol-preserved specimen and we were reluctant to risk degradation from drying the body. Fur colour could also have altered during a century of preservation. Dorsal fur colour is uniformly dark from the head and shoulders to the rump (Fig. 2). The ventral surface also lacks a colour gradation from anterior to posterior, but has paler fur in the inguinal region. The ear margin terminates near the angle of the mouth in a simple, unenlarged join similar to that of *C. nigrogriseus*. A thin projection of skin exists on the lower lip near the angle of the mouth, forming a horizontal ledge with a linear, i.e. unwrinkled, outer margin. The upper incisors are not worn and there is no sign of a secondary cusp on I<sup>1</sup>. A small anterior lingual cusp is present on P<sup>4</sup>.

Selected cranial and dental measurements taken from the holotype are given in Table 1. Additional measurements (mm) made of the holotype are: bulla length, 3.22; least inter-bullae distance, 2.33; C<sub>1</sub>–M<sub>3</sub> length, 5.77; dentary length (anterior tip to posterior tip of angular process), 11.12; dentary height (coronoid process to ventral margin of dentary), 3.83. Digit 3 metacarpal length, 30.63 from inside wing (32.12 from anterior margin of FA); phalanx 1 length, 12.78; phalanx 2 length, 10.75; phalanx 3 length, 5.49; Digit 4, metacarpal, 29.81 mm (32.53); phalanx 1, 11.83; phalanx 2, 9.14; Digit 5, metacarpal, 27.8 (30.08); phalanx 1, 7.82; phalanx 2, 5.66; Tibia length, 13.63.

Our measurements of the holotype skull and wing digits taken by AD are a close match with those given in the original description. It is apparent that Revilliod (1914) measured wing metacarpals from the leading edge of the wing at the wrist. Notable differences are our CM<sup>3</sup> of 5.4 mm compared to 5.7 mm given by Revilliod and his measurement of 6.0 mm for CM<sub>3</sub> against our 5.77 mm. These discrepancies presumably reflect measurement error, slight differences in the placement of calliper blades or calliper precision. Our FA measurements of the holotype and a specimen of *C. nigrogriseus* (NMB 235) are about 1 mm greater than those of Revilliod.



**FIGURE 2.** Alcohol-preserved body of NMB 1751, holotype male of *C. neocaledonicus*: A, dorsal view; B, ventral view (images: AD).

### Morphological comparisons of the type series of *venatoris* and *neocaledonicus*

**External criteria.** Koopman (1971) drew his conclusions largely from examining skins and skulls of the holotype and four paratypes of *C. gouldii venatoris* along with seven skins and skulls of *C. neocaledonicus* from Tiare in the NHML. In addition, he examined a small series from near Townsville, Queensland assigned to *venatoris* by Tate (1942) and one alcohol-preserved specimen of *C. neocaledonicus*, all in the AMNH.

**TABLE 1.** Selected external, skull and dental measurements for specimens of *C. neocaledonicus* and *C. gouldii venatoris*. \* = holotypes.

Registration number	Sex	FA	GL	CON	BASL	C <sup>1</sup> -C <sup>1</sup>	M <sup>3</sup> -M <sup>3</sup>	PAL	CM <sup>3</sup>	ZYG	POC	MASB	BUL	BTB
<i>C. neocaledonicus</i>														
NHML 1919.10.8.16	M	38.7	14.28	14.03	12.39	5.13	7.11	6.87	5.54	10.16	4.46	8.40		
NHML 1919.10.8.17	F	37.8	13.81	13.56	11.80	4.91	6.43	6.52	5.21	9.79	4.45	8.16		
NHML 1919.10.8.18	F	36.7	13.80	13.58	12.11	5.17	6.95	6.66	5.49	10.13	4.62	8.51		
NHML 1919.10.8.19	F	38.7	13.43	13.16	11.79	4.62	6.62	6.48	5.25	9.74	4.45	8.08		
NHML 1919.10.8.20	F	37.6	13.78	13.50	12.05	4.73	6.71	6.58	5.30	9.15	4.57	7.98		
NHML 1919.10.8.21	F	39.7	13.84	13.41	11.97	4.68	6.28	6.34	5.33	9.60	4.48	8.16		
NHML 1919.10.8.22	F	35.9	13.83	13.75	12.22	4.84	6.69	6.42	5.39	10.08	4.38	8.50		
MNHN 2006-650	M	-	14.29	14.03	12.39	5.11	7.01	6.53	5.47	10.33	4.49	8.57	3.29	2.26
MNHN 2006-652	F	-	14.28	14.25	12.45	5.44	7.10	6.93	5.52	10.59	4.57	8.77	3.29	2.35
NMB 1751*	M	36.1	13.71	13.57	12.22	5.13	6.89	6.43	5.39	10.20	4.56	8.45	3.22	2.33
<i>C. gouldii venatoris</i>														
NHML 1906.3.9.4*	F	40.0	13.66	13.85	11.87	5.03	6.80	6.69	5.46	10.33	4.72	8.65		
NHML 1906.3.9.2	M	39.1	13.87	13.93	12.62	5.21	6.87	6.58	5.75	9.65	4.41	8.52		
NHML 1906.3.9.3	M	38.9	14.36	14.28	12.92	-	7.01	7.00	5.63	10.45	4.85	8.70		
NHML 1906.3.9.5	F	39.0	13.81	13.94	12.51	5.26	7.01	6.69	5.49	10.50	4.51	9.03		
NHML 1907.1.4.4	M	39.0	13.87	13.89	12.66	4.85	6.75	6.66	5.51	10.06	5.07	8.96		

In his carefully reasoned decision, Koopman believed that the enlarged terminal ear margin in *gouldii* was a variable, and therefore unreliable character, based on the few alcohol specimens that he examined from Australia. However, at least among Australian taxa, this character is now widely recognised as unique to *C. gouldii* (e.g., Dixon & Lumsden 2008; Baker 2013). Although less easily seen in dried skins, it is clearly visible in the holotype of *venatoris* and the four paratype skins. This feature is quite different in the seven skins of *C. neocaledonicus* from Tiare, in which the outer ear margin terminates in a relatively small skin flap, similar to the condition in the holotype of *C. neocaledonicus* and quite unlike the enlarged flap of *C. gouldii*.

A second diagnostic feature of *C. gouldii* examined by Koopman was the gradient in dorsal fur colour from dark head and shoulders to paler brown rump. Koopman believed that this feature was present in some of the skins from Tiare, thereby negating its diagnostic value for separating *C. gouldii* and *C. neocaledonicus*. We noticed a conspicuous difference in body fur colouration in the type series of *venatoris* compared to the seven skins of *C. neocaledonicus* in the NHML. The head and shoulders of the holotype of *venatoris* are very dark, near black, abruptly changing to a much paler brown on the back and rump. The colour change is also obvious on the ventral surface, where the dark fur of the head and chest changes to paler brown fur but is prominently tipped with pale grey (Fig. 3A–B). Similar fur colouration is evident on dorsal and ventral surfaces of the four paratypes of *venatoris*. Fur colour of the seven skins of *C. neocaledonicus* are quite different from the type series of *venatoris*. Although the seven skins are possibly faded, both ventral and dorsal fur remains a uniform dark red-brown from head to rump and all lack a distinct change to paler fur on the lower half of the body (Fig. 3C–D). These specimens do not approach the sharp demarcation of black shoulders, which grade to the contrasting paler brown rump in the type series of *venatoris*. However, in October 2017 one of us (GH) examined and measured 41 live, adult female *C. neocaledonicus* from a colony in a church in Tendo, north-east Grande Terre and a definite gradient to paler rump fur was evident on the dorsum of at least some of these individuals (Fig. 3E), although this is far less distinct than the contrast typical in *C. gouldii*. In live adult female *C. neocaledonicus* from Tendo, the ventral surface generally graded from a warmer light brown under the chin and neck to a grey-brown in the abdominal area (Fig. 3F).

In summary, we found pronounced differences in fur colour patterns and development of the outer termination of the ear margin between *C. neocaledonicus* and the type series of *C. gouldii venatoris*. The lobe formed by the terminal ear margin is present but rudimentary in *C. neocaledonicus* yet conspicuously enlarged in *C. gouldii venatoris*, as it is in hundreds of live caught and vouchered *C. gouldii gouldii* that we have examined. The sharp contrast in dorsal fur colour between shoulders and rump seen in the type series of *C. gouldii venatoris* is either absent or only weakly developed in *C. neocaledonicus*.

**Cranial and dental criteria.** Koopman was unable to find cranial or dental criteria to distinguish *venatoris* from *neocaledonicus* and this is the final reason cited by him for his decision to relegate *neocaledonicus* to subspecific status. We noticed several differences between the type series of *venatoris* and the ten skulls examined of *C. neocaledonicus*. Our comparisons were based on photographs and require evaluation by direct skull comparisons and measurements. The height of the main cusp of the second upper incisor above the cingulum is nearly half the height of I<sup>1</sup> in *C. neocaledonicus* but in the three *venatoris* skulls that have unworn incisors, I<sup>2</sup> is scarcely a third the height of I<sup>1</sup>. The upper third molars of *C. neocaledonicus* appear to have relatively longer crowns than in the type series of *venatoris*, while the last upper premolar (P<sup>4</sup>) extends closer lingually to a line drawn between the lingual margins of the canine and M<sup>1</sup> in *venatoris* (Fig. 4). The mesopterygoid fossa is relatively broader in all five skulls of *venatoris*, being distinctly wider than long, but is longer than wide in *C. neocaledonicus* (Fig. 4), although occasionally subequal as in the holotype.

### Metric comparisons

**The type series of *venatoris*.** Summary statistics for selected cranial and dental measurements for the type series of *venatoris* and specimens of *C. neocaledonicus* are given in Table 2. Measurement ranges of the type series of *C. gouldii venatoris* either abut or extensively overlap with those of *C. neocaledonicus* for all external and cranial measurements other than D3p1, for which *venatoris* exceeds *C. neocaledonicus* (Table 2), but means for all measured characters of *C. neocaledonicus* are smaller.

Differences in skull proportions between these taxa are evident from bivariate plots, and for the external characters that we measured. Mastoid breadth (MASB) is relatively greater in *venatoris*, as seen in a plot of ZYG vs. MASB (Fig. 5), reflecting a trend for *C. neocaledonicus* of equivalent ZYG to have a narrower braincase than in the type series of *C. gouldii venatoris*. We did not measure bulla length (BUL) in the type series of *venatoris* or in





**FIGURE 3.** Dorsal and ventral pelage colour in holotype of *C. gouldii venatoris* A, dorsal view; and B, ventral view; *C. neocaledonicus* (NHML 1919.10.8.20, female) from Tiare; C, dorsal view; and D, ventral view (images: AD); E and F, adult female *C. neocaledonicus* from Tendo (image: GH). Scale bar = 4 mm.

**TABLE 2.** Summary statistics for selected external and cranial measurements for *Chalinolobus* spp, sexes combined unless otherwise indicated. \* field measurements. Body weights are of non-gravid adult females. Abbreviations for summary statistics are SE, standard error of the mean; SD, standard deviation and CV, coefficient of variation.

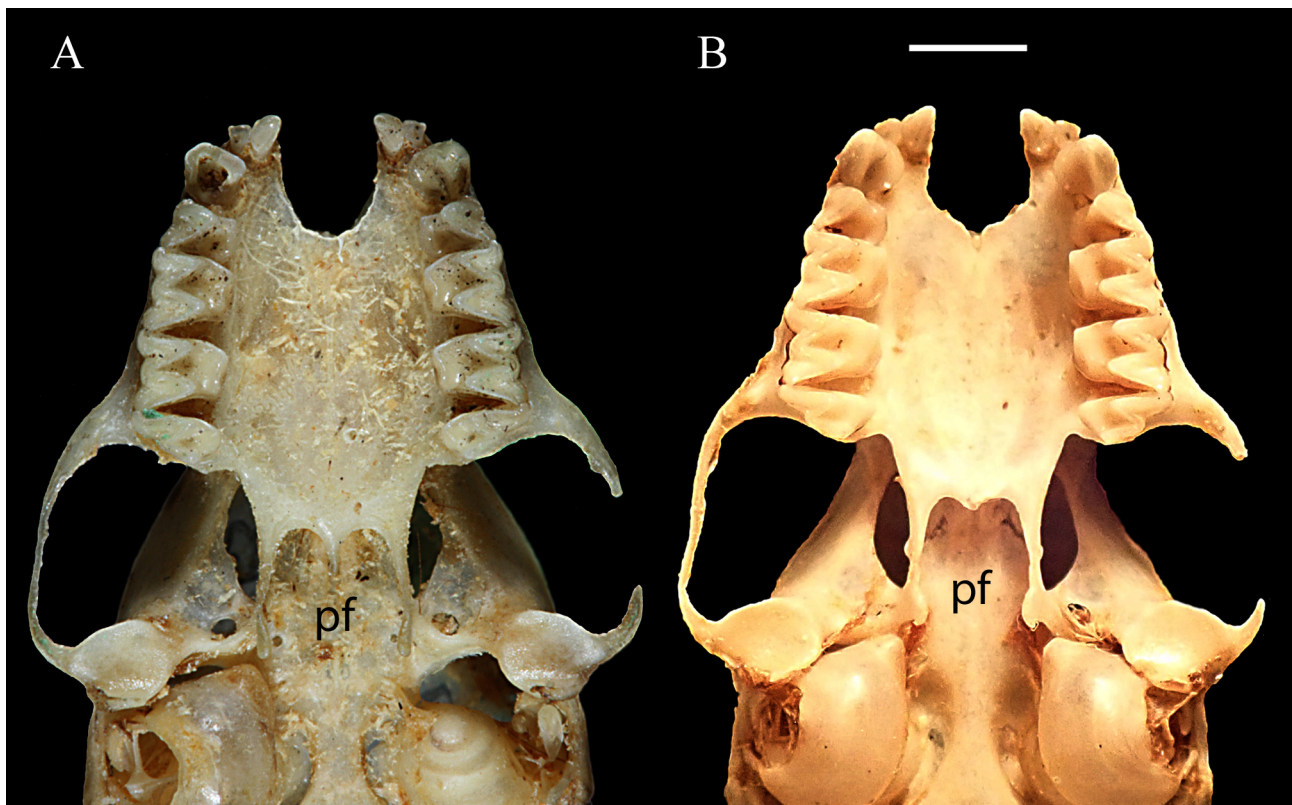
<i>Chalinolobus neocaledonicus</i>							
	Min	Max	Mean	SE	SD	CV	N
<b>FA</b>	35.9	39.7	37.65	0.474	1.341	3.56	8
<b>FA, females*</b>	35.8	40.6	37.71	0.161	1.029	2.73	41
<b>D3p1</b>	13.0	15.3	14.29	0.251	0.710	4.97	8
<b>GL</b>	13.43	14.29	13.905	0.091	0.287	2.06	10
<b>CON</b>	13.16	14.25	13.684	0.105	0.331	2.42	10
<b>BASL</b>	11.79	12.45	12.139	0.075	0.238	1.96	10
<b>C<sup>1</sup>-C<sup>1</sup></b>	4.62	5.44	4.976	0.083	0.262	5.26	10
<b>M<sup>3</sup>-M<sup>3</sup></b>	6.28	7.11	6.779	0.089	0.282	4.16	10
<b>PAL</b>	6.34	6.93	6.576	0.061	0.193	2.93	10
<b>CM<sup>3</sup></b>	5.21	5.54	5.389	0.036	0.115	2.14	10
<b>ZYG</b>	9.15	10.59	9.977	0.131	0.413	4.14	10
<b>POC</b>	4.38	4.62	4.503	0.023	0.074	1.64	10
<b>MASB</b>	7.98	8.77	8.358	0.079	0.251	3.00	10
<b>WT, females*</b>	7.8	11.0	9.46	0.095	0.610	6.45	41
<i>Chalinolobus gouldii venatoris</i> type series							
	Min	Max	Mean	SE	SD	CV	N
<b>FA</b>	38.9	40.0	39.20	0.198	0.442	1.13	5
<b>D3p1</b>	16.5	17.5	16.92	0.166	0.370	2.19	5
<b>GL</b>	13.66	14.36	13.914	0.118	0.264	1.90	5
<b>CON</b>	13.85	14.28	13.978	0.077	0.173	1.23	5
<b>BASL</b>	11.87	12.92	12.516	0.175	0.391	3.13	5
<b>C<sup>1</sup>-C<sup>1</sup></b>	4.85	5.26	5.088	0.093	0.187	3.67	4
<b>M<sup>3</sup>-M<sup>3</sup></b>	6.75	7.01	6.888	0.053	0.119	1.73	5
<b>PAL</b>	6.58	7.00	6.724	0.072	0.161	2.39	5
<b>CM<sup>3</sup></b>	5.46	5.75	5.568	0.054	0.121	2.16	5
<b>ZYG</b>	9.65	10.50	10.198	0.157	0.351	3.44	5
<b>POC</b>	4.41	5.07	4.712	0.118	0.264	5.61	5
<b>MASB</b>	8.52	9.03	8.772	0.096	0.215	2.46	5
<b>WT</b>							0
<i>Chalinolobus nigrogriseus nigrogriseus</i>							
	Min	Max	Mean	SE	SD	CV	N
<b>FA</b>	31.9	38.0	35.57	0.131	1.145	3.22	76
<b>FA, females*</b>	33.8	37.5	35.98	0.164	0.852	2.37	27
<b>FA, males*</b>	31.9	38.0	35.35	0.176	1.230	3.48	49
<b>D3p1</b>	14.0	16.4	15.19	0.214	0.676	4.45	10
<b>CON</b>	12.00	13.00	12.627	0.083	0.276	2.19	11
<b>C<sup>1</sup>-C<sup>1</sup></b>	4.10	4.80	4.417	0.058	0.199	4.51	12
<b>M<sup>3</sup>-M<sup>3</sup></b>	5.90	6.40	6.163	0.040	0.137	2.22	12
<b>CM<sup>3</sup></b>	4.70	5.10	4.900	0.041	0.147	3.00	13
<b>ZYG</b>	9.10	9.60	9.278	0.068	0.205	2.21	9
<b>POC</b>	3.80	4.50	4.125	0.064	0.222	5.38	12
<b>WT, females*</b>	5.5	7.5	6.51	0.212	0.672	10.31	10
<b>WT, males*</b>	5.0	7.0	6.10	0.134	0.656	10.76	24

the series of *C. neocaledonicus* from Tiare; however Tidemann's (1986) data indicate that mean BUL is larger in *venatoris* (Fig. 6). Although ranges of FA overlap, specimens of *venatoris* have longer D3p1 relative to FA than *C. neocaledonicus* (Fig. 7).

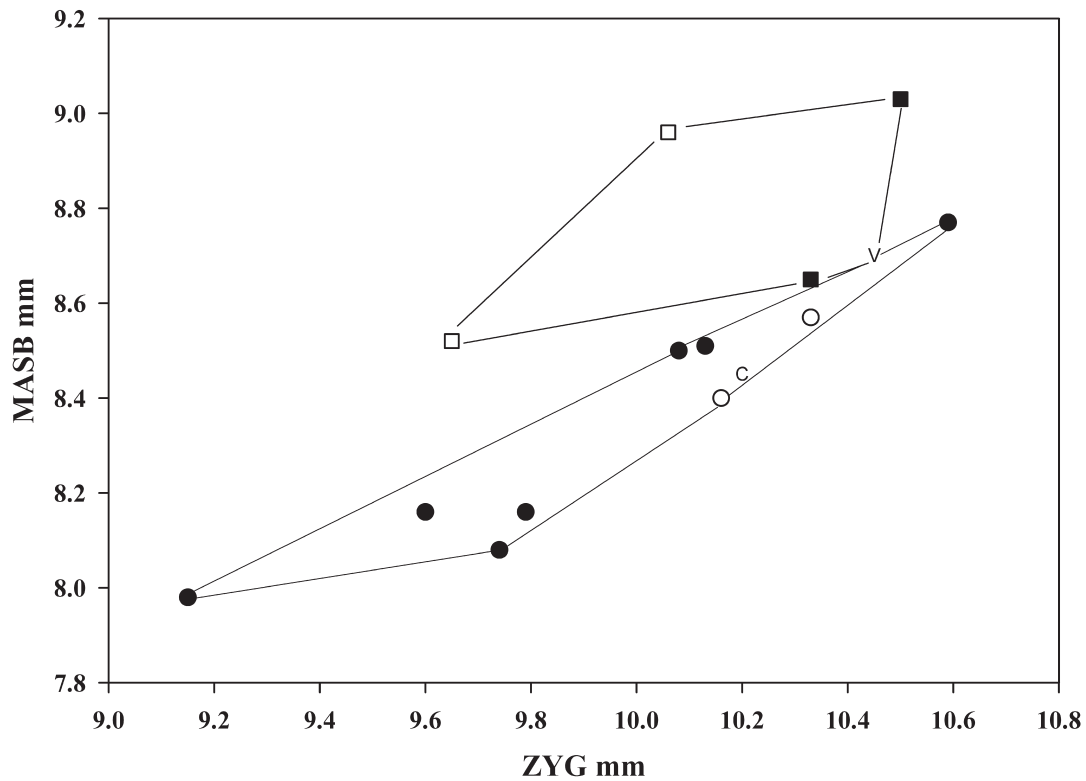
Multivariate analyses of eight cranial measurements were used to determine whether skulls of the type series of *venatoris* could be separated from *neocaledonicus* but there was no separation. Partial overlap of both taxa was found on the first two axes of a PCA using a correlation matrix (Fig. 8A). The first two PC axes accounted for a large proportion (63.3%) of the variance in these measurements and although the two groups overlapped, the direction of variation within each group was highly divergent on these axes. This possibly reflects differences in skull shape. Alternatively, it might be an artefact of the high positive score of an outlier specimen of *venatoris* on PC axis 2. Character loadings on the first two PC axes (Table 3) and inspection of individual measurements for each specimen (Table 1) suggest that the first PC axis reflected an overall increase in absolute skull size. Specimen scores on the second axis are dominated by a trend of an inverse relationship between POC relative to both  $CM^3$  and  $M^3-M^3$ , i.e. specimens of *venatoris* tend to have longer  $CM^3$  and proportionately broader POC.

Specimen scores of both taxa formed discrete groups on the first two axes in a further PCA that included FA in addition to the eight cranial measurements (Fig. 8B). Character loadings reveal that this separation was driven on the first axis largely by an overall increase in skull size, as indicated by positive loadings of similar magnitude for cranial characters but with little contribution from FA, combined with a second axis largely reflecting an inverse relationship between FA and POC against remaining characters (Table 4). The character loadings on the first two PC axes can be interpreted to indicate that individuals with the largest skulls tend to have proportionately longer FA and POC, in this instance, *venatoris* of similar skull size to *neocaledonicus* tend to have longer FA and broader POC (Table 1). Individuals of each group overlapped on the third and all subsequent PC axes of this analysis.

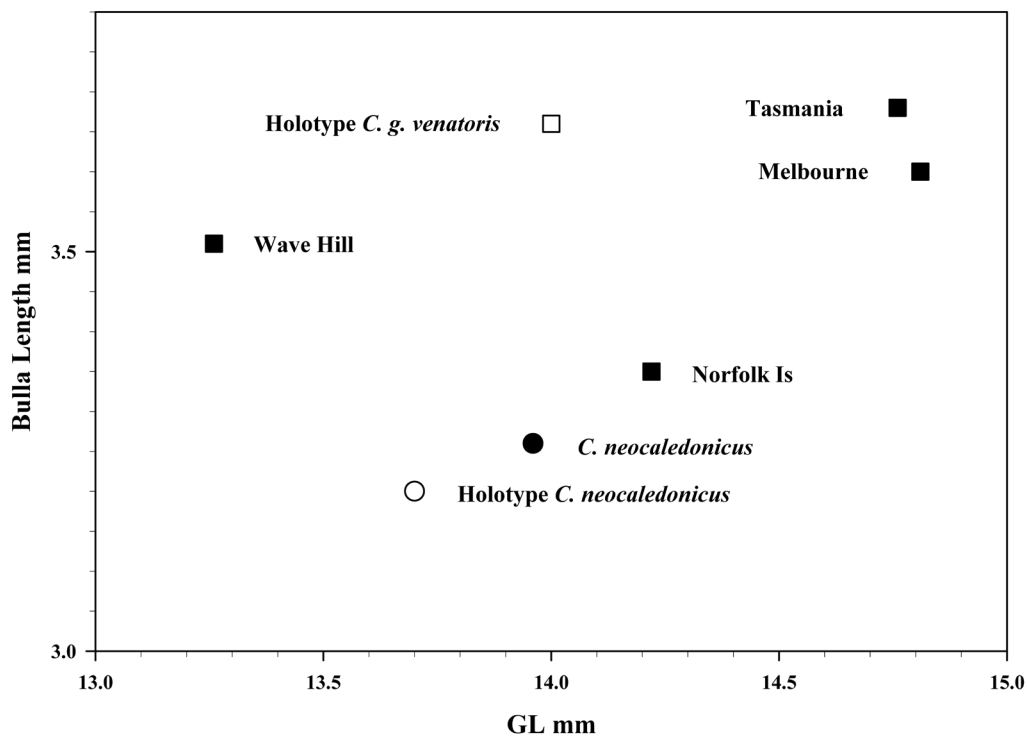
In summary, skulls of the type series of *venatoris* could not be clearly distinguished from those of *C. neocaledonicus* solely on the eight measurements used in these analyses. Both groups are distinguished in the PCA using FA in combination with cranial measurements and in a plot of FA vs. D3p1.



**FIGURE 4.** Differences in the relative breadth of the mesopterygoid fossa (pf) in skulls of A, *C. gouldii venatoris* (NHML 1906.3.9.4, holotype female; image: GH); B, *C. neocaledonicus* (NHML 1919.10.8.22, female; image: AD). Scale bar = 2 mm.



**FIGURE 5.** Plot of zygomatic breadth (ZYG) vs. mastoid breadth (MASB) showing trend for relatively broader MASB in type series of *C. gouldii venatoris* (squares) compared to *C. neocaledonicus* (circles). V = holotype female of *C. g. venatoris*, C = holotype male of *C. neocaledonicus*. Open symbols are males, solid symbols are female.



**FIGURE 6.** Mean greatest skull length (GL) vs. mean bulla length showing smaller mean bulla length of *C. neocaledonicus* compared with sample means of *C. gouldii* (squares) from Tidemann (1986): Tasmania (n = 10), Melbourne, Victoria (n = 9), Norfolk Island (n = 4) and Wave Hill, Northern Territory (n = 9), plus measurements for the holotypes of *C. gouldii venatoris* (open square) and *C. neocaledonicus* (open circle).

**Comparisons with *C. nigrogriseus nigrogriseus*.** All previous authors have treated *C. nigrogriseus* as a species distinct from *neocaledonicus* but morphological comparisons of these taxa have not been published other than the original description of *neocaledonicus* by Revilliod (1914). He believed that *C. neocaledonicus* most resembled *C. nigrogriseus* and that both shared a uniform dorsal fur colouration and a similar, unenlarged flap on the terminal outer ear margin. However, his assessment was based on one specimen of *neocaledonicus* and two that he regarded to be *C. nigrogriseus*. He regarded the smaller form *rogersi* to be a valid species. Specimens of *neocaledonicus* examined in this study leave little doubt that *neocaledonicus* and *nigrogriseus* are distinct taxa. We set out other differences that we observed below, which will need to be verified using larger samples, and we do not attempt a comprehensive morphological comparison in this study.

**TABLE 3.** Character loadings and percentage of variance of each axis in a PCA based on a correlation matrix of eight cranial measurements of *C. neocaledonicus* and the type series of *C. gouldii venatoris*.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8
CON	0.406	-0.080	-0.055	-0.090	-0.643	0.157	0.435	-0.436
BASL	0.380	0.032	0.372	0.308	-0.369	-0.564	-0.282	0.296
M <sup>3</sup> -M <sup>3</sup>	0.375	-0.320	0.014	-0.279	0.531	-0.515	0.202	-0.303
PAL	0.351	0.114	0.221	-0.704	-0.022	0.306	-0.462	0.105
CM <sup>3</sup>	0.341	-0.347	0.430	0.364	0.285	0.520	0.208	0.226
ZYG	0.356	-0.045	-0.673	-0.063	-0.005	0.001	0.175	0.620
POC	0.208	0.856	0.163	0.038	0.239	-0.015	0.372	0.021
MASB	0.376	0.151	-0.381	0.432	0.174	0.164	-0.514	-0.429
Eigenvalue	5.064	1.000	0.723	0.583	0.287	0.189	0.090	0.065
% variance	63.30	12.50	9.03	7.28	3.59	2.36	1.13	0.81

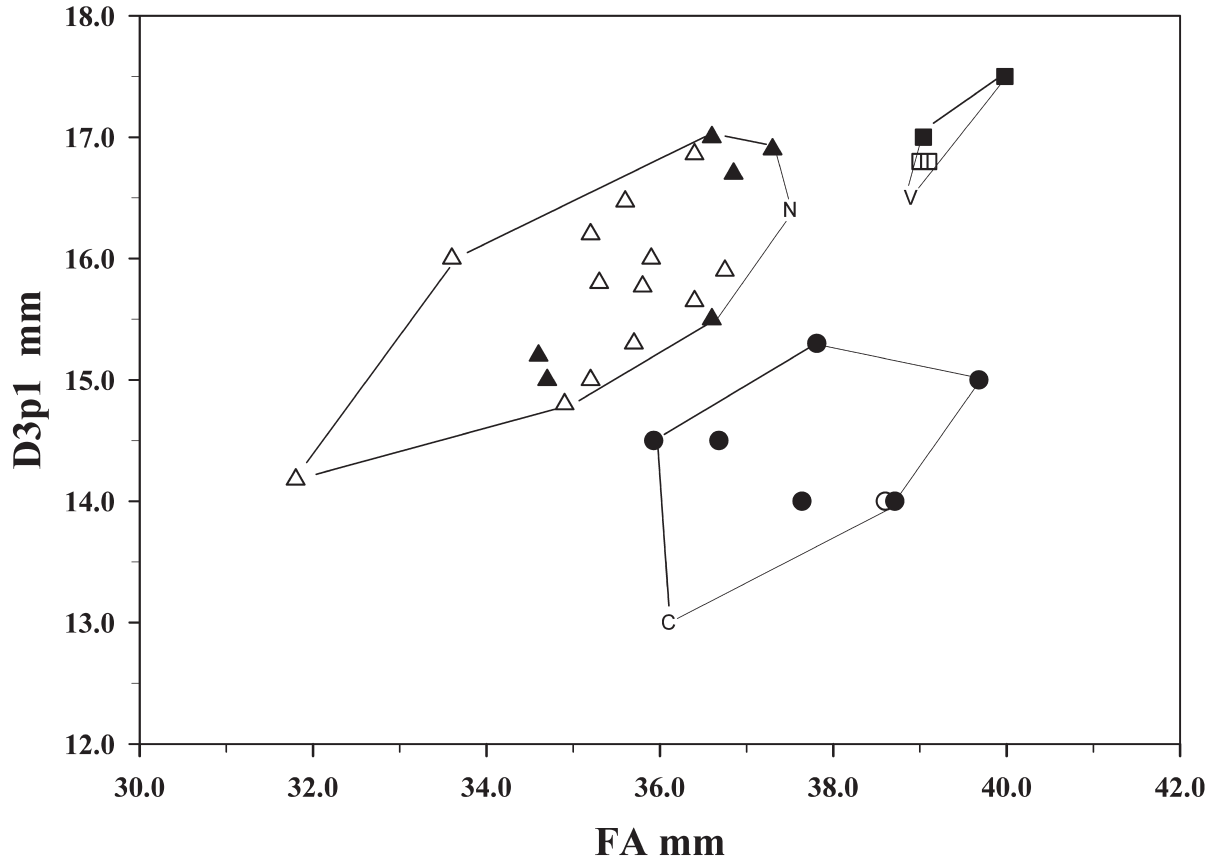
**TABLE 4.** Character loadings and percentage of variance of each axis in a PCA based on a correlation matrix of FA and eight cranial measurements of *C. neocaledonicus* and the type series of *C. gouldii venatoris*.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
FA	0.040	0.750	0.345	0.310	0.320	0.016	0.198	0.116	0.256
CON	0.405	-0.079	0.023	-0.004	0.115	-0.639	-0.445	-0.127	0.440
BASL	0.380	0.060	0.132	-0.131	-0.511	-0.393	0.592	0.183	-0.134
M <sup>3</sup> -M <sup>3</sup>	0.372	-0.315	0.144	-0.251	0.117	0.509	0.266	0.032	0.578
PAL	0.353	0.160	0.042	-0.532	0.509	-0.006	0.040	-0.269	-0.482
CM <sup>3</sup>	0.341	0.008	0.567	0.114	-0.314	0.302	-0.504	0.152	-0.286
ZYG	0.354	-0.224	-0.322	0.402	0.375	0.001	0.042	0.605	-0.225
POC	0.210	0.501	-0.589	-0.292	-0.307	0.229	-0.264	0.199	0.129
MASB	0.376	0.031	-0.260	0.531	-0.131	0.184	0.125	-0.659	-0.086
Eigenvalue	5.070	1.354	0.879	0.608	0.561	0.287	0.122	0.071	0.047
% variance	56.34	15.05	9.77	6.75	6.23	3.19	1.36	0.79	0.52

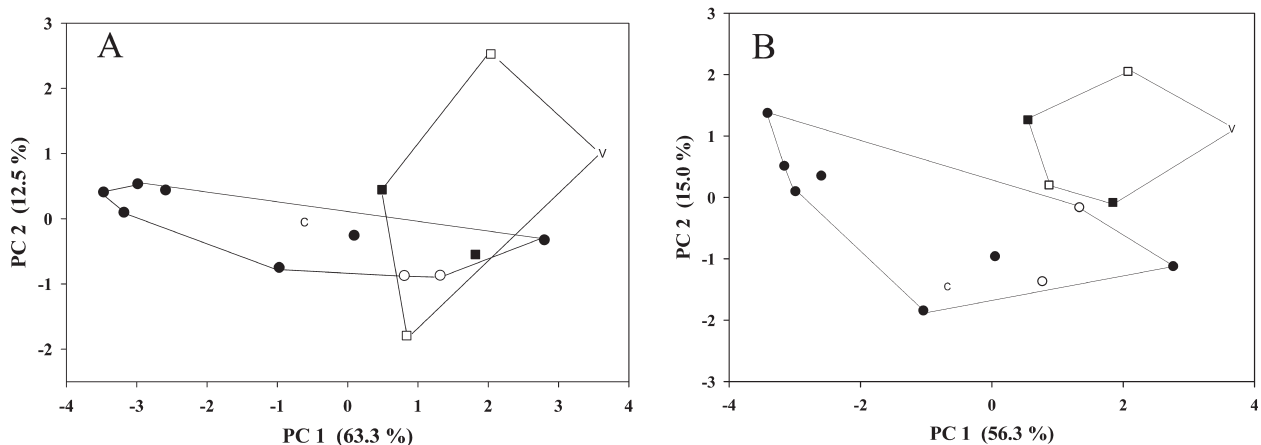
Based on photographs taken from multiple angles, we observed several pronounced differences between the holotype skulls of the unsexed adult *C. nigrogriseus* and the adult male *C. neocaledonicus*. In profile, the braincase of *C. nigrogriseus* drops gradually anteriorly to the rostrum but is a steep descent in *C. neocaledonicus*. The infra-orbital swellings are not only more enlarged but also more robust in *C. neocaledonicus*. The second upper incisor of the holotype of *C. nigrogriseus* is smaller relative to I<sup>1</sup>, similar to that of the holotype of *C. gouldii venatoris*. The upper third molars are distinctly less “reduced” in the holotype of *C. nigrogriseus* and another specimen of that species examined by Revilliod (NMB 235), compared to those of *C. neocaledonicus*, as noted by Revilliod (1914). Specifically, crown length of M<sup>3</sup> is shorter relative to breadth although M<sup>3</sup> morphology is otherwise similar in both species.

The ranges of measurements for FA, D3p1 and six skull characters of *C. nigrogriseus* abut or overlap with those of *C. neocaledonicus* but means for all measurements of *C. nigrogriseus* are smaller, with the exception of

D3p1 (Table 2). Although there is extensive overlap in FA measurements between both taxa, *C. neocaledonicus* of equivalent FA length have longer skulls (CON) and longer tooththrows (CM<sup>3</sup>), see Fig. 9. Mean D3p1 is larger (Table 2), and D3p1 is longer relative to FA, in *C. nigrogriseus* (Fig. 7). However, there is a possibility that this difference is an artefact of preservation. Whereas all *C. nigrogriseus*, other than the holotype, were measured from alcohol-preserved specimens, all *venatoris* and most *C. neocaledonicus* were measured from scaled photographs of skins. It is therefore possible that D3p1 could have been shorter if taken from dry specimens, due to potential bone or cartilage shrinkage (Arata 1968).

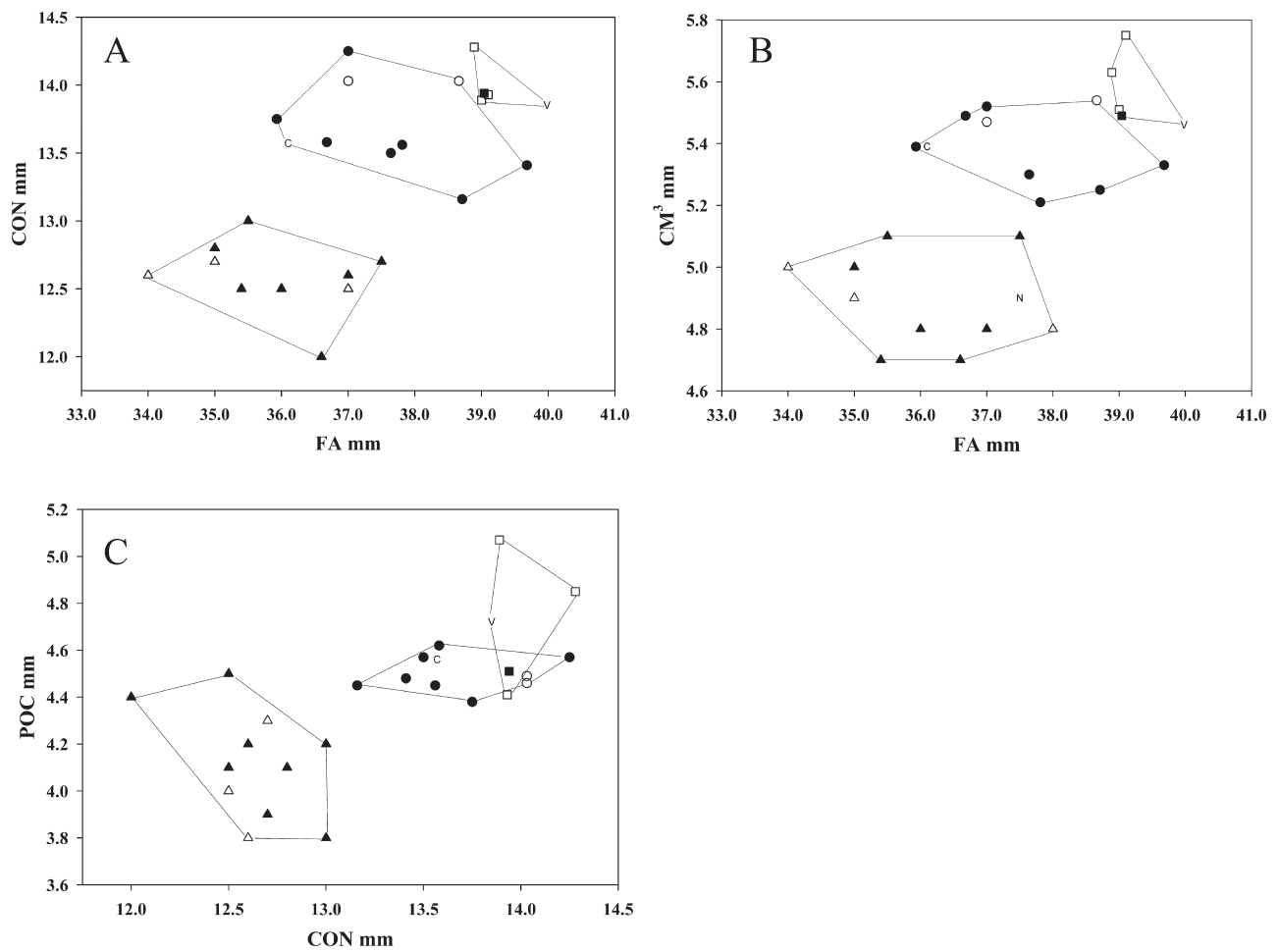


**FIGURE 7.** Plot of forearm length (FA) vs. length of first phalanx of third digit (D3p1) showing separation of type series of *C. g. venatoris* (squares), *C. neocaledonicus* (circles), and *C. nigrogriseus* (triangles). Holotypes are: V, *C. g. venatoris* female; C, *C. neocaledonicus* male, and N, *C. nigrogriseus* indeterminate sex. Open symbols are males, solid symbols are females.

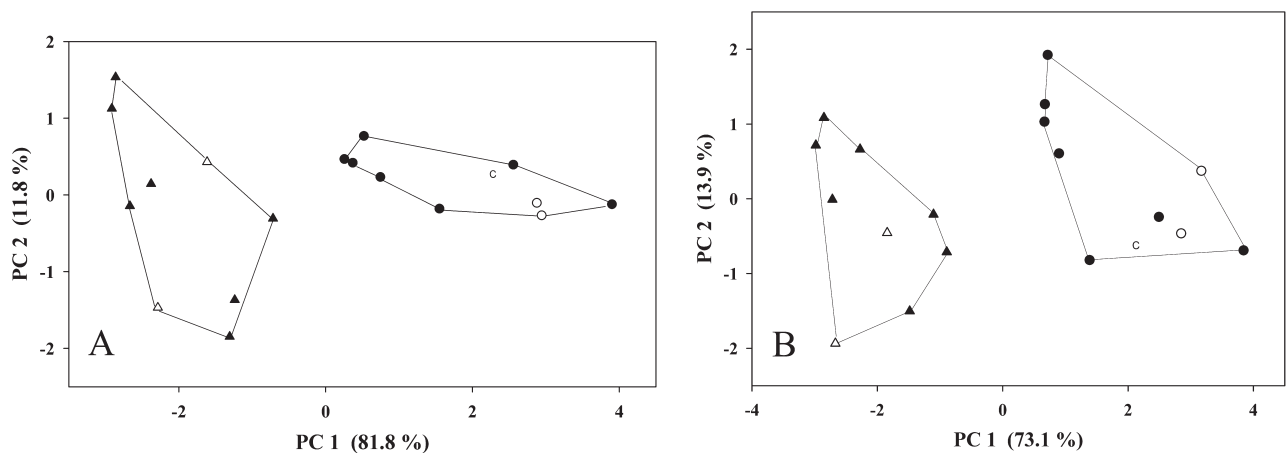


**FIGURE 8.** Plot of specimen scores on the first two axes of a PCA using a correlation matrix of A, eight cranial measurements; B, the same eight characters and FA. Symbols are: the type series of *C. gouldii venatoris* (squares), *C. neocaledonicus* (circles), holotype female of *C. g. venatoris* (V) and holotype male of *C. neocaledonicus* (C). Open symbols are males, solid symbols are females.

Although measurement ranges for CON and  $CM^3$  abut and overlap for POC (Table 2), the majority of skulls of both species can be reliably separated by the larger size of *C. neocaledonicus*: e.g.,  $CON > 13.1$  mm,  $CM^3 > 5.1$  mm (Fig. 9A–C).



**FIGURE 9.** Species separation on plots of FA (forearm length) vs. A, CON (condylo-basal skull length) and B, canine-posterior molar length ( $CM^3$ ); and C, CON vs. post-orbital constriction (POC). Symbols are: the type series of *C. g. venatoris* (squares), *C. neocaledonicus* (circles) and *C. nigrogriseus* (triangles). V = holotype female of *C. g. venatoris*, and C = holotype male of *C. neocaledonicus* (CON not available for incomplete holotype skull of *C. nigrogriseus*). Open symbols are males, solid symbols are females.



**FIGURE 10.** Plot of specimen scores on the first two axes of a PCA using a correlation matrix of A, six cranial measurements; B, the same six characters and FA. Symbols are *C. neocaledonicus* (circles, C is holotype) and *C. nigrogriseus* (triangles). Open symbols are males, solid symbols are females.

Clear separation of *C. nigrogriseus* and *C. neocaledonicus* is evident on the first axis of a PCA based on the six available cranial measurements (Fig. 10A). Character loadings suggest that PC 1 largely reflects overall size while scores on PC 2 are dominated by POC (Table 5). A PCA involving FA and the six craniodental measurements produced a similar pattern of separation between specimens of *C. nigrogriseus* and *C. neocaledonicus* on the first two PC axes (Fig. 10B), with the first axis reflecting skull size and the second dominated by FA and POC (Table 6). The second axis of both PCAs are interpreted to indicate a relatively smaller increase in FA and POC with increasing absolute size, compared to remaining characters.

**TABLE 5.** Character loadings and percentage of variance for each axis in a PCA based on a correlation matrix of six cranial measurements of *C. neocaledonicus* and *C. nigrogriseus*.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
CON	0.435	-0.065	0.352	0.533	-0.125	-0.618
ZYG	0.421	-0.053	-0.841	0.243	-0.217	0.077
POC	0.271	0.947	0.066	0.016	0.101	0.123
CM <sup>3</sup>	0.433	-0.188	0.403	-0.001	-0.448	0.644
C <sup>1</sup> -C <sup>1</sup>	0.430	-0.243	0.039	0.027	0.844	0.202
M <sup>3</sup> -M <sup>3</sup>	0.433	-0.047	-0.018	-0.810	-0.117	-0.376
Eigenvalue	4.910	0.710	0.166	0.112	0.066	0.036
% variance	81.83	11.84	2.76	1.86	1.10	0.60

**TABLE 6.** Character loadings and percentage of variance for each axis in a PCA based on a correlation matrix of FA and six cranial measurements of *C. neocaledonicus* and *C. nigrogriseus*.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7
FA	0.220	0.764	-0.562	0.213	0.027	0.035	-0.076
CON	0.425	-0.086	-0.049	-0.362	-0.566	-0.180	-0.571
ZYG	0.405	-0.211	0.166	0.836	-0.182	-0.175	0.025
POC	0.275	0.535	0.765	-0.143	-0.030	0.091	0.150
CM <sup>3</sup>	0.424	-0.108	-0.218	-0.304	-0.013	-0.433	0.693
C <sup>1</sup> -C <sup>1</sup>	0.417	-0.225	-0.139	-0.067	-0.036	0.850	0.167
M <sup>3</sup> -M <sup>3</sup>	0.421	-0.126	0.041	-0.086	0.802	-0.133	-0.370
Eigenvalue	5.118	0.977	0.561	0.134	0.111	0.065	0.033
% variance	73.12	13.95	8.01	1.92	1.59	0.93	0.47

In summary, *C. neocaledonicus* is a larger species than *C. nigrogriseus*. This is reflected in mean body weight of females, for which *C. neocaledonicus* is considerably heavier (9.46 vs. 6.51 g, see Table 2).

## Discussion

The consistent morphological differences that we found between the type series of *C. gouldii venatoris* and *C. neocaledonicus* clearly supports recognition of *C. neocaledonicus* as a distinct species. Although *C. neocaledonicus* was recognised as a valid species prior to our study, that arrangement was tentative and its past synonymy with Australian *C. gouldii* meant that its status has remained uncertain. We provide the first study to resolve its status and clarify the confusion with *C. gouldii* that has persisted since Koopman (1971) proposed *neocaledonicus* as a subspecies of *C. gouldii*. The unenlarged flap, or lobe, formed by the relatively short, downturned ear margin in all voucher specimens of *C. neocaledonicus* that we examined is similar to that of *C. nigrogriseus*, but distinct from the enlarged condition which is now widely recognised as unique to *C. gouldii*. These distinctions alone, would suggest that *C. gouldii* and *C. neocaledonicus* are different species. The condition of the flap formed by the terminal ear margin is not easily interpreted from the dried skins of *C. neocaledonicus* from Tiare in the NHML, but we drew from familiarity with ear structure in all species of Australian *Chalinolobus* through extensive field experience of



live animals. Past taxonomic assessments did not recognise the significance of this feature, which is probably the primary source of taxonomic confusion surrounding *C. neocaledonicus*. Koopman (1971) examined this character but did not recognise its significance, and it is not mentioned by Tidemann (1986). Flannery (1995) was uncertain whether the terminal ear lobe of *C. neocaledonicus* resembled the enlarged condition of *C. gouldii*.

Our conclusions support the assessment by Revilliod (1914), that his new species *C. neocaledonicus* had an unenlarged terminal ear margin similar to *C. nigrogriseus*, in marked contrast to the enlarged terminal ear margin of *C. gouldii*. He also believed that both species differed from *C. gouldii* in having uniform rather than contrasting dorsal fur colouration, but his assessment of fur colour was presumably based on a specimen in alcohol in which a colour gradient, unless pronounced, would be hard to detect. Revilliod (1914) made only a passing reference to *C. gouldii*, perhaps because he believed that it was so distinct from *C. neocaledonicus* and *C. nigrogriseus* that it did not warrant further comment. However, although a colour gradient in dorsal fur is not evident in the alcoholic holotype of *C. neocaledonicus*, it is apparent that a colour gradient exists in some of the live specimens examined by one of us (GH) but this gradient is not nearly as distinct as is typically found in *C. gouldii*. It is possible that fur colour has faded in the *C. neocaledonicus* skins from Tiare in the NHML, particularly if the skins were prepared from specimens initially preserved in alcohol. Revilliod (1914) based his assessment on very few specimens and did not diagnose his new species with respect to *C. gouldii venatoris*, the type series of which approximates *C. neocaledonicus* in skull and body size. Although described six years earlier by Thomas (1908), *venatoris* is not mentioned in Revilliod's (1914) paper. We examined most of the material used by Koopman (1971) in his evaluation of *C. neocaledonicus* and *C. gouldii venatoris*, i.e. the seven skins of *C. neocaledonicus* from Tiare and the holotype skin and four paratype skins of *C. gouldii venatoris* in the NHML. Contrary to Koopman, we found that the enlarged ear margin was present in the type series of *venatoris*, and invariably greatly reduced in the seven *C. neocaledonicus* from Tiare. We suspect that both taxa can be distinguished from each other by the relatively larger P<sup>4</sup> and relatively broader meso-pterygoid fossa in *venatoris* (features not mentioned by Koopman), but our assessment is based on photographs and requires confirmation by direct comparison of skulls.

To fully re-diagnose *C. neocaledonicus* our study needs to be expanded by a more comprehensive morphological comparison of cranial, dental and external criteria. This is necessary both to test the validity of our diagnostic criteria in larger samples, and to explore other likely differences between these taxa that we could not resolve. A number of cranial characters that are regarded as potentially informative for diagnosing species of the genus should be examined. These include relative size of I<sup>2</sup>, morphology of third molars, relative braincase height, the degree of inflation of the supra-orbital processes, the relative breadth of inter-orbital to post-orbital breadths and bullae size (Tate 1942; Ryan 1966). Several external features should also be assessed, including possible differences in tragus shape, degree of wrinkling of the lips, and differences in the proportions of wing elements and body proportions. These are best done on alcohol-preserved or live animals. Species comparisons should also be extended to include the New Zealand endemic *C. tuberculatus*. There has been a rapid expansion of ecological knowledge of *C. tuberculatus* (reviewed by O'Donnell 2005), but we found insufficient descriptive information or measurements of *C. tuberculatus* in the traditional taxonomic literature to enable inclusion in our assessment of *C. neocaledonicus*. We have not found cranial measurements or descriptive morphological studies of the species, other than geographic variation in forearm length and body weight between the north and south islands (summarised by O'Donnell 2005), a brief description of the skull and dentition of one skull of *C. tuberculatus* in the AMNH (Koopman 1971), and a small number of cranial measurements incidentally given by Tate (1942). Both species are of similar size, based on measurements of forearm length, condylo-basal length and body weight summarised by O'Donnell (2001, 2005).

The relationships of *C. neocaledonicus* to other species of the genus are poorly understood and best explored using DNA techniques. We suggest that molecular investigations should prioritise comparisons of *C. nigrogriseus nigrogriseus*, *C. tuberculatus* and both northern and southern Australian samples of *C. gouldii*. Samples of *C. gouldii* from latitudes north of c. 20°S have the best chance of sampling *C. gouldii venatoris*, if it is a valid entity, as discussed below. The status of *C. rogersi* Thomas, 1909 is unresolved, but is currently treated as a synonym of *C. nigrogriseus* by most authors, either as a western subspecies (e.g., Simmons 2005), or as a synonym of *C. nigrogriseus nigrogriseus* (e.g., Burbidge *et al.* 2014). Consequently, we recommend that samples of *C. nigrogriseus* are sourced from localities away from potential overlap with *C. nigrogriseus rogersi*, i.e. either southern Queensland or New South Wales, or north-eastern Queensland, along with material of *C. nigrogriseus* from Western Australia. Van Deusen & Koopman (1971) suggest both forms potentially intergrade in a region from west of the Dividing Range to the Gulf of Carpentaria, but if they are distinct taxa, this will be an overlap zone.

The distinction between the enlarged terminal ear flap of *C. gouldii* and the comparatively rudimentary condition found in *C. neocaledonicus* and its diagnostic value has been misunderstood. We recommend that this character is carefully examined in any future identification of *Chalinolobus* from New Caledonia to ensure that additional, overlooked species are not present. We examined this character in eight of the 13 museum voucher specimens of *C. neocaledonicus* known to us. Although we examined and measured skulls of two of the three Paris specimens, we were unable to examine their alcohol bodies to check this feature, and we did not examine the remaining two specimens, viz, one each at AMNH and ANUZ. The extent of morphological variation within *C. neocaledonicus* remains to be defined, partly because it is so poorly represented in research collections. Half of the voucher specimens in world collections were obtained from a tree hollow in Tiare, and those specimens are faded or bleached, and are dried skins, thereby hindering a comprehensive assessment of external morphology. In particular, variation of adult males remains poorly defined. The insectivorous bat fauna of New Caledonia remains comparatively poorly known and needs further targeted bat surveys that use live capture techniques such as mist-nets and harp traps.

**The status of *C. gouldii venatoris*.** The validity of a smaller, darker subspecies *C. gouldii venatoris* from northern Australia was widely accepted in the past but many authors have not recognised *venatoris* following publication of the influential study by Tidemann (1986). He conducted a multivariate analysis of cranial and wing measurements and concluded that *neocaledonicus* was the same species as *C. gouldii* and argued that subspecies recognition within *C. gouldii* was meaningless. He found that sample means of 24 cranial and wing measurements from northern Australian localities were smaller than southern localities, which he interpreted as reflecting size gradients that correlate with latitude and to a lesser extent with longitude. Significantly, Tidemann's (1986) conclusion that *neocaledonicus* and *venatoris* were the same species as *C. gouldii* seems to have been based entirely on measurements, given that non-metric criteria are not mentioned.

Our primary focus of resolving the status of *C. neocaledonicus* required a re-assessment of the original material and justifications used by Koopman (1971) for his decision to synonymise *C. neocaledonicus* with *C. gouldii*. This could be achieved by restricting our taxon comparisons to the type series of *venatoris* without inclusion of additional material from northern Australia. Although we do not attempt to resolve the taxonomic validity of *venatoris*, we provide a re-interpretation of the results of Tidemann's study. We suggest that his data can be interpreted as providing support for recognition of *venatoris*, although previous assessments have invoked his study as evidence that *venatoris* is not a valid entity.

Tidemann (1986) selected FA to illustrate geographic trends in his fig. 3 plots of FA against latitude and longitude. We have reconstructed his fig. 3, but have excluded his samples from Norfolk Island and New Caledonia so that geographic trends in mainland Australia are more apparent (Fig. 11). Two distinct trends are evident in his fig. 3 which could be interpreted as suggesting two groups of *C. gouldii*: a southern group with a continuum of decreasing average size north to about latitude 24°S (his sample from Alice Springs, Northern Territory), followed by an abrupt shift to a smaller size north of about 21°S (his samples from Mount Isa, Queensland and Wave Hill, Northern Territory). Tidemann's sample from Karonie (south-western Western Australia) adds to the impression of a possible difference in FA (and overall size) between our speculated far northern and southern groups in his plot of FA vs. longitude. Further, Tidemann's fig. 3 suggests that the smaller northern group have FA less than 41 mm, with minor size overlap with more southern animals. The stepped size cline does not appear to be a product of sexual size dimorphism from samples biased by sex. The magnitude of differences between mean FA for samples north and south of about latitude 21°S far exceeds mean FA differences of less than 1 mm between each sex reported for large samples from southern Australia (e.g., Taylor *et al.* 1987; Lumsden & Bennett 1995; Young & Ford 2000).

Whether the trends in Tidemann's analysis are maintained with larger data sets remains to be tested, but our interest is in examining the basis upon which Tidemann reached his conclusions about the status of *venatoris*. He does not specifically address the validity of *venatoris* in relation to the sharp reduction in size over a span of four degrees latitude that is noted here.

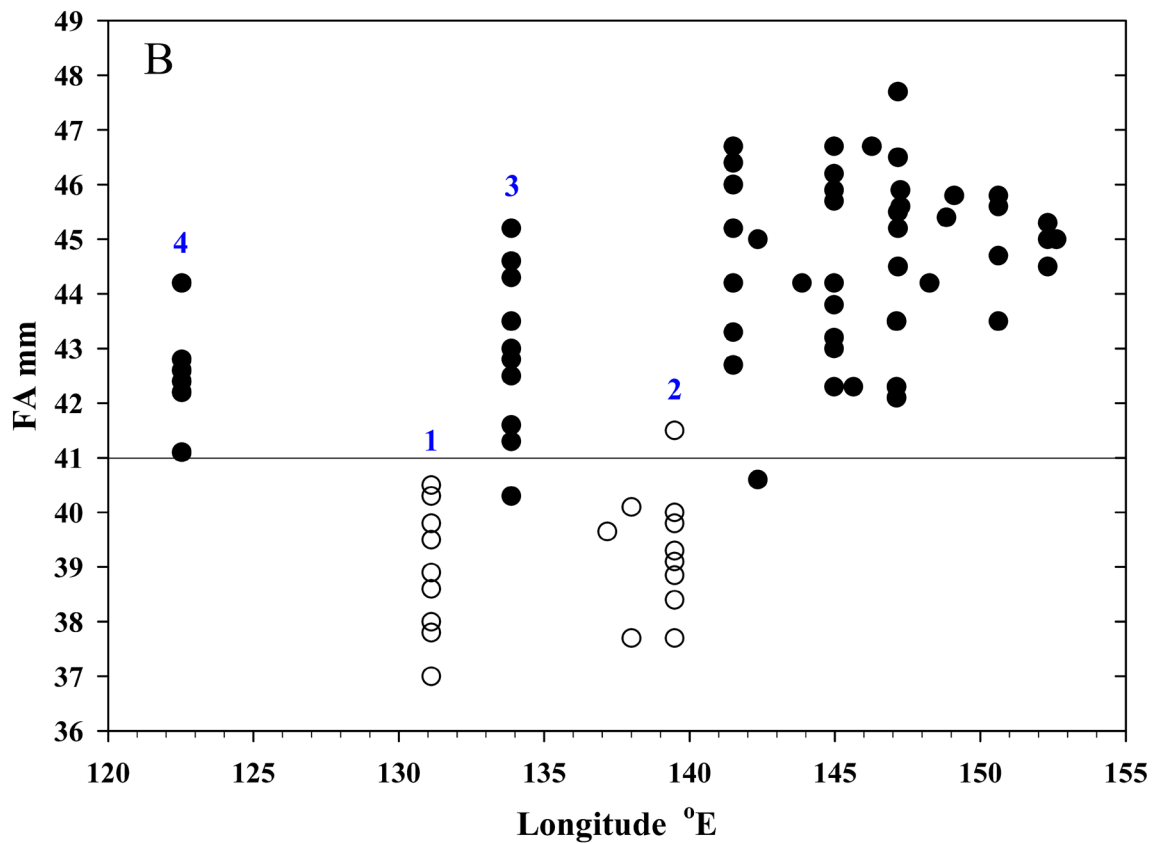
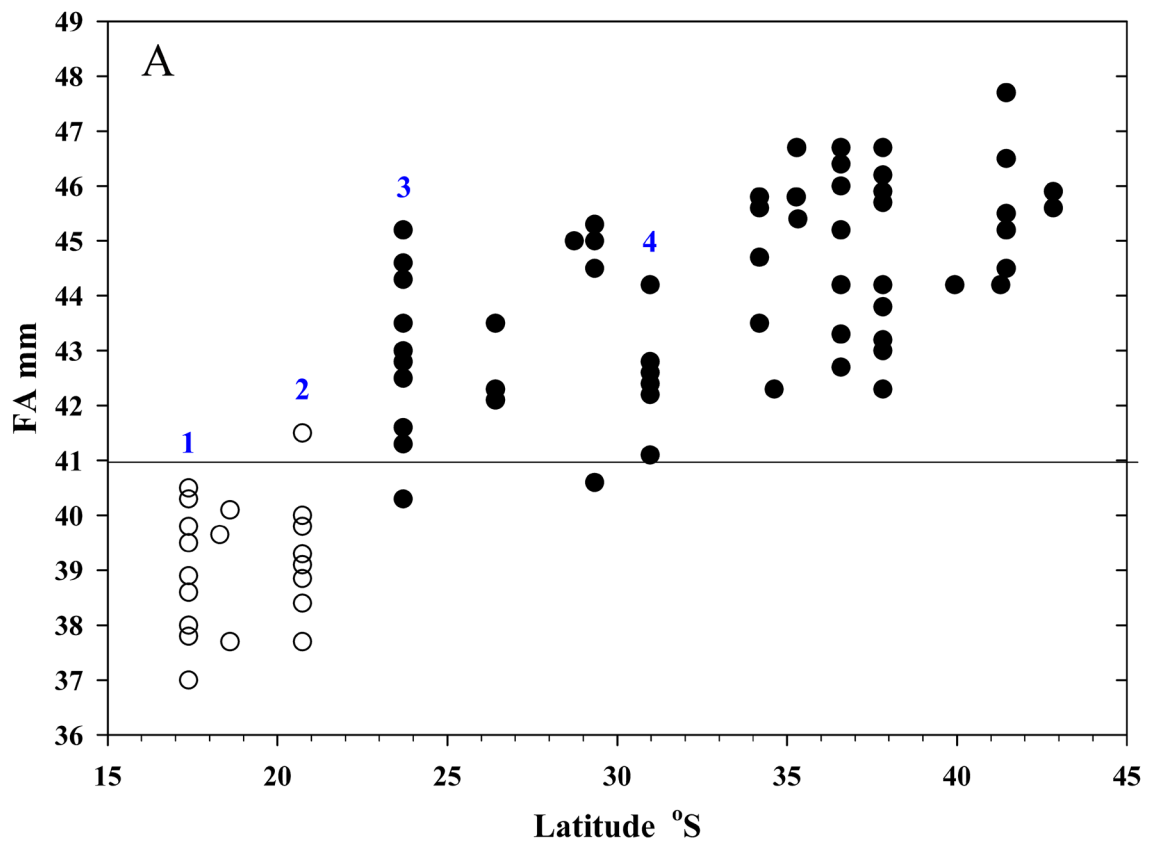
Tidemann (1986) expressed the view that the use of subspecies within *C. gouldii* (including *neocaledonicus*) had little meaning beyond the geographic designation of populations, yet that is a primary purpose of subspecific nomenclature. Significantly, he did not reject the concept that northern Australian populations of *C. gouldii* averaged smaller than more southern Australian populations, as his data clearly indicate this trend. His rejection of *venatoris* appears to be based on an incorrect assumption of a continuum of latitudinal decrease in average size on mainland Australia (or a rejection of the use of subspecies), yet his data clearly demonstrate a departure from that trend, with smaller animals at localities north of about latitude 22°S.

It is likely that a more complicated pattern of morphological variation in *C. gouldii* would emerge from analysis of a greater number of samples than the 89 specimens included in Tidemann's analysis, particularly as he was unable to include adequate samples from key areas such as northern Queensland and far northern Northern Territory. Although *C. gouldii* from southern Australian locations are well represented in collections, there are relatively few specimens from the far north of the continent. We did not attempt such an analysis but have reproduced fig. 3 of Tidemann (1986), to which we have added FA for the following: the type series of *venatoris*; two adult females with FA of 43 mm from far northern Northern Territory reported by Johnson (1964) from Douglas River (c. 13° 45'S, 131° 17'E), and specimens from eight other localities from south-western Australia, northern Australia and south-eastern Australia (Fig. 12). Although not represented in Tidemann's samples, adult individuals with FA as small as 38 mm also occur in south-eastern Australia, as indicated by a sample of 57 adults measured at the same locality on 19 April, 1994 near Windbar (30° 51' 17"S, 144° 52' 04"E), inland New South Wales. FA measurements for this sample are: males, mean = 42.43 (37.9–45.0 mm, n = 27), females 42.59 (38.7–45.3 mm, n = 30). This would not necessarily invalidate subspecific recognition of *venatoris*, which is based on population average size. Another important consideration is to establish whether individuals from northern Australia with larger FA have skulls of equivalent size to smaller northern animals and, conversely, whether southern animals with unusually small FA also have small skulls. We cannot resolve this but note that the limited skull measurements given by Johnson (1964) for an adult female (FA = 43 mm) from Douglas River (northern Northern Territory) fall within the range for the type series of *venatoris* (e.g., CON = 14.2 mm vs. 13.8–14.3 mm) while his measurements for two females (FA = 42, 43 mm) from the Alice Springs region (Wigley Water Hole, Horse Shoe Bend) exceed those of the type series of *venatoris* for CON (14.6, 15.3 mm) and ZYG (10.7, 11.3 mm vs. 9.6–10.5 mm).

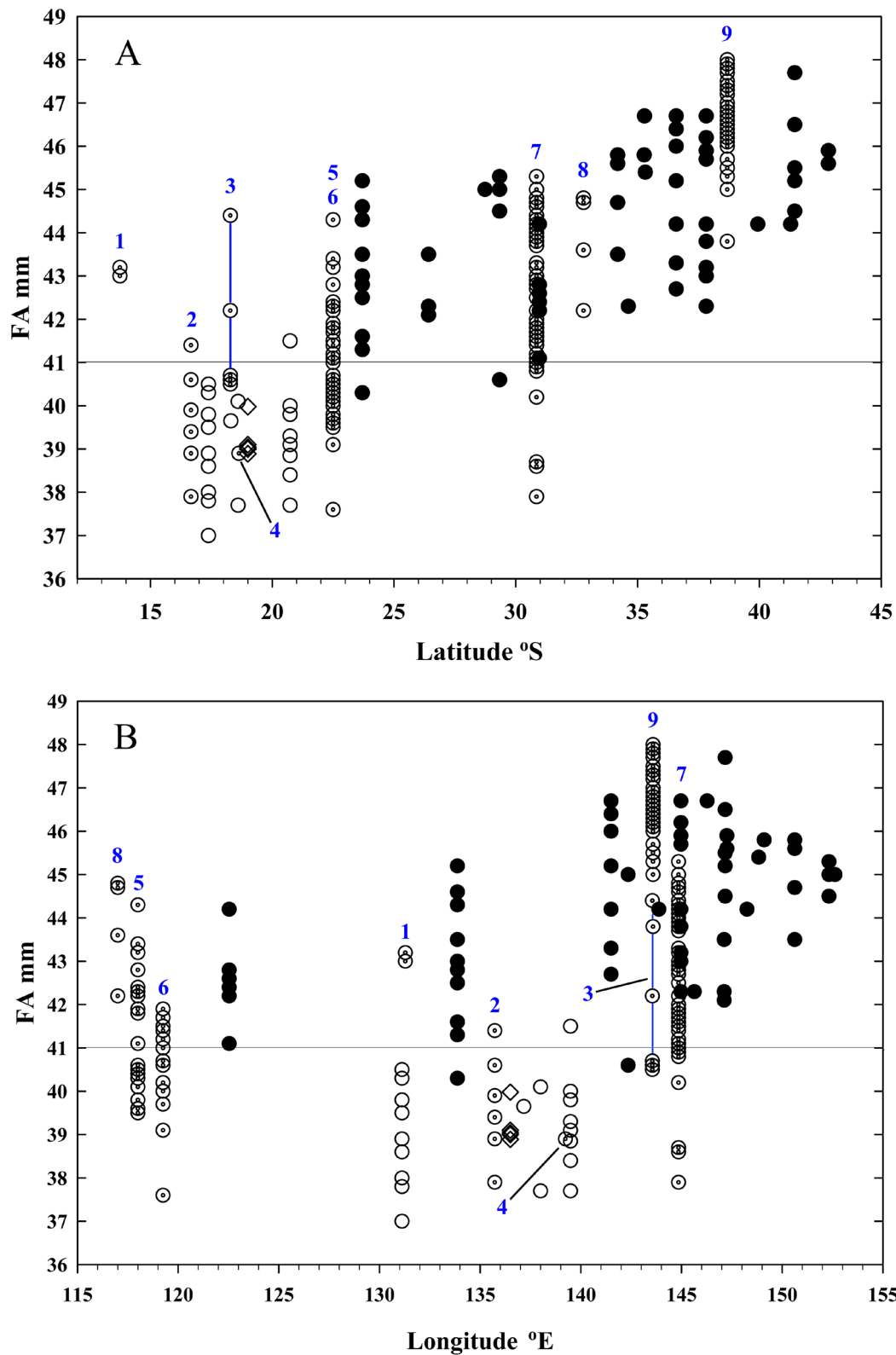
Our interpretation of Tidemann's analysis of geographic variation for mainland *C. gouldii* is that it implies the presence of two groups of mainland *C. gouldii* differing in average size, with smaller mainland animals found north of about latitude 22°S. The stepped size cline implied by Tidemann's data approximates the transition from the southern arid zone to the wet-dry tropics, which in the Northern Territory is north of about latitude 18°S, but the boundary is not parallel with latitude (Milne & Pavey 2011). Whether these trends are real and *venatoris* is a distinct biological entity or a sampling artefact of Tidemann's study remains to be determined. Alternatively, it could reflect adaptive changes by northern populations of *C. gouldii* to a monsoonal tropical environment. The latter interpretation was invoked by Bullen & McKenzie (2004), who found smaller flight-muscle mass ratios for northern Australian versus temperate samples of *C. gouldii*. Echolocation call parameters of northern populations might also differ from southern populations (Reinhold *et al.* 2001).

It is not surprising that many authors doubt the subspecific validity of *venatoris*. Scepticism about recognition of subspecies has prevailed among Australian mammalogists for decades (see the discussion by Aplin *et al.* 2015), no doubt resulting in a reluctance to adopt trinomial nomenclature unless populations are allopatric. The use of subspecies in vertebrate taxonomy remains contentious. One school of thought treats the subspecies as a pragmatic interim step that flags potential hidden diversity through the application of subspecific names. This acts as a warning to non-taxonomists of possible unrecognised cryptic diversity and is a significant consideration for physiologists, ecologists and biodiversity managers (see Jackson & Groves 2015: 6). In this approach, recognition of the subspecific status of *venatoris* would seem to have a reasonable foundation in the analysis of Tidemann (1986), despite his interpretation to the contrary.

We suggest that the widely held assumption that latitudinal variation in mainland *C. gouldii* represents a gradual, unbroken continuum has also hindered the wider acceptance of the validity of *venatoris*. Our re-interpretation of Tidemann's (1986) data suggests, at least in relation to metric characters, that latitudinal variation implies either two taxa, or a stepped cline. This has prompted us to re-examine other published observations of *venatoris*, in relation to the trends we see in this data. When Thomas (1908) first proposed *venatoris* as a subspecies, he remarked that animals from southern Australia seemed to be intermediate in overall size between *venatoris* and *C. gouldii* from Tasmania. McKean (quoted in Parker 1973: 37) believed that populations of *C. gouldii* from central Australia were variable but formed a cline between *venatoris* and southern *C. gouldii*. We note that McKean was an experienced taxonomist who did extensive field collecting of *C. gouldii* in both southern and northern Australia, observing live animals from which external criteria are more readily apparent than in voucher specimens. Under an assumption of continuous, gradual clinal variation from southern to northern Australia, the observations of Thomas and McKean are likely to be mis-interpreted as further evidence that *venatoris* is not valid. We suggest that Thomas and McKean were postulating a different scenario: that southern Australian populations of *C. gouldii* formed a gradual latitudinal cline that abutted the separate entity *venatoris*.



**FIGURE 11.** Variation in forearm length (FA) of adult Australian and Tasmanian *C. gouldii* with A, latitude °S; and B, longitude °E. Adapted from fig. 3 of Tidemann (1986). Open symbols are individuals from sites north of latitude 22°S. Localities: 1, Wave Hill, Northern Territory; 2, Mount Isa, Queensland; 3, Alice Springs, Northern Territory and 4, Karonie, Western Australia.



**FIGURE 12.** Variation in forearm length (FA) of adult Australian and Tasmanian *C. gouldii* with A, latitude °S; and B, longitude °E. Adapted from fig. 3 of Tidemann (1986) with additional specimens: solid circles, Tidemann's measurements; diamonds, type series of *C. gouldii venatoris* Thomas, 1908; open circles, additional field measurements: 1, Douglas River, Northern Territory (Johnson 1964); 2, Cape Cleveland, Northern Territory (n = 6); 3, Georgetown, Queensland (n = 6); 4, Gregory River Downs, Queensland (n = 1); 5, Tom Price, Pilbara, Western Australia (n = 20); 6, Marillana Station, Pilbara, Western Australia (n = 19); 7, Windbar, inland New South Wales (n = 57); 8, Dryandra Woodlands, Western Australia (n = 5) and 9, Otway Ranges, Victoria (n = 56).

Speculation about the validity of *venatoris* could be swiftly resolved by appropriate genetic analyses, provided samples were included from appropriate regions, and by morphometric analyses that utilised the large number of *C. gouldii* now in Australian collections. In the interim, our re-interpretation of latitudinal trends in morphological variation of Australian *C. gouldii* from the data of Tidemann (1986), previously overlooked, provides a useful working hypothesis for further analyses and a refinement on past concepts of *venatoris*. It suggests a more restricted geographic range than has previously been recognised for *venatoris* which should be considered when selecting locations for genetic analyses. In particular, we suggest that sampling should include the northern third of the Northern Territory, well within the monsoonal tropics. Our interpretation that Tidemann's (1986) data suggest a discontinuity in latitudinal variation north of c. 20°S means that support for recognition of *venatoris* has existed since publication of that paper. His data not only suggest the distributional limit of that form, but also indicate, at least from that data set, that the small form typically has FA less than c. 41 mm. The failure of previous authors to note these differences is probably due to the reluctance of many Australian zoologists to recognise subspecies under what we suggest is a misplaced assumption of a continuum of variation.

In summary, geographic variation in *C. gouldii* requires a comprehensive study to test for the possible existence of cryptic, sympatric taxa. Although latitudinal size gradients in *C. gouldii* can be interpreted as intraspecific clinal variation that includes a stepped cline in northern Australia, it could equally reflect two broadly sympatric species, with a smaller northern species that extends into southern Australia. Consequently, although it is possible to interpret Tidemann's (1986) data as support for the subspecific status of *venatoris*, and that such an interpretation could have been justified prior to our study, we await evaluation of variation in mainland *C. gouldii* that includes gene sequencing and morphometric analyses. In the interim, we suggest that recognition of *venatoris* as the northern subspecies of *C. gouldii* is justified because it reflects current understanding of the divergent morphology of *C. gouldii* in northern Australia, and has merit for those who adopt a pragmatic approach to the application of subspecies.

## Acknowledgements

We thank Dr Tim Flannery for comments to the manuscript and Dr Benoit Delvinquier for his translational nuances of Revilliod's paper (which he undertook in 1989), also Dave Milledge, Harry Hines and Terry Reardon who shared their field measurements of Australian *Chalinolobus*. AD thanks: Dr Roberto Portela Miguez (Natural History Museum, London Senior Curator, mammals) who went above and beyond to allow access to collections and set up further meetings with other museum departments of the Natural History Museum, London; the very friendly and helpful assistance of Mr Eduard Stöckli, Naturhistorisches Museum, Basel for access to the mammal collection; Dr Jean-Marc Pons (Institut de Systématique, Evolution, Biodiversité), who facilitated the visit, and Dr Cécile Callou (Chargée de conservation des types de Mammifères et des lagomorphes) for arranging access to mammal specimens in the Muséum national d'Histoire naturelle, Paris. Travel expenses of AD were defrayed by an award from the Australian Museum. GH wishes to thank Louise Tomsett of the Natural History Museum, London for facilitating his visit and allowing access to the collection and Margaret Hoyer for her unstinting love, help and companionship during that visit and generally. We thank Prof. Sue Hand and two anonymous reviewers for suggesting substantial improvements to the manuscript. Thanks also to AMRI for support and funding to enable open access.

## References

- Aplin, K.P., Rhind, S.G., Have, J.T. & Chesser, R.T. (2015) Taxonomic revision of *Phascogale tapoatafa* (Meyer, 1793) (Dasyuridae; Marsupialia), including descriptions of two new subspecies and confirmation of *P. pirata* Thomas, 1904 as a 'Top End' endemic. *Zootaxa*, 4055 (1), 1–73.  
<https://doi.org/10.11646/zootaxa.4055.1.1>
- Arata, A.A. (1968) Discrepancy between 'Dry' and 'Fresh' forearm measurements in bats. *Journal of Mammalogy*, 49 (1), 155–156.  
<https://doi.org/10.2307/1377750>
- Baker, A. (2013) Identification keys. In: Van Dyck, S., Gynther, I. & Baker, A. (Eds.), *Field Companion to The Mammals of Australia*. New Holland Publishers, Sydney, pp. 239–556.
- Bonaccorso, F.J. (1998) *A field guide to the bats of Papua New Guinea*. Conservation International, Washington, D.C., 489 pp.
- Brescia, F. (2008) *Chalinolobus neocaledonicus*. *The IUCN Red List of Threatened Species 2008: e.T4420A10868334*. Available from: <https://doi.org/10.2305/IUCN.UK.2008.RLTS.T4420A10868334.en> (accessed 21 February 2020)

- Bullen, R.D. & McKenzie, N.L. (2004) Bat flight-muscle mass: implications for foraging strategy. *Australian Journal of Zoology*, 52 (6), 605–622.  
<https://doi.org/10.1071/zo04036>
- Burbidge, A.A., Eldridge, M.D.B., Groves, C.P., Harrison, P.L., Jackson, S.M., Reardon, T.B., Westerman, M. & Woinarski, J.C.Z. (2014) A list of native Australian mammal species and subspecies. In: Woinarski, J.C.Z., Harrison, P.L. & Burbidge, A.A. (Eds.), *The Action Plan for Australian Mammals 2012*. CSIRO Publishing, Melbourne, pp. 15–32.
- Burgin, C.J. (2019) New Caledonian Wattled Bat. In: Wilson, D.E. & Mittermeier, R.A. (Eds.), *Handbook of the Mammals of the World. Vol. 9. Bats*. Lynx Edicions, Barcelona, pg. 797.
- Chruszcz, B. & Barclay, R.M.R. (2002) *Chalinolobus gouldii*. *Mammalian Species*, 690, 1–4.  
<https://doi.org/10.1644/0.690.1>
- Churchill, S. (2008) *Australian Bats. Second edition*. Allen & Unwin, Crows Nest, New South Wales, 255 pp.
- Dixon, J.M. & Lumsden, L.F. (2008) Gould's Wattled Bat. In: Van Dyck, S. & Strahan, R. (Eds.), *The Mammals of Australia*. Reed New Holland, Sydney, pp. 533–534.
- Dobson, G.E. (1878) *Catalogue of the Chiroptera in the Collection of the British Museum*. Trustees of the British Museum, London, xlii + 567 pp., 525 pls.  
<https://doi.org/10.5962/bhl.title.55341>
- Flannery, T.F. (1995) *Mammals of the South-West Pacific and Moluccan Islands*. Australian Museum/Reed Books, Chatswood, New South Wales, 464 pp.
- Forster, J.R. (1844) *Descriptiones animalium quae in itinere ad Maris Australis terras per annos 1772, 1773 et 1774 suscepto*. Ex Officina Academica, Berlin, 424 pp.  
<https://doi.org/10.5962/bhl.title.63900>
- Gould, J. (1852) *The Mammals of Australia. Part 4*. John Gould, London, 15<sup>th</sup> pl., 1 pg. (unnumbered text). [= 1863, Vol. 3, pl. 43, 1 pg. (unnumbered text)]
- Gould, J. (1856) *The Mammals of Australia. Part 8*. John Gould, London, 15<sup>th</sup> pl., 1 pg. (unnumbered text). [= 1863, Vol. 3, pl. 44, 1 pg. (unnumbered text)]
- Gray, J.E. (1841) Contributions towards the geographical distribution of the Mammalia of Australia, with notes on some recently discovered species, a letter addressed to the Author. Appendix C. In: Grey, G. (Ed.), *Journals of Two Expeditions of Discovery in north-west and Western Australia, During the Years 1837, 38, and 39, Under the Authority of Her Majesty's Government. Describing many newly discovered, important, and fertile districts, with observations on the moral and physical condition of the aboriginal inhabitants, &c. &c. Vol. 2*. T. & W. Boone, London, pp. 397–414.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4 (1), 1–9. Software available from: <http://folk.uio.no/ohammer/past/> (accessed 21 February 2020).
- Hand, S.J. & Grant-Mackie, J.A. (2012) Late-Holocene bats of Mé Auré Cave, New Caledonia: Evidence of human consumption and a new species record from the recent past. *The Holocene*, 22 (1), 79–90.  
<https://doi.org/10.1177/0959683611409783>
- Hill, J.E. & Harrison, D.L. (1987) The baculum of the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus. *Bulletin of the British Museum (Natural History) Zoology*, 52 (7), 225–305.
- How, R.A., Cooper, N.K. & Bannister, J.L. (2001) Checklist of the mammals of Western Australia. *Records of the Western Australian Museum Supplement*, 63, 91–98.  
<https://doi.org/10.18195/issn.0313-122x.63.2001.091-098>
- Hoye, G. (2011) The status of microbats on Norfolk Island, southwest Pacific In: Law, B., Eby, P., Lunney, D. & Lumsden, L. (Eds.), *The Biology and Conservation of Australasian Bats*. Royal Zoological Society of NSW, Mosman, New South Wales, pp. 297–307.  
<https://doi.org/10.7882/fs.2011.030>
- Jackson, S.M. & Groves, C.P. (2015) *Taxonomy of Australian Mammals*. CSIRO Publishing, Melbourne, Victoria, 529 pp.  
<https://doi.org/10.1071/9781486300136>
- Johnson, D.H. (1964) Mammals of the Arnhem Land Expedition. In: Specht, R.L. (Ed.), *Records of the American-Australian Scientific Expedition to Arnhem Land. Vol 4. Zoology*. Melbourne University Press, Melbourne, pp. 427–515.
- Kirsch, R.A., Tupinier, Y., Beuneux, G. & Rainho, A. (2002) *Contributions à l'inventaire chiroptérologique de la Nouvelle-Calédonie: Chiroptera Pacifica, Missions 2000 & 2001. Rapport final et recommandations*. Unpublished report by SFPEM, Groupe Chiroptères Outre-Mer. Available from: <https://doi.org/10.13140/RG.2.1.1730.6640> (accessed 1 April 2020)
- Koopman, K.F. (1971) Taxonomic notes on *Chalinolobus* and *Glauconycteris* (Chiroptera, Vespertilionidae). *American Museum Novitates*, 2451, 1–10.
- Koopman, K.F. (1993) Order Chiroptera. In: Wilson, D.E. & Reeder, D.M. (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference. Second Edition*. Smithsonian Institution Press, Washington, pp. 137–241.
- Kutt, A.S., Milne, D.J. & Allison, F.R. (2008) Hoary Wattled Bat. In: Van Dyck, S. & Strahan, R. (Eds.), *The Mammals of Australia*. Reed New Holland, Sydney, pp. 537–538.
- Lumsden, L.F. & Bennett, A.F. (1995) Bats of a semi-arid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildlife Research*, 22 (2), 217–239.  
<https://doi.org/10.1071/wr9950217>

- Menkhorst, P. & Knight, F. (2011) *A Field Guide to the Mammals of Australia. Third edition.* Oxford University Press, Melbourne, 274 pp.
- Millon, L., Colin, C., Brescia, F. & Kerbiriou, C. (2018) Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. *Ecological Engineering*, 112, 51–54.  
<https://doi.org/10.1016/j.ecoleng.2017.12.024>
- Milne, D.J. & Pavey, C.R. (2011) The status and conservation of bats in the Northern Territory. In: Law, B., Eby, P., Lunney, D. & Lumsden, L. (Eds.), *The Biology and Conservation of Australasian Bats*. Royal Zoological Society of NSW, Mosman, New South Wales, pp. 208–225.  
<https://doi.org/10.7882/fs.2011.024>
- O'Donnell, C.F.J. (2001) Advances in New Zealand mammalogy 1990–2000: Long-tailed bat. *Journal of the Royal Society of New Zealand*, 31 (1), 43–57.  
<https://doi.org/10.1080/03014223.2001.9517638>
- O'Donnell, C.F.J. (2005) New Zealand Long-tailed Bat. In: King, C.M. (Ed.), *The Handbook of New Zealand Mammals. 2<sup>nd</sup> Edition*. Oxford University Press, Melbourne, pp. 95–109.
- Parker, S.A. (1973) An annotated checklist of the native land mammals of the Northern Territory. *Records of the South Australian Museum*, 16 (11), 1–57.
- Parnaby, H.E. (1992) An Interim Guide to the Identification of Insectivorous bats of South-eastern Australia. *Technical Reports of the Australian Museum*, 8, 1–33.  
<https://doi.org/10.3853/j.1031-8062.8.1999.1528>
- Parnaby, H.E. (2002) A new species of long-eared bat (*Nyctophilus*: Vespertilionidae) from New Caledonia. *Australian Mammalogy*, 23 (2), 115–124.  
<https://doi.org/10.1071/AM01115>
- Reinhold, L., Herr, A., Lumsden, L., Reardon, T., Corben, C., Law, B., Prevett, P., Ford, G., Conole, L., Kutt, A., Milne, D. & Hoyer, G. (2001) Geographic variation in the echolocation calls of Gould's Wattled Bat *Chalinolobus gouldii*. *Australian Zoologist*, 31 (4), 618–624.  
<https://doi.org/10.7882/AZ.2001.008>
- Revilliod, P. (1914) Les mammifères de la Nouvelle-Calédonie et des îles Loyalty. In: Sarasin, F. & Roux, J. (Eds.), *Nova Caledonia*, A, Zoologie, 1, pp. 341–365, pl. x.  
<https://doi.org/10.5962/bhl.title.6790>
- Ryan, R.M. (1966) A new and some imperfectly known Australian *Chalinolobus* and the taxonomic status of African *Glauconycteris*. *Journal of Mammalogy*, 47 (1), 86–91.  
<https://doi.org/10.2307/1378072>
- Simmons, N.B. (2005) Order Chiroptera. In: Wilson, D.E. & Reeder, D.M. (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference. Third edition.* The Johns Hopkins University Press, Baltimore, pp. 312–529.
- Tate, G.H.H. (1942) Results of the Archbold Expeditions. No 47. Review of the vespertilionine bats, with special attention to genera and species of the Archbold collections. *Bulletin of the American Museum of Natural History*, 80 (7), 221–297.
- Taylor, R.J., O'Neill, M.G. & Reardon, T. (1987) Tasmanian bats: identification, distribution and natural history. *Papers and Proceedings of the Royal Society of Tasmania*, 121, 109–119.  
<https://doi.org/10.26749/rstpp.121.109>
- Thomas, O. (1905) On some Australasian mammals. *Annals and Magazine of Natural History*, Series 7, 16, 422–428.  
<https://doi.org/10.1080/03745480509442882>
- Thomas, O. (1908) New bats and rodents in the British Museum Collection. *Annals and Magazine of Natural History*, Series 8, 2, 370–375.  
<https://doi.org/10.1080/00222930808692496>
- Thomas, O. (1909) Some mammals from N.E. Kimberley, Northern Australia. *Annals and Magazine of Natural History*, Series 8, 3, 149–152.  
<https://doi.org/10.1080/00222930908692558>
- Tidemann, C.R. (1986) Morphological variation in Australian and Island populations of Gould's Wattled Bat, *Chalinolobus gouldii* (Gray) (Chiroptera: Vespertilionidae). *Australian Journal of Zoology*, 34 (4), 503–514.  
<https://doi.org/10.1071/zo9860503>
- Troughton, E.L.G. (1926) Bats of Australia and New Guinea. In: Le Souef, A.S. & Burrell, H. (Eds.), *The Wild Animals of Australasia: Embracing the mammals of New Guinea and the Nearer Pacific Islands. With a chapter on the bats of Australia and New Guinea by Ellis Le G. Troughton.* G.G. Harrap, Sydney, pp. 21–88.
- Van Deusen, H.M. & Koopman, K.F. (1971) Results of the Archbold Expeditions. No. 95. The genus *Chalinolobus* (Chiroptera, Vespertilionidae). Taxonomic review of *Chalinolobus picatus*, *C. nigrogriseus*, and *C. rogersi*. *American Museum Novitates*, 2468, 1–30.
- Van Dyck, S. & Strahan, R. (Eds.) (2008) *The Mammals of Australia*. Reed New Holland, Sydney, Australia, 887 pp.
- Wood Jones, F. (1925) *The Mammals of South Australia*. South Australian Government Printer, Adelaide, 458 pp.
- Young, R.A. & Ford, G.I. (2000) Bat fauna of a semi-arid environment in central western Queensland, Australia. *Wildlife Research*, 27 (2), 203–215.  
<https://doi.org/10.1071/WR98071>