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A new species of lobe-lipped bat (*Chalinolobus*: Vespertilionidae) from southern Papua New Guinea

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Abstract

The Hoary Bat *Chalinolobus nigrogriseus* is the only species of the genus known from the island of New Guinea. A new species of *Chalinolobus* from Papua New Guinea is described based on DNA sequence and morphological criteria using material previously assigned to *C. nigrogriseus*. The new species most resembles the eastern Australian subspecies of the Hoary Bat *C. n. nigrogriseus* in general size and appearance but is easily distinguished by an enlarged, rather than rudimentary lobe at the terminal outer ear margin. The new species might also be confused on external characters with smaller individuals of Australian Gould's Wattle Bat *C. gouldii*, from which it differs in having bifid first upper incisors and uniform dark dorsal fur. The inclusion of *C. nigrogriseus* in the bat fauna of New Guinea is now in doubt, pending a re-assessment of the identity of *Chalinolobus* specimens in world museum collections. Locality records of all *Chalinolobus* spp. from Papua New Guinea are reviewed. Most localities are below 60 m elevation in coastal savannah and woodlands. The identity of specimens of *C. nigrogriseus* and *C. gouldii* from northern Australia should be reviewed to determine whether the new species also occurs in Australia.

Key words: *Chalinolobus nigrogriseus*, *Chalinolobus gouldii*, Trans-Fly, savannah, woodland, taxonomy, morphology, genetics

Introduction

The Hoary Bat *Chalinolobus nigrogriseus* (Gould, 1856) is the only species of *Chalinolobus*, the lobe-lipped bats, reported from the island of New Guinea. The species is known from relatively few records, all from the subcoastal savannah woodlands of southern Papua New Guinea (PNG), east to Fergusson Island, all from below 300 m altitude (Bonaccorso 1998). Although the genus does not seem to have been reported from Indonesian Papua, the savannah woodlands of the southern Trans-Fly that extend west to the Merauke region is potentially suitable habitat, but the mammal fauna of that region is poorly known (Helgen 2007). The Hoary Bat is widely distributed across northern Australia (Kutt & Milne 2023) but there are no confirmed records from islands of the Torres Strait (Lavery *et al.* 2012). Two subspecies are often recognised in Australia: *C. nigrogriseus nigrogriseus* (type locality Morton Bay environs, Brisbane) from north-eastern NSW through eastern Queensland to Cape York and *C. n. rogersi* Thomas, 1909 (type locality of Parry's Creek, Wyndham, WA) from northern Western Australian, northern Northern Territory and north-western Queensland. The taxonomic status of *rogersi* remains unresolved but it was differentiated by Thomas (1909) by its smaller size, a more inflated braincase, and a strong "frosting" of the dorsal fur tips.

In the most recent taxonomic review of *C. nigrogriseus*, Van Deusen & Koopman (1971) included material from PNG in their comparisons with northern Australian specimens. They tentatively assigned New Guinean material to

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C. n. nigrogriseus rather than *C. n. rogersi* based on larger overall size and lack of frosting of dorsal pelage, noting that New Guinean material averaged larger than Australian *C. n. nigrogriseus* and had a high frequency of bifid first upper incisors, in contrast to unicuspidate incisors in Queensland and NSW specimens. The morphological differences of New Guinean *Chalinolobus* were neglected in a subsequent diagnosis by Koopman (1994), who specified unicuspidate first upper incisors for both subspecies of *C. nigrogriseus*.

This current study stems from an attempt to identify a specimen of *Chalinolobus* captured near Serki village by SH in 2006 during an opportunistic survey of bats from the Trans-Fly region, Western Province, PNG. The specimen has an enlarged lobe formed by the outer ear margin where it terminates near the angle of the mouth. This feature was thought to be uniquely diagnostic of Australian Gould's Wattled Bat *Chalinolobus gouldii* (Gray, 1841), a species not recorded from the island of New Guinea, and sharply contrasts with the small terminal ear lobe of *C. nigrogriseus*. However, unlike either species, the specimen has bifid upper first incisors. This prompted a review of the taxonomic status of *Chalinolobus* from PNG and the review of *Chalinolobus* from New Caledonia (Parnaby *et al.* 2020). It was immediately evident that the Serki specimen was likely to be an unnamed taxon but its status as subspecies or species was unclear as it had characters diagnostic of both Australian *C. n. nigrogriseus* and *C. gouldii*. Our comparisons with the latter species focus on populations from the northern half of Australia which average smaller than southern populations (Tidemann 1986), and potentially have a higher proportion of small individuals that approach the size of the largest individuals of *Chalinolobus* from PNG.

A key diagnostic feature of *Chalinolobus* is the presence of a skin lobe that projects horizontally from the lower lip near the angle of the mouth (Dobson 1878). This feature should not be confused with the enlarged lobe characteristic of *C. gouldii*, which is formed by an expansion of the ear margin into a downwardly projecting flap, at the termination of the outer ear margin near the angle of the mouth. The ear margin terminates in a small lobe in other species of the genus, i.e. *C. neocaledonicus* Revilliod, 1914 from New Caledonia (see illustration by Parnaby *et al.* 2020) and *C. tuberculatus* (Forster, 1844) from New Zealand, and the Australian species *C. nigrogriseus*, *C. morio* (Gray, 1841), and *C. picatus* (Gould, 1852). The terminal ear lobe of the Australian *C. dwyeri* Ryan, 1966 is larger than those species yet conspicuously smaller compared to *C. gouldii*. The five Australian species of *Chalinolobus* are readily distinguished from each other using other external criteria including fur colour, relative ear size, the number and relative size of skin lobes on the lips, the relative size of upper incisors and the presence or absence of a secondary cusp on the first upper incisor (Churchill 2008). Of particular relevance to this study is that, although both subspecies of *C. nigrogriseus* are usually defined as having unicuspidate first upper incisors, this neglects the observations by Van Deusen & Koopman (1971), who found a high incidence of bifid upper incisors in New Guinean specimens (10 of 13), and a significant occurrence in Northern Territory and Western Australian specimens they assigned to *C. n. rogersi* (5 of 20). The statement by Milledge *et al.* (1992: 56) that two specimens of *C. n. nigrogriseus* from northern NSW (AM M.25437 and M.26598) have notched first upper incisors is a *lapsus* and should have read both "do *not* have notched first upper incisors".

Bonaccorso (1998) stated that *C. nigrogriseus* is infrequently encountered in PNG. To our knowledge, *Chalinolobus* have been recorded from four general localities (Fig. 1): Western Province in the Trans-Fly region at Bandaber (Bonaccorso 1998) and Serki (this study), 97 km apart; six localities in the Port Moresby environs (Fig. 1), Kupiano, Central Province (Bonaccorso 1998), and Fergusson Island (Van Deusen & Koopman 1971). Van Deusen & Koopman (1971) cite a 19th century record from Eastern Cape, Milne Bay Province, but were mistakenly informed that the specimen (AM A.3176) was lost, but it remains in the AM collection and is the holotype of the bat *Scotorepens sanborni* (Troughton, 1937), see Parnaby *et al.* (2017).

Our cursory tally of New Guinean *Chalinolobus* in world museum collections indicates that there are at least 55 adult specimens, of which the majority (c. 71%) are adult females from two collection events at maternity colonies in the Port Moresby area in 1968 (5 adults) and 1969 (35 adults) as reported by Menzies (1971). He lists 47 specimens that he lodged with collections: the Papua New Guinea Museum and Art Gallery, Port Moresby (PNGM, 6); ten specimens each to the Natural History Museum, London (NHMUK) and the American Museum of Natural History, New York (AMNH) and 21 registered in the University of Papua New Guinea, Port Moresby (UPNG), with an unspecified number of remaining specimens lodged unregistered, in the later institution (presumably all juveniles). Six of Menzies' specimens from UPNG were subsequently donated to the Australian Museum, Sydney (AM) and registered in 1977. A further six of Menzies' specimens, that could include juveniles, are lodged in the Australian National Research Collection, Canberra. The Bernice P. Bishop Museum, Honolulu (BPBM) has seven adult females and three males not previously discussed in the literature. All were taken from a colony in the roof of the PNG Museum & Art Gallery on 27th March 1985 by Andrew Engilis, Jnr. (Curator, Museum of Wildlife and Fish Biology, University of California, Davis, pers. comm. 1 March 2024). To our knowledge the Serki specimen reported here is the only one collected this century.

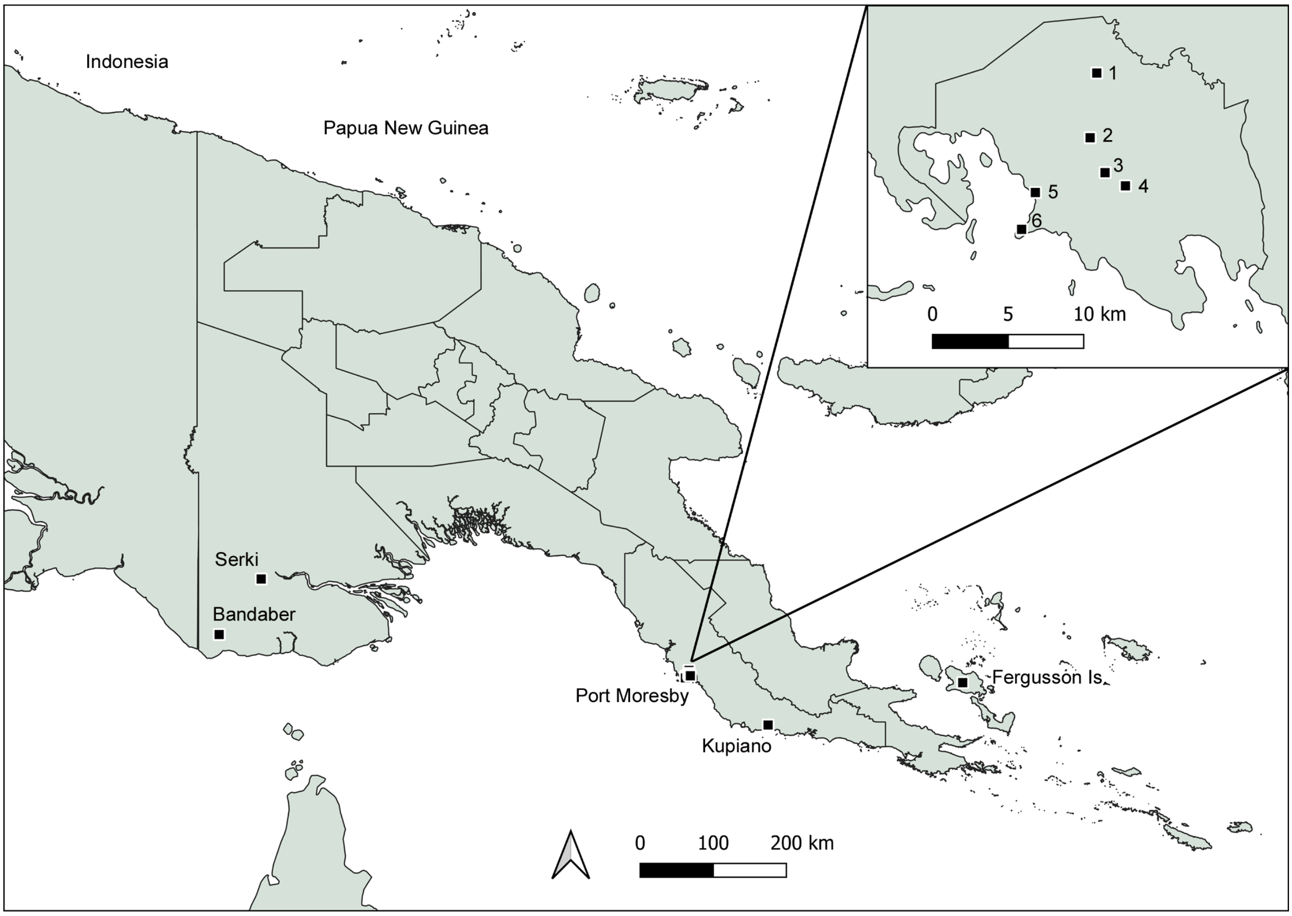

FIGURE 1. Locality records of *Chalinolobus* from Papua New Guinea, showing Province boundaries. Six localities from Port Moresby environs (inset map) are: 1, Waigani Sewerage works, 2, National Museum & Art Gallery roof, 3, Gordon, 4, Saraga, 5, Champion House, and 6, Paga Hill Court House.

Materials and methods

DNA sequencing

Tissue samples or published DNA sequences were available for all seven currently recognised species of *Chalinolobus* (Table 1).

Total genomic DNA was extracted from 10 mg of tissue using the *Isolate II Genomic DNA Kit* (Bioline Australia) following manufactures protocol. Fragments of two mitochondrial DNA genes, cytochrome b (CytB) and cytochrome oxidase 1 (COI), were PCR amplified using the following primers: CytB - L14841 (F), AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA, H15149 (R) AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA (Kocher *et al.* 1989); COI-BAK1490 (F) CTCAACCAAC CACAAAGACATCGG, BAK2198 (R) TAGACTTCTGGGTGGCCGAAGAATCA (Neaves *et al.* 2018). PCRs were performed in 25 µl reactions using 10–20 ng of genomic DNA, 1 × *MyTaq Red Reagent Buffer* (Bioline, Australia), 2 pmol primers and 0.5Units *MyTaq Red DNA polymerase* (Bioline Australia). Thermocycling was performed on an *Eppendorf Mastercycler Nexus Gradient* (Eppendorf, Hamburg, Germany) under the following conditions: initial denaturation 94°C (3 min), 38 cycles of denaturation at 94°C (20 s), annealing at 54°C (40 s) and extension at 72°C (40 s) with a final extension step of 72°C for 5 min. Sequences were edited using *Sequencher v5.4* (Gene Codes Corporation, Ann Arbor, USA) and aligned using *ClustalW* in MEGA 11 (Tamura *et al*. 2021). The evolutionary history of haplotypes was inferred using Maximum Likelihood based on the HKY model and 1000 bootstraps. The most appropriate evolutionary model was determined using the "Find Best Model Fit" in MEGA 11 (Tamura *et al.* 2021). Initial trees for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. Sequence divergence amongst haplotypes (*p*-distance) was calculated in MEGA 11 (Tamura *et al.* 2021). Homologous sequence data from GenBank of a representative of the related vespertilionid genus *Pipistrellus* was used as an outgroup (Table 1).

TABLE 1. Details of the samples used in genetic comparisons.

AM Registration number	GenBank number	Taxon	Location
AM M.49359	MT216514, MT246593	*Chalinolobus dwyeri*	Coolah Tops, NSW
AM M.22089	MT216512, MT246604	*Chalinolobus gouldii*	Pilbara, WA
AM M.34595	MT216511	*Chalinolobus gouldii*	Empire Bay, NSW
AM M.36162	MT216513, MT246603	*Chalinolobus gouldii*	White Cliffs, NSW
AM M.47820	MT216510, MT246602	*Chalinolobus gouldii*	Wisemans Ferry, NSW
AM M.47821	MT216509	*Chalinolobus gouldii*	Somersby, NSW
AM M.23971	MT216508, MT246600	*Chalinolobus morio*	Billilimbra State Forest, NSW
AM M.39844	MT216507, MT246598	*Chalinolobus morio*	Eagle Rock, WA
AM M.49341	MT216504, MT246601	*Chalinolobus morio*	Coolah Tops, NSW
AM M.25363	MT216500, MT246593	*Chalinolobus picatus*	Enngonia, NSW
	MF038571, MF038472	*Chalinolobus neocaledonicus*	New Caledonia
AM M.22087	MT216502, MT246595	*Chalinolobus nigrogriseus rogersi*	Napier Downs, Kimberly, WA
AM M.49709	MT216501, MT246594	*Chalinolobus* sp.	Serki, Western Province, PNG
	NC002626.1	*Chalinolobus tuberculatus*	New Zealand
	HM914966, OL513431	*Pipistrellus javanicus*	Vietnam

Morphological comparisons

Taxonomic units

Specimens were assigned to five groups in the morphological analyses:

1) *C.* sp.: an unnamed form of *Chalinolobus* from Port Moresby and Trans-Fly, PNG — determined from non-metric characters to be either a subspecies of Australian *C. gouldii* or Australian *C. nigrogriseus*, or a new species;

2) *C. n. nigrogriseus*: from northern NSW and Qld. Subspecific identity was determined by locality but as the eastern extent of *C. n. rogersi* in Queensland is not known we cannot be certain that all our Qld specimens are *C. n. nigrogriseus*;

3) northern *C. gouldii*: from northern Australia, defined as localities north of latitude 23° S;

4) southern *C. gouldii*: from southern mainland Australia and Tasmania, defined as localities south of latitude 23° S;

5) *C.* sp. indet.: specimens of *Chalinolobus* from Papua New Guinea for which forearm and cranial measurements are given by Van Deusen & Koopman (1971). Previously assigned to *C. n. nigrogriseus* but now of indeterminate status. Possibilities include *C. n. nigrogriseus*, small individuals of *C. gouldii* as are found in northern Australia, or a new species. This group was included in the analyses to evaluate their identity.

The latitudinal demarcation of northern and southern groups of *C. gouldii* was arbitrarily selected to remove the influence of larger mean size of southern individuals (Tidemann 1986), thus refining comparisons between smaller northern Australian *C. gouldii* with individuals of the otherwise smaller *Chalinolobus* from PNG. The northern group of *C. gouldii* does not necessarily equate to the northern subspecies *C. gouldii venatoris* Thomas, 1908, for which the status and distribution requires clarification.

Measurements

Measurements were taken with Vernier callipers to the nearest 0.05 mm. Abbreviations for measurements used in the text are: **GL**, Greatest length of skull: from the most anterior extension of the premaxilla to the posterior of the lambdoidal crest; **CON**, condylo-basal skull length: from posterior of occipital condyles to anterior most point of premaxilla; **CM^3** and **CM$_3$**, Length of maxillary tooth rows: from anterior cingulum of canine to posterior cingulum of third molar; **C^1–C^1**, Outer breadth across upper canines from cingula; **ZYG**, Zygomatic breadth: maximum breadth across zygomatic arches; **INT**, Least inter-temporal breadth; **M^3–M^3**, Maximum breadth from left M^3 to right M^3, from labial cingula; **MASB**, mastoid breadth: maximum breadth across mastoids; **PAL**, Palatal length, from anterior most projection of premaxilla to most anterior margin of interpterygoid fossa; **BUL**, Bulla length, from base of eustachian tube when present, taken along the long axis of the bulla; **DL (con.)**, Dentary length from condyle: from anterior projection of dentary to posterior of condyle along the dentary axis; **DL (ang.)**, Dentary length from angular process: from anterior projection of dentary to posterior of angular process along the dentary axis. **Ear Length**, taken from the junction of outer ear margin near the jaw; **FA**, forearm length, from the posterior tubercle of the radius; **HL**, lower hind leg length, taken with the lower leg with the ankle and knee joints bent (note that HL is not equivalent to tibia length), and **WT**, field body weight, taken in the field for vouchers or capture-released animals, or from museum tags.

Univariate summary statistics and Principal Components Analyses (PCA) were run using the Paleontological Statistics (PAST) software package version 4.14 (Hammer *et al.* 2001). PCAs used a correlation matrix with specimens unassigned to groups. Specimens with missing values were excluded from the PCAs. In most cases sexes were combined due to small sample size but sexual size dimorphism of *Chalinolobus* species is anticipated for many characters, with females averaging larger, e.g. for FA and WT (see Results).

Results

DNA sequencing

For the COI sequence data (581 bp), the sequence divergence between currently recognised species of *Chalinolobus* ranged from 2.2% between *C. picatus* and *C. dwyeri* to 17% between *C. morio* and *C. tuberculatus* (Table 2). Intraspecific sequence divergences (sd) were 0–1.4% amongst five specimens of *C. gouldii* and 2.4–4.5% amongst three specimens of *C. morio* (Table 2). The specimen of *C.* sp. from the Trans-Fly differed by an average of 6.96% from sampled specimens of *C. gouldii* and 7.4% from an exemplar of *C. nigrogriseus* (Table 2). The sampled *C. gouldii* and *C. nigrogriseus* differed by an average of 5.86% (Table 2). The partial CytB sequence data (287 bp) yielded a similar pattern of divergences.

Under phylogenetic analysis of the COI data, two well supported lineages were resolved; one comprising *C. morio* and the other containing the other seven sampled species (Fig. 2). Within this second group the inter-relationships amongst the sampled taxa was not well resolved, apart from the strongly supported sister relationship of *C. picatus* and *C. dwyeri* which formed the basal lineage to the other five species (Fig. 2). The partial CytB sequence data yielded a tree of similar topology.

Morphometric comparisons

In overall body size, *C.* sp. is intermediate between the two species with which it is most likely to be confused, viz. Australian *C. n. nigrogriseus* and northern Australian *C. gouldii*. This is evident from plots of FA vs. C^1–C^1 (Fig. 3a) and FA vs. WT (Fig. 3b). Maximum and minimum values of all characters of *C.* sp. overlap or abut those of Australian *C. n. nigrogriseus*, which has smaller mean values for all characters except GL, CON and CM^3 but for which ranges completely overlap (other than MASB, with small sample size), and northern *C. gouldii* which have larger mean values for all measurements except MASB (Tables 3 & 4). Northern Australian *C. gouldii* of equivalent forearm length to *C.* sp. tend to have larger skulls, e.g. CON typically greater than 12.9 mm, C^1–C^1 usually greater than 4.8 mm (Fig. 3a) and CM^3 greater than 5.0 mm. Australian *C. n. nigrogriseus* tend to have proportionately longer CM^3 relative to FA compared to *C.* sp.: whereas mean FA is smaller than *C.* sp., mean CM^3 is similar (Tables 3 & 4). The smaller average size of *C. nigrogriseus rogersi* from Western Australian and Northern Territory relative to *C. n. nigrogriseus* is evident from a plot of FA vs. WT for adult females (Fig. 3b).

TABLE 2. DNA sequence divergence for COI among sampled *Chalinolobus* specimens.

	C. gouldii **M.22089**	***C. gouldii*** **M.34595**	***C. gouldii*** **M.47820**	***C. gouldii*** **M.47821**	***C. gouldii*** **M.36162**	***C. neocaledonicus*** **MF038571**	***C. tuberculatus*** **NC002626.1**	***C. morio*** **M.23971**	***C. morio*** **M.39844**	***C. morio*** **M.49341**	***C. nigrogriseus rogersi*** **M.22087**	***Chalinolobus*** **sp. M.49709**	***C. picatus*** **M.25363**	***C. dwyeri*** **M.49359**	***Pipistrellus javanicus*** **MH914966 Vietnam**
C. gouldii **M.22089 Pilbara, WA**															
C. gouldii **M.34595 Empire Bay, NSW**	0.010														
C. gouldii **M.47820 Wisemans Ferry, NSW**	0.010	0.000													
C. gouldii **M.47821 Central Coast, NSW**	0.014	0.003	0.003												
C. gouldii **M.36162 White Cliffs, NSW**	0.010	0.000	0.000	0.003											
C. neocaledonicus **MF038571 New Caledonia**	0.057	0.060	0.060	0.062	0.060										
C. tuberculatus **NC002626.1 New Zealand**	0.108	0.108	0.108	0.107	0.108	0.107									
C. morio **M.23971 Billilimbra State Forest, NSW**	0.146	0.143	0.143	0.141	0.143	0.155	0.170								
C. morio **M.39844 Eagle Rock Goldfields, WA**	0.151	0.151	0.151	0.150	0.151	0.151	0.165	0.024							
C. morio **M.49341 Coolah Tops. NSW**	0.155	0.155	0.155	0.153	0.155	0.157	0.162	0.038	0.045						
C. nigrogriseus rogersi **M.22087 Napier Downs, WA**	0.059	0.059	0.059	0.057	0.059	0.065	0.076	0.155	0.151	0.155					
Chalinolobus **sp. M.49709 Serki, WP, PNG**	0.074	0.069	0.069	0.067	0.069	0.079	0.107	0.143	0.139	0.153	0.074				
C. picatus **M.25363 Enngonia, NSW**	0.110	0.110	0.110	0.108	0.110	0.117	0.124	0.139	0.145	0.138	0.117	0.105			
C. dwyeri **M.49359 Coolah Tops, NSW**	0.119	0.115	0.115	0.114	0.115	0.122	0.129	0.139	0.148	0.138	0.126	0.103	0.022		
Pipistrellus javanicus **MH914966 Vietnam**	0.182	0.182	0.182	0.181	0.182	0.172	0.174	0.162	0.164	0.170	0.176	0.169	0.170	0.176	

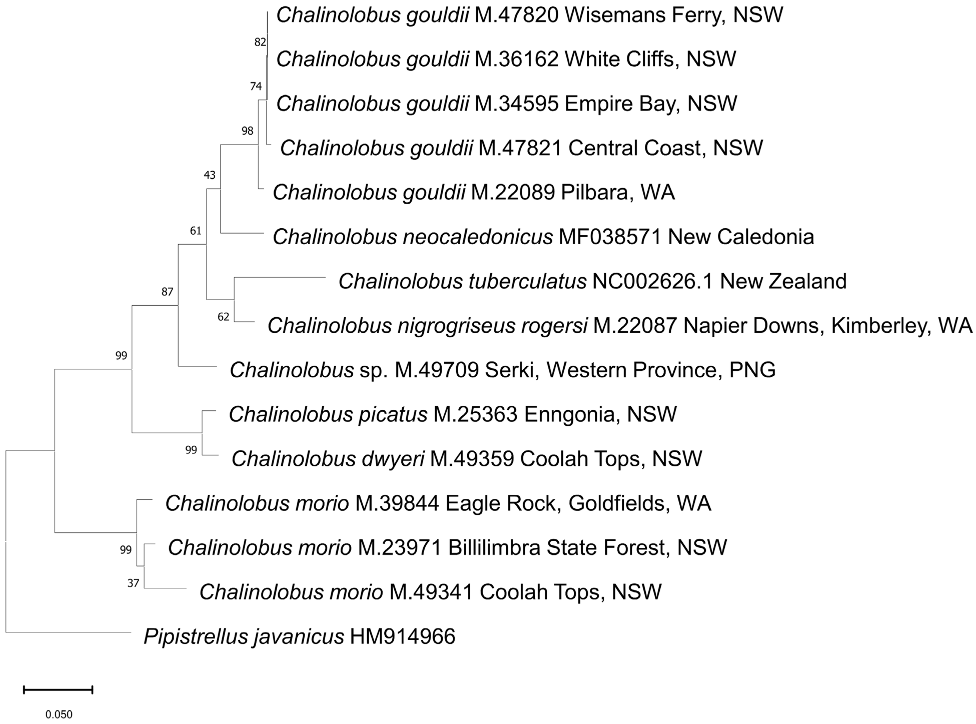

FIGURE 2. Phylogenetic relationships (ML) amongst sampled *Chalinolobus* haplotypes based on 581 bp of COI sequence. Bootstrap support (%) shown at branch nodes. All M. numbers refer to AM specimens except where indicated. Partial CytB sequence data yielded a tree of similar topology.

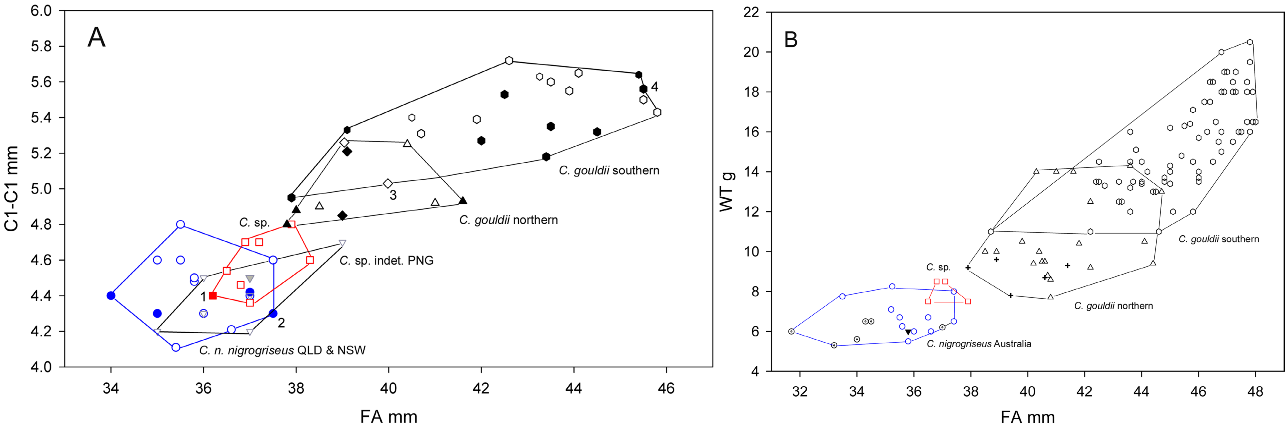

FIGURE 3. Intermediate body size of *C.* sp. (rectangles) between *C. nigrogriseus* and *C. gouldii* exemplified by: **a)**, Forearm length (FA) vs. Outside breadth across upper canines (C^1–C^1) for adult males (solid symbols) and females (open symbols). Type specimens are: 1, *C. orarius* **sp. nov.** holotype; 2, *C. nigrogriseus* holotype, sex unknown; 3, *C. gouldii venatoris* holotype, and 4, *C. gouldii* lectotype, sex unknown; and **b)**, field forearm length (FA) vs. field body weight (WT) for adult females. Symbols are: Australian *C. nigrogriseus* (circles), *C.* sp. indet. PNG (inverted triangles); *C. gouldii* from southern Australia (hexagons), and northern Australia (triangles) including the type series of *C. gouldii venatoris* (diamonds). Additional symbols for Fig. 3b are: *C. nigrogriseus* from WA, NT and Gulf of Carpentaria (dotted circles); *C. gouldii* northern from Cape Cleveland, NT (crosses, n = 5, Glenn Hoye pers. comm.), and an adult female from Port Essington, NT from Calaby & Keith (1974), solid inverted triangle.

Bivariate plots reveal trends in differing skull proportions between groups. Compared to northern *C. gouldii*, skulls of *C.* sp. have relatively broader INT because northern *C. gouldii* of comparable INT have larger CON (Fig. 4a). The braincase of *C.* sp. tends to be relatively much broader than northern and southern *C. gouldii*, and *C. n. nigrogriseus* as seen from a plot of CON vs. MASB (Fig. 4b). This trend is clear, despite the small sample sizes for

MASB and is also evident from group means of MASB and CON (Table 3). Skulls of *C.* sp. tend to have broader ZYG than *C. n. nigrogriseus* (Fig. 4c) and to a lesser extent, broader INT (Fig. 4a). The palate is also relatively broader posteriorly in *C.* sp. compared to northern *C. gouldii*, based on M^3–M^3 as a proxy for rear palatal breadth. Consequently, northern *C. gouldii* of comparable M^3–M^3 to *C.* sp. have larger C^1–C^1 (Fig. 5a). The rear palate of *C.* sp. also tends to be slightly broader than *C. n. nigrogriseus*, as seen from plots of M^3–M^3 vs. C^1–C^1 (Fig. 5a) and CM^3 vs. M^3–M^3 (Fig. 5b).

TABLE 3. Summary statistics of cranial and dental characters for adult *Chalinolobus*, sexes combined. Abbreviations are s.e, standard error of the mean, s.d. standard deviation, Med., median and CV, coefficient of variation.

	C. orarius **sp. nov.**									*Chalinolobus* sp. indet. PNG							
	N	Mean	Min	Max	s.e.	s.d.	Med.	CV		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
GL	4	12.63	12.48	12.83	0.074	0.149	12.61	1.18	GL	2	12.45	12.34	12.56	0.110	0.156	12.45	1.25
CON	4	12.53	12.40	12.72	0.069	0.137	12.51	1.10	CON	7	12.55	12.08	13.40	0.162	0.428	12.40	3.41
ZYG	4	9.48	9.38	9.60	0.050	0.099	9.47	1.05	ZYG	6	9.10	8.52	9.50	0.163	0.398	9.30	4.38
INT	4	4.26	4.12	4.47	0.076	0.151	4.22	3.55	INT	7	4.16	4.10	4.26	0.024	0.064	4.18	1.53
CM^3	4	4.80	4.70	4.90	0.052	0.104	4.80	2.18	CM^3	7	4.85	4.76	5.00	0.039	0.104	4.80	2.15
C^1–C^1	8	4.57	4.36	4.84	0.059	0.166	4.57	3.63	C^1–C^1	7	4.41	4.20	4.70	0.066	0.176	4.40	3.99
M^3–M^3	4	6.33	6.16	6.53	0.076	0.153	6.31	2.41	M^3–M^3	7	6.17	6.04	6.30	0.032	0.085	6.20	1.39
MASB	4	8.87	8.31	9.36	0.248	0.496	8.91	5.59	MASB	2	7.89	7.83	7.95	0.060	0.085	7.89	1.08
	C. gouldii northern Australia									*C. gouldii* southern Australia							
	N	Mean	Min	Max	s.e.	s.d.	Med.	CV		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
GL	8	13.76	12.91	14.40	0.160	0.452	13.84	3.28	GL	17	14.57	13.56	15.30	0.098	0.406	14.64	2.78
CON	11	13.80	13.00	14.50	0.151	0.501	13.89	3.63	CON	6	14.51	13.68	15.20	0.209	0.512	14.58	3.53
ZYG	14	10.15	9.65	10.50	0.079	0.295	10.10	2.90	ZYG	17	10.87	10.12	11.33	0.078	0.321	10.98	2.95
INT	10	4.62	4.41	5.07	0.068	0.217	4.51	4.70	INT	18	4.80	4.48	5.45	0.051	0.217	4.76	4.53
CM^3	16	5.53	5.05	6.00	0.060	0.239	5.51	4.32	CM^3	22	5.86	5.50	6.22	0.038	0.180	5.89	3.07
C^1–C^1	10	5.00	4.80	5.26	0.055	0.174	4.93	3.48	C^1–C^1	19	5.42	4.95	5.72	0.043	0.189	5.43	3.48
M^3–M^3	11	6.76	6.31	7.01	0.066	0.217	6.75	3.22	M^3–M^3	14	7.29	6.80	7.80	0.075	0.281	7.31	3.86
MASB	8	8.69	8.33	9.03	0.079	0.224	8.67	2.57	MASB	6	9.29	8.90	9.59	0.106	0.261	9.25	2.81
	C. nigrogriseus Australia																
	N	Mean	Min	Max	s.e.	s.d.	Med.	CV									
GL	2	12.74	12.53	12.94	0.205	0.290	12.74	2.28									
CON	13	12.69	12.02	13.00	0.079	0.284	12.70	2.24									
ZYG	12	9.21	9.00	9.60	0.062	0.213	9.13	2.31									
INT	14	4.09	3.80	4.50	0.059	0.219	4.10	5.36									
CM^3	20	4.87	4.60	5.10	0.036	0.159	4.85	3.27									
C^1–C^1	14	4.43	4.11	4.80	0.049	0.183	4.40	4.14									
M^3–M^3	19	6.13	5.80	6.66	0.048	0.208	6.10	3.40									
MASB	2	7.87	7.79	7.95	0.080	0.113	7.87	1.44									

Multivariate analyses were constrained by our dataset which had missing values for the majority of specimens of each group. Several PCAs were run using different combinations of characters and specimens to check for stable patterns of group separation. A PCA based on four cranial characters (INT, CM^3, C^1–C^1 and M^3–M^3) enabled inclusion of the maximum specimen number (n = 47). The PCA captured a high proportion of variance on the first two PC axes and demonstrated a separation of *C.* sp. from *C. gouldii* on PC 1. However, specimen scores extensively overlapped between *C.* sp., Australian *C. n. nigrogriseus*, and *C.* sp. indet. from PNG on PC 1 while all five groups overlapped on PC 2 (Fig. 6a). The similar character loadings on the first axis (Table 5) suggest an influence of increasing overall size. PC 3 scores for *C.* sp. separate but abut those of Australian *C. n. nigrogriseus*, and *C.* sp. indet. from PNG (Fig. 6b). Character loadings on PC 3 (Table 5) were strongly influence by an inverse relationship between CM^3 and M^3–M^3. As previously noted, the four specimens of *C.* sp. have relatively larger

M^3–M^3, i.e. proportionately broader rear palates, compared to northern *C. gouldii*, and to a lesser extent, also to *C. n. nigrogriseus* (Fig. 5a).

TABLE 4. Summary statistics of Forearm Length (FA) and field body weight (WT) for adult *Chalinolobus* species.

C. orarius **sp. nov.**									
		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
Females	FA	8	37.24	36.5	38.3	0.210	0.595	37.10	1.60
	WT	4	8.00	7.5	8.5	0.289	0.577	8.00	7.22
Male	FA	1		36.2					
	WT	1		6.0					
C. gouldii northern Australia									
		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
Females	FA	66	40.97	37.0	44.7	0.189	1.533	40.70	3.74
	WT	26	10.13	7.5	14.3	0.373	1.903	9.55	18.79
Males	FA	29	40.07	37.4	43.0	0.318	1.710	39.70	4.27
	WT	20	8.77	7.0	11.0	0.269	1.204	8.75	13.74
C. gouldii southern Australia									
		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
Females	FA	101	45.80	38.7	48.0	0.175	1.760	46.40	3.84
	WT	103	15.55	11.0	20.5	0.224	2.271	16.00	14.61
Males	FA	113	44.18	37.9	47.8	0.165	1.758	44.30	3.98
	WT	111	12.74	10.0	18.0	0.157	1.652	12.50	12.97
C. nigrogriseus (QLD and NSW)									
		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
Females	FA	38	35.70	31.7	37.5	0.194	1.199	35.70	3.36
	WT	17	6.89	5.5	8.3	0.209	0.862	6.70	12.52
Males	FA	74	35.23	31.9	38.0	0.137	1.180	35.25	3.35
	WT	37	6.06	5.0	7.0	0.106	0.642	6.00	10.60
Chalinolobus sp. indet. PNG									
		N	Mean	Min	Max	s.e.	s.d.	Med.	CV
Females	FA	17	36.75	34.5	39.0	0.313	1.292	36.50	3.52
	WT	7	7.14	6.5	7.5	0.143	0.378	7.00	5.29
Males	FA	1		37.0					
	WT	3	6.67	6.5	7.0	0.167	0.289	6.50	4.33

A second PCA used seven characters (FA, CON, ZYG, CM^3, INT, C^1–C^1, and M^3–M^3) but southern *C. gouldii* was excluded to check for the possible influence of that group on overall spatial relationships. The first two axes captured 86.95 % of the variance, and group separation on PC 1 (Fig. 7a) was similar to the initial PCA, but unlike the first analysis, scores of *C.* sp. fell entirely within the bounds of *C. n. nigrogriseus* on PC 3 (Fig. 7b). The spatial relationships of specimen scores on a plot of PC 1 vs. PC 2 was similar to the first PCA derived from four characters, as were the character loadings. This indicates that, despite the increase in characters, group separation on PC 1 arose primarily from overall size (Table 6). A third PCA using only the six cranial characters produced very similar results (not shown) with one notable exception. A specimen of *C.* sp. indet. (AMNH 193793) that was an outlier on the first axis based on seven characters and closest to northern *C. gouldii* (Fig. 7a), fell on the group boundary of *C. n. nigrogriseus* in the analysis using six cranial characters (not shown). This suggests that its outlier status arose mainly from FA.

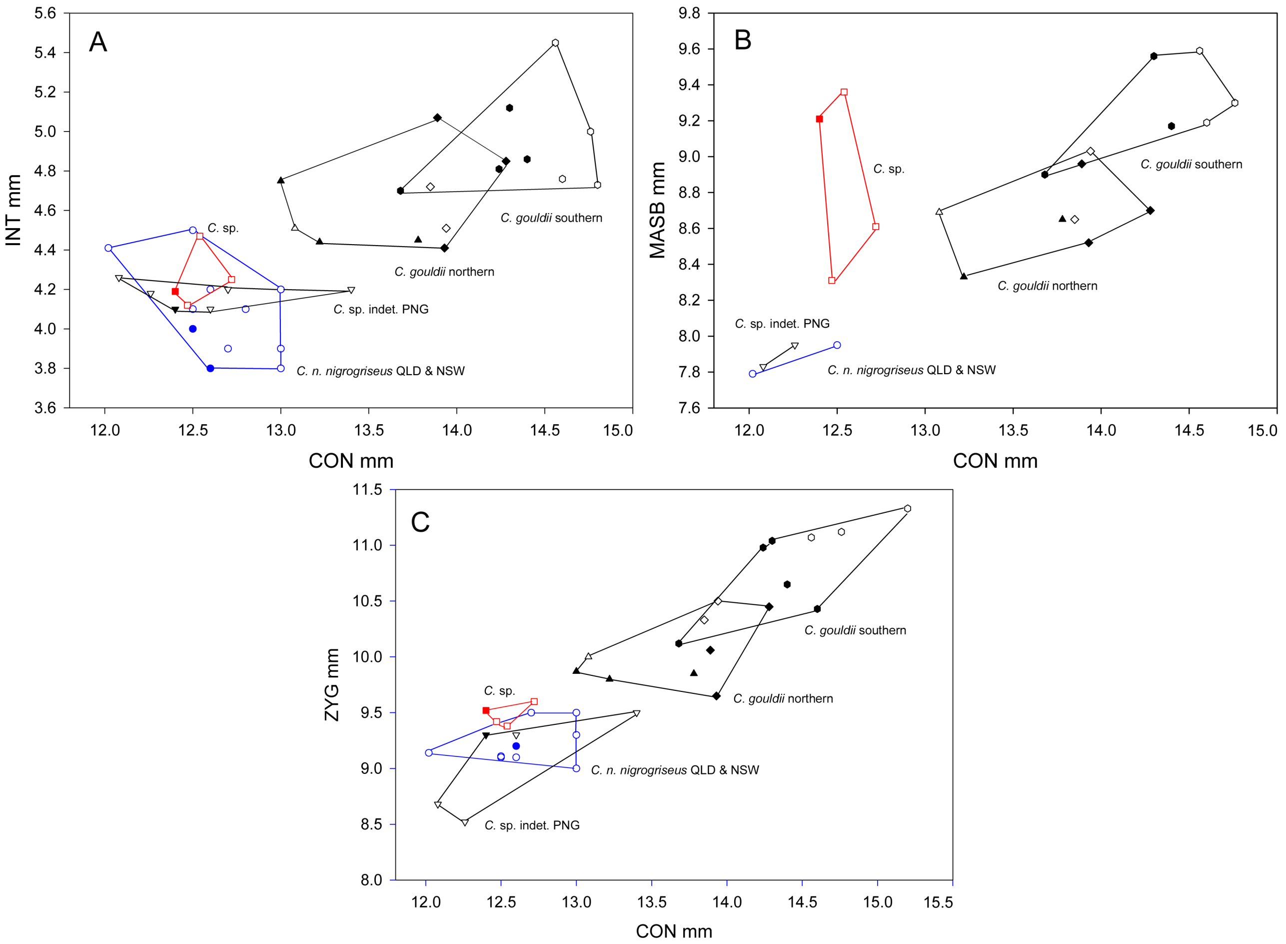

FIGURE 4. Trends in differing skull proportions of *C.* sp.: **a)**, least intertemporal breadth (INT) vs. condylobasal length (CON), showing relatively broader INT than northern *C. gouldii*; **b)**, CON vs. mastoid breadth (MASB) showing relatively broader MASB than northern *C. gouldii* and *C. nigrogriseus*; **c)**, CON vs. zygomatic breadth (ZYG) showing relatively broader ZYG than northern *C. gouldii* and *C. nigrogriseus*.

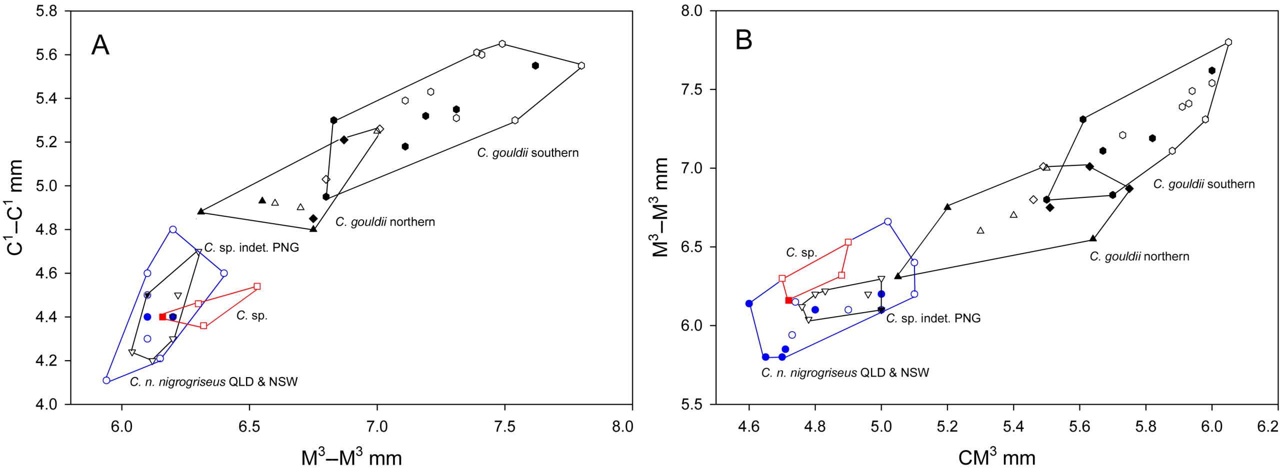

FIGURE 5. Trends of a relatively broader rear palate of *C.* sp. compared to: **a)**, northern *C. gouldii* as seen in a plot of maximum breadth from left M^3 to right M^3 (M^3–M^3) vs. Outer breadth across upper canines (C^1–C^1); and **b)**, *C. nigrogriseus*, from a plot of maxillary tooth row length (CM^3) vs. M^3–M^3.

Both PCAs included measurements from Van Deusen & Koopman (1971) of six females and one male from PNG which they assigned to *C. n. nigrogriseus* (our indeterminate group). PCA scores of those specimens extensively overlap with both *C.* sp. and Australian *C. nigrogriseus* (Figs. 6 & 7) and might include one or both taxa. Summary statistics for the PNG specimens using their measurements (Tables 3 & 4) also overlap with both taxa for all measurements. The specimen with the largest FA (AMNH 193793, adult female), an outlier in Fig. 7a, had bifid I^1 but worn teeth, thus potentially confounding their assessment of a secondary cusp. We are unable to resolve the identity of their PNG specimens from these measurements, nor can we exclude the possibility (if remote) that the small form of *C. gouldii* from northern Australia might also be present in the sample.

TABLE 5. Character loadings, eigen values and percentage of total variance per axis on the four axes of a PCA using four cranial and dental characters of 47 specimens of *Chalinolobus*.

	PC 1	**PC 2**	**PC 3**	**PC 4**
INT	0.465	0.855	0.124	0.195
CM^3	0.511	-0.299	0.719	-0.363
C^1–C^1	0.506	-0.420	-0.162	0.736
M^3–M^3	0.517	-0.062	-0.664	-0.537
Eigenvalue	3.62	0.294	0.044	0.0355
% variance	90.65	7.36	1.17	0.887

TABLE 6. Character loadings, eigen values and percentage of total variance per axis for a PCA using FA and six cranial and dental characters of 29 specimens of *Chalinolobus*.

	PC 1	**PC 2**	**PC 3**	**PC 4**	**PC 5**	**PC 6**	**PC 7**
FA	0.359	0.143	0.865	-0.287	-0.030	-0.037	-0.131
CON	0.396	-0.280	-0.048	0.341	0.585	0.250	-0.491
ZYG	0.385	0.128	-0.380	-0.656	0.388	-0.309	0.124
INT	0.285	0.833	-0.088	0.392	0.073	0.144	0.195
CM^3	0.398	-0.288	0.045	0.450	-0.125	-0.668	0.305
C^1–C^1	0.404	-0.326	-0.036	-0.086	-0.168	0.611	0.566
M^3–M^3	0.404	0.048	-0.306	-0.088	-0.676	0.027	-0.524
Eigenvalue	5.339	0.747	0.364	0.265	0.163	0.067	0.054
% variance	76.273	10.677	5.203	3.784	2.324	0.960	0.778

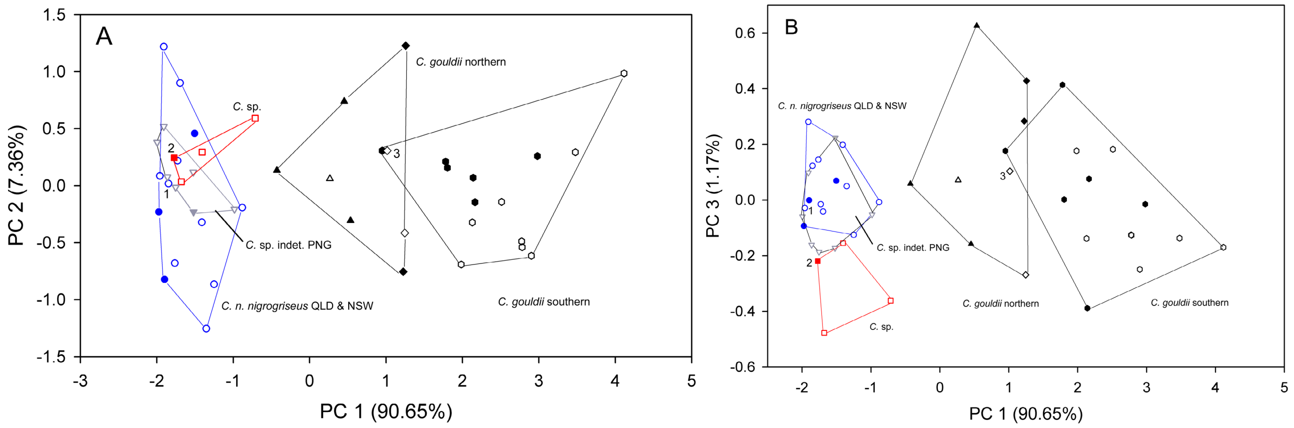

FIGURE 6. Plot of specimen scores for the first three axes of a PCA based on a correlation matrix of four skull and dental measurements of 47 *Chalinolobus* skulls: **a)** PC 1 vs. PC 2, and **b)**, PC 1 vs. PC 3. Symbols are: *C. orarius* **sp. nov.** (rectangles), Australian *C. nigrogriseus* (circles), *Chalinolobus* from PNG of indeterminate species previous referred to *C. nigrogriseus* (inverted triangles), and *C. gouldii* from southern Australia (hexagons) and northern Australia (triangles), including the type series of *C. gouldii venatoris* (diamonds). Solid symbols are male, open symbols female. 1, holotype of *C. nigrogriseus*, 2, holotype of *C. orarius* **sp. nov.** and 3, holotype of *C. gouldii venatoris*.

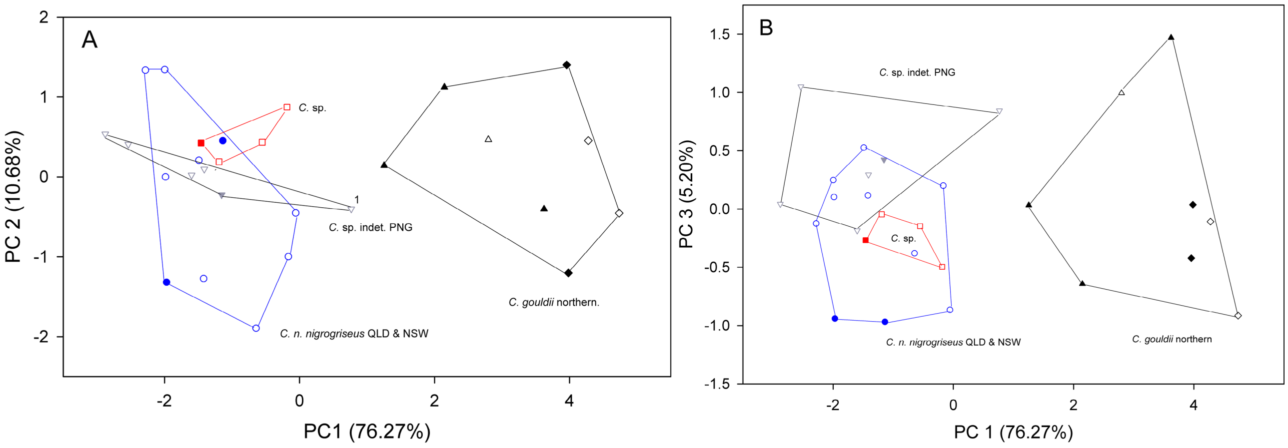

FIGURE 7. Plot of specimen scores for the first three axes of a PCA based on a correlation matrix of FA and six skull and dental measurements of 29 *Chalinolobus* skulls: **a)** PC 1 vs. PC 2, and **b)**, PC 1 vs. PC 3. Symbols are: *C. orarius* **sp. nov.** (rectangles), Australian *C. nigrogriseus* (circles), *Chalinolobus* from PNG of indeterminate species previous referred to *C. nigrogriseus* (inverted triangles), and *C. gouldii* from northern Australia (triangles) including the type series of *C. gouldii venatoris* (diamonds). Solid symbols are male, open symbols female. 1, *C.* sp. indet. (AMNH 193793 female) from Port Moresby, PNG.

Systematics

Chalinolobus orarius sp. nov.

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Figs. 8–10. Tables 2–4, 7.

Holotype. AM M.15114, (field number H13), male, body in alcohol, skull extracted, captured in a mist-net on 7 June 1984 by H. Parnaby and Peter Wilson, Gordon, -9.446°, 147.199° (a suburb of Port Moresby), Central Province, Papua New Guinea. Tissue samples stored in liquid nitrogen taken in the field have the same field number as the body and were lodged in the South Australian Museum.

Paratypes (n = 8). Champion House, Goldie Street, -9.458°, 147.157°, Port Moresby, Papua New Guinea, all adult females collected by Dr James I. Menzies from a roof cavity: M.10385, (UPNG no. 461), male, study skin & extracted skull, collected 3 Nov 1969; M.10386, (UPNG no. 462), female, study skin & extracted skull, collected 4 Nov 1969; M.10387, (UPNG no. 467), female, body in alcohol with skull in situ., collected 3 Nov 1969; M.10388, (UPNG no. 469), female, body in alcohol with skull in situ., collected 3 Nov 1969; M.10389, (UPNG no. 471), female, body in alcohol with skull in situ., collected 3 Nov 1969, M.10390, (UPNG no. 471) female, body in alcohol with skull in situ, humerus extracted, collected 3 Nov, 1969; M.15115, (field number H91), female, body in alcohol with skull in situ., collected 17 June 1984 by H. Parnaby and Peter Wilson from the type locality; M.49709, (field number of body R12245, PNGM 28231 on long term loan to AM), female, body in alcohol with extracted skull, M.49709.001, frozen tissue, field liver sample number CHNI1, AM EBU tissue number 99826, collected in a mist-net on 9 Nov 2006 by Steve Hamilton from a survey base camp at -8.236°, 141.808° approx. 4 km E of new Serki village, Western Province, Papua New Guinea.

Measurements of the type series are given in Table 7.

Diagnosis. Distinguished from all other species of *Chalinolobus* by the combination of an enlarged ear margin which terminates as a lobe near the angle of the mouth (Fig. 8), and the presence of a secondary cusp on I^1 (Fig. 9). Further differentiated by DNA sequence divergence of at least 6.7% in the mtDNA COI gene from other sampled *Chalinolobus* species. Distinguished from Australian *C. gouldii gouldii, C. gouldii venatoris* and Norfolk Island *C. cf. gouldii*, the only other *Chalinolobus* in which the enlarged ear terminal lobe is present, by smaller mean body size, e.g. mean FA = 37.24 mm (n = 8 females) vs. northern Australian *C. gouldii* 40.97 mm (n = 66 females) (Table 4). Northern Australian *C. gouldii* (north of latitude 20° S) of equivalent forearm length to *C. orarius* **sp. nov.** tend to have larger skulls, e.g. CON typically greater than 12.9 mm, C^1–C^1 usually greater than 4.8 mm and CM^3 greater than 5.0 mm (Table 3).

Distribution. Recorded from Serki, Western Province and Port Moresby, Central Province, Papua New Guinea.

Biology. The limited information about New Guinean *Chalinolobus* summarised by Bonaccorso (1998) is now in doubt, pending clarification of how many species of the genus occur in PNG. Twins have been recorded from *C. orarius* **sp. nov.** at Port Moresby in a maternity colony located in the roof of a building. The species is suspected to roost in tree hollows and is known to roost in buildings. Bonaccorso (1998) states that *C. nigrogriseus* forage in riparian gallery forest and might not travel far into adjoining forest and woodland but this could have been drawn from Australian studies. If those observations were made in PNG, it raises the possible association of *C. orarius* **sp. nov.** with gallery forest in addition to the open habitats discussed below.

Etymology. Derived from the Greek adjective *oraria* meaning "of the coast", a reference to the species distribution in the coastal and subcoastal eucalypt savannahs of southern New Guinea.

Common name. Coastal Lobe-lipped Bat is suggested as a vernacular name for this species.

Remarks. Although Australian *C. n. nigrogriseus* has the closest overall resemblance in external features and general body size to *C. orarius* **sp. nov.**, it is readily distinguished by the ear margin which terminates in a rudimentary skin lobe near the angle of the mouth and the secondary cusp on I^1 is invariably absent. Smaller individuals of *C. gouldii* with forearm length less than 40 mm, especially those from far northern NT and north Qld can be separated from *C. orarius* **sp. nov.** by the invariant absence of a secondary cusp on I^1 and which have relatively larger skulls. The two-tone dorsal fur colouration, grading from dark shoulders to lighter rump fur typical of northern Australian *C. gouldii* contrasts with the more uniform dark dorsal fur of *C. orarius* **sp. nov.** (Fig. 10). Although dorsal fur colouration is a potentially useful guide in distinguishing *C. orarius* **sp. nov.** from northern *C. gouldii*, individuals of the latter species occasionally have uniform dorsal fur colour. Melanistic individuals aside, the two-tone dorsal fur gradation can also be absent during stages of fur moult.

The conspicuously enlarged terminal ear lobe is present in only three other *Chalinolobus* taxa: *C. gouldii* from mainland Australia and Tasmania including the type series of *C. gouldii venatoris* Thomas, 1908 from Alexandria NT, and the presumably extinct Norfolk Island *Chalinolobus* sp., assigned to *C. gouldii* in the past. The ear lobe of *C. dwyeri*, though enlarged, does not approach the relative size of *C. gouldii*.

The dentition of the holotype of *C. orarius* **sp. nov.** broadly resembles that of the holotypes of *C. n. nigrogriseus* and *C. gouldii venatoris*, based on comparisons with photographs of the upper toothrows of the latter two holotypes. Thus, the first upper premolars are minute, an antero-lingual cusp is present on the second upper premolars and the third molars are unreduced. The pronounced secondary antero-lateral cusp on I^1 is absent in the latter holotypes and is also absent in the holotype of *C. nigrogriseus rogersi*, which also lacks an antero-lateral cusp on the second upper premolars (Van Deusen & Koopman 1971). A detailed assessment of the diagnostic value of dental characters is premature and requires a better understanding of infra-specific variation within these taxa.

FIGURE 8. Similarity of the enlarged lobe (white arrow) formed by the downwardly directed, lower ear margin near the angle of the mouth of **a)** and **b)**, AM M.49709 (PNGM 28231), adult female from Serki, Western Province PNG, paratype of *C. orarius* **sp. nov.**; and **c)**, southern Australian *C. gouldii*, AM M.16073, adult male, Barakula State Forest, NW of Chincilla, Qld. Not to scale. (Photos: a and b, Steve Hamilton; c, Ron Lovatt, AM Digivols).

FIGURE 9. Holotype of *C. orarius* **sp. nov.**, AM M.15114 adult male from Port Moresby, PNG. (Photo: Ron Lovatt, AM Digivols).

FIGURE 10. Pelage colour of **a)**, dorsal, and **b)**, ventral surface of paratype of *C. orarius* **sp. nov.**, AM M.10385 adult female study skin from Port Moresby, PNG, compared to variation in northern *C. gouldii* from the Gulf of Carpentaria, Qld: **c)**, AM M.8515 adult female, and **d)**, AM M.8516 adult male. (Photos: Harry Leung, AM).

TABLE 7. External and cranial measurements for the holotype (AM M.15114) and paratypes of *C. orarius* **sp. nov.**

	AM M.15114	**PNGM M28231**	**AM M.10385**	**AM M.10386**	**AM M.10387**	**AM M.10388**	**AM M.10389**	**AM M.10390**	**AM M.15115**
Sex	male	female	female	female	female	female	female	female	female
GL	12.48	12.65	12.83	12.57					
CON	12.40	12.47	12.72	12.54					
ZYG	9.52	9.42	9.60	9.38					
INT	4.19	4.12	4.25	4.47					
CM^3	4.72	4.70	4.88	4.90					
C^1–C^1	4.40	4.46	4.36	4.54	4.60		4.70	4.70	4.84
M^3–M^3	6.16	6.30	6.32	6.53					
PAL	6.07	5.80	5.96	6.04					
MASB	9.31	8.31	8.61	9.36					
BUL	3.36	3.35	3.24	3.26					
CM$_3$	5.01	5.05	5.07	5.43					
DL (con.)	10.19	9.52	10.05	9.90					
DL (ang.)	10.28	9.98	10.40	10.14					
FA	36.20	36.80	37.00	36.50	38.30	37.30	36.90	37.20	37.90
WT	6.00	8.50	8.50	7.50					7.50
Ear	11.7	13.8							12.5
HL	17.3								17.4

Distribution and habitat of *Chalinolobus* in Papua New Guinea

Records attributed to *C. nigrogriseus* from Papua New Guinea are summarised by Bonaccorso (1998) as having a coastal distribution, postulated to be below 300 m elevation by Ziegler (1982) and Bonaccorso (1998). It remains to be established what proportion represent *C. orarius* **sp. nov.** but a review of all *Chalinolobus* locality records is potentially informative.

A summary of locality data for PNG *Chalinolobus* (Table 8) indicates that the likely elevation for most is below 100 m, and most of these are probably below 50 m. The precise location is not available for some records but the lowland context within an arbitrarily selected, 5 km radius of the general locality places an upper elevational limit. For example, the record from "Six Mile Saraga" is in a suburb of Port Moresby in which most land is below 100 m, with limited hills and ridges to c. 150 m.

Locality records were examined in relation to the broad vegetation classes mapped by Paijmans (1975) using the vegetation shape files of the analysis of Joseph *et al.* (2019). All localities were dominated by open vegetation classes within 5 km radius of the estimated site, mainly savannah, woodland, swamp vegetation, grassland or mosaics of these classes (Fig. 11, Table 8). Kupiano was the only site where extensive mangroves were mapped within 5 kms. This indicates that, in the context of the relatively coarse scale of vegetation mapping, the distribution of *Chalinolobus* in PNG is associated with open habitats. The influence of gallery forest needs to be examined but was not mapped by Paijmans (1975).

The broad distribution of potentially suitable habitat was examined by amalgamating the dominant vegetation classes surrounding locality records into two categories: savannah and savannah mosaics, and woodland and woodland mosaics. An overlay of these categories with elevation below 150 m reveals a limited and disjunct distribution of these vegetation categories through the lowlands of southern PNG (Fig. 12), as demonstrated by Joseph *et al.* (2019).

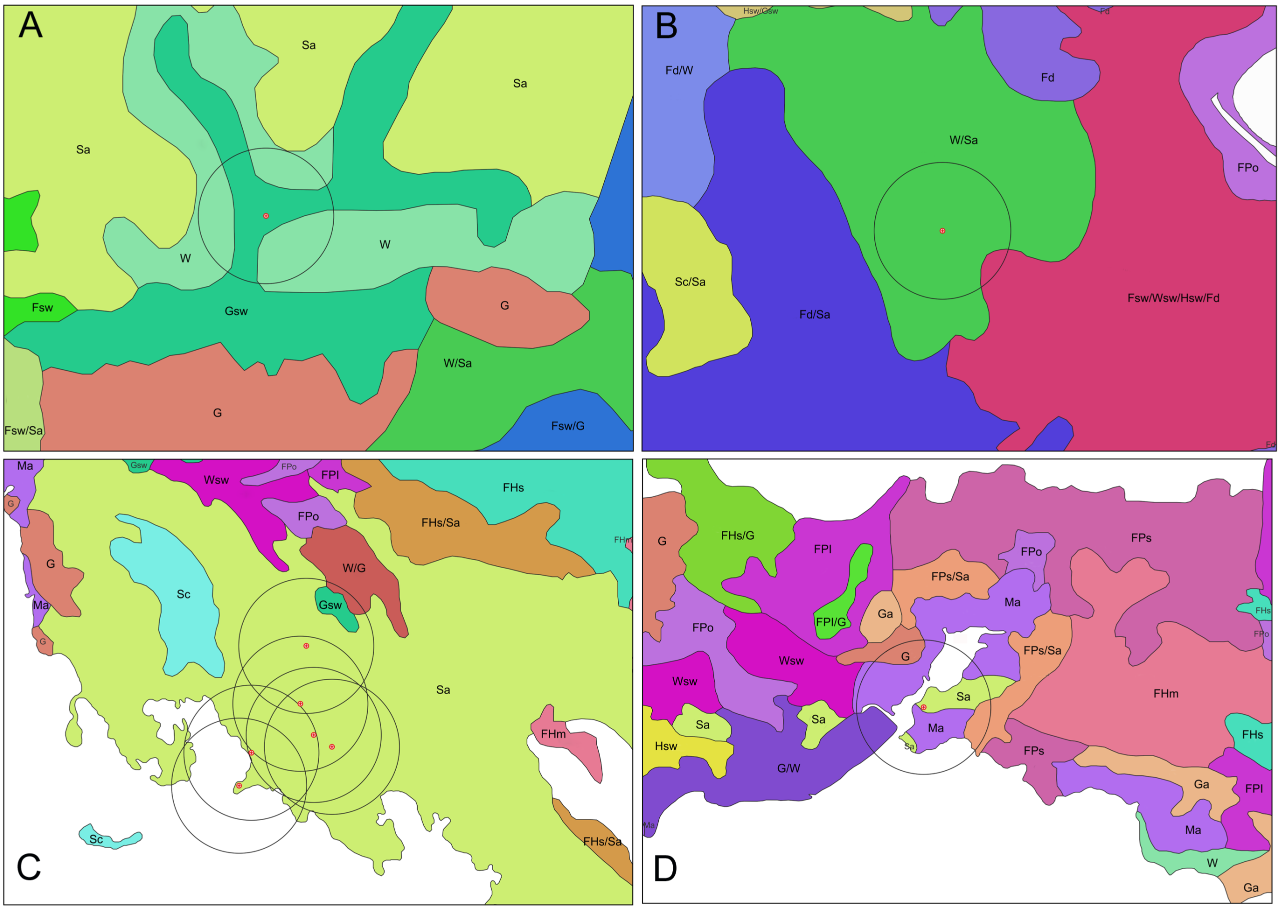

FIGURE 11. Localities of PNG *Chalinolobus* with vegetation categories of Paijmans (1975), showing 5 km radius circle around locations. **a)**, Bandaber, **b)**, Serki, **c)**, Port Moresby and **d)**, Kupiano. Based on vegetation shape file of Joseph *et al.* (2019). Abbreviations for vegetation classes are: Sa, savannah; W, woodland, Wsm, swamp woodland; G, grassland, Ga, current and abandoned gardens and plantations, Gsw, swamp grassland; Hsw, herbaceous swamp vegetation; Ma, mangrove; Sc, scrub; FB, littoral forest; Fd, dry evergreen forest; Fsw, swamp forest; FHs, small-crowned lowland hill forest; FHm, medium-crowned lowland hill forest; FPo, open forest on plains; FPs, small crowned forest on plains; FPI, large to medium-crowned forest on plains.

TABLE 8. Estimated elevation of locality records of PNG *Chalinolobus* spp. and vegetation classes within 5 km radius of site using vegetation classes of Paijmans (1975). Asterisks indicate *C. orarius* **sp. nov.**

Site	**Latitude**	**Longitude**	**Est. elev. (m)**	**Nu of veg types 5 km radius**	**Vegetation categories of Paijmans (1975)**
Bandaber	-8.935	141.279	< 20	2	-Swamp grassland -Woodland
Serki*	-8.236	141.808	< 20	6	-Woodland/Savannah -Swamp forest/Swamp woodland/ Herbaceous swamp vegetation/Dry evergreen forest
Kupiano community school	-10.073	148.19	< 30	5	-Savannah -Mangrove -Small crowned forest/Savannah -Grassland/Woodland -Grassland
Fergusson Is			?		Site unknown.

...continued on the next page

TABLE 8. (Continued)

Site	Latitude	Longitude	Est. elev. (m)	Nu of veg types 5 km radius	Vegetation categories of Paijmans (1975)
Champion house*, Goldie St	-9.458	147.157	< 50	1	-Savannah, urban
Waigani sewerage works (assumed to be Moitaka ponds)	-9.386	147.194	< 50	4	-Savannah, -Swamp grassland, -Woodland/Grassland
Paga Hill Court House	-9.4802	147.1487	< 20	1	-Savannah, urban
PNG National Museum & Art Gallery (roof)	-9.4255	147.1900	c. 55	1	-Savannah, urban
Gordon	-9.446	147.199	50-60	1	-Savannah, urban
Saraga (Six mile)	-9.454	147.2113	< 150	1	-Savannah, urban

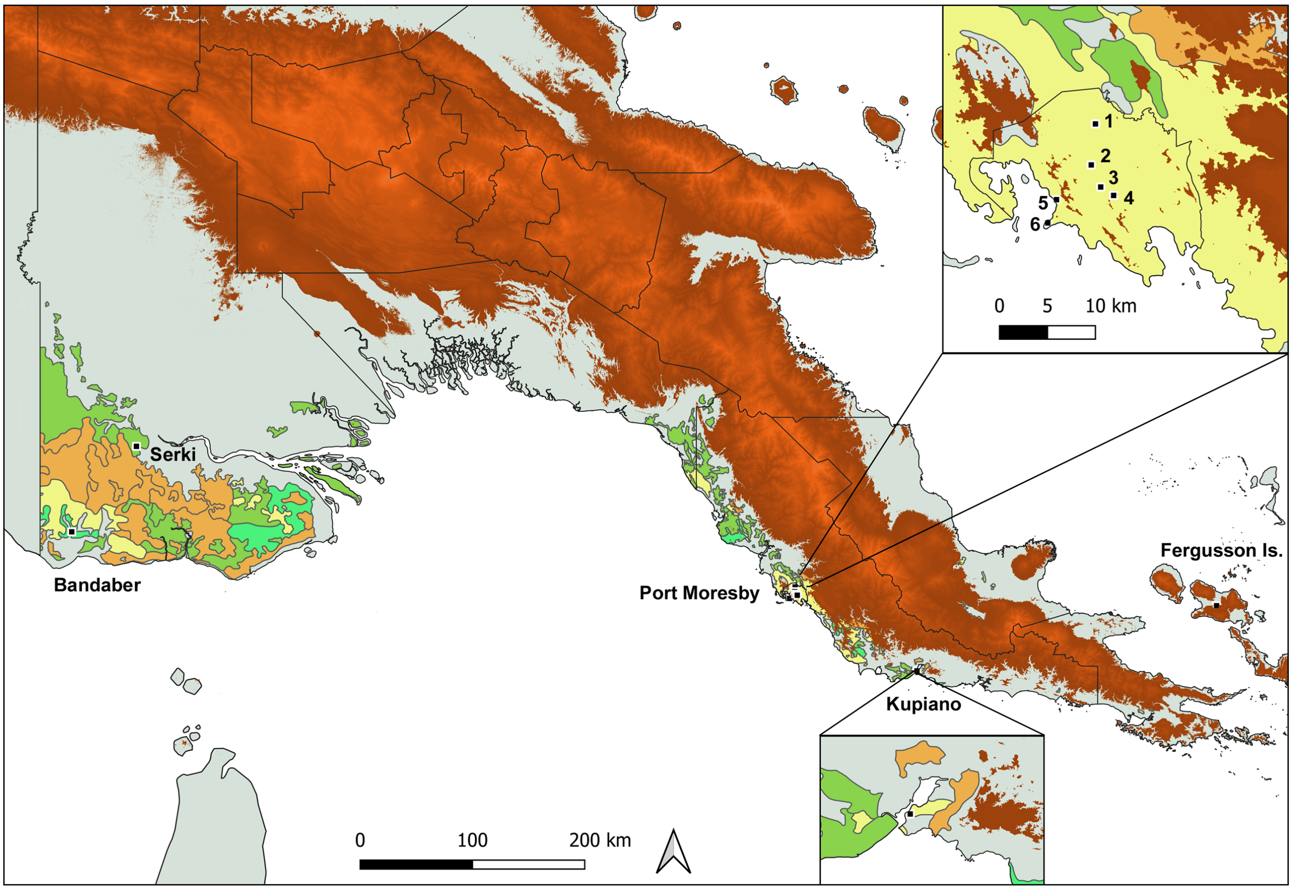

FIGURE 12. Locality records of *Chalinolobus* from the island of New Guinea showing amalgamations of Paijmans vegetation categories: savannah (yellow); mosaics with savannah (orange); woodland (pale green) and mosaics containing woodland (dark green). Elevations above 150 m are in dark red. Six localities from Port Moresby environs (map inset) are: 1, Waigani Sewerage works, 2, PNG Museum & Art Gallery roof, 3, Gordon, 4, Saraga, 5, Champion House and 6, Paga Hill. Second inset shows environs of Kupiano. Vegetation map modified from figure 1 of Joseph *et al.* (2019) using a vegetation shape file kindly provided by Christopher Wilson, CSIRO Canberra.

Discussion

The discovery of a new species of *Chalinolobus* from PNG necessitates a review of the identity of remaining New Guinean material of the genus in world collections. In the interim, the presence of *C. nigrogriseus* on the island of New Guinea remains in doubt although it would not be surprising, given the number of bat species shared between the eucalypt savannahs of northern Australia and southern New Guinea. Several specimens from Port Moresby examined by Van Deusen & Koopman (1971) lacked a secondary cusp on I^1 and are possibly *C. n. nigrogriseus* or *C. gouldii*, the latter species not reported from New Guinea. If *C. gouldii* occurs in New Guinea, populations might average smaller than those from northern Australia, following a trend of decreasing size with latitude documented from mainland Australia (e.g. Tidemann 1986). If so, a higher proportion of smaller individuals might approach the size of *C. orarius* **sp. nov.** than in northern Australian populations.

The possible occurrence of *C. orarius* **sp. nov.** in northern Australia should also be investigated. It could have been mistaken for *C. nigrogriseus* or *C. gouldii*, depending on which identification criteria were prioritised. If body size and dorsal fur colour were the primary criteria it could be confused with *C. nigrogriseus* but if the identification prioritised the relative size of the terminal ear lobe, then *C. orarius* **sp. nov.** could be confused with smaller individuals of *C. gouldii*, particularly if the bifid upper incisor was overlooked. Calaby & Keith (1974) recorded a small adult female from Danger Point, Cobourg Peninsula, Northern Territory which they assigned to *C. gouldii* and for which they cite registration numbers in the Museum and Art Gallery of the Northern Territory (Darwin) as NTM 363 (now U2115) for the body in alcohol, and NTM 3650 (now U2116) for the extracted skull. We have not been able to locate that specimen but suspect that Calaby identified it based on the presence of an enlarged terminal ear lobe, given that they captured *C. nigrogriseus* in the same area. Its forearm length (35.8 mm) and body weight (6 g) fall within the range of *C. orarius* **sp. nov.** (see Fig. 3b) but whether the specimen has an enlarged ear lobe and bifid I^1 remains to be determined. Milne & Pavey (2011) mention a small form of *C. gouldii* from far northern NT which they suspect is a distinct subspecies and its status relative to *C. orarius* **sp. nov.** needs to be examined.

Our study was constrained by a lack of comparative material to evaluate morphological variation within taxa. Although a large number of specimens of *C. gouldii* reside in research collections, there are fewer from far northern Australia and we accessed few skulls of Australia *C. nigrogriseus*. Further, most material of *Chalinolobus* from PNG is held in overseas collections. Assembling the comparative material would entail a major project. We chose to publish the material at hand to accelerate research into the distribution, biology and conservation status of *C. orarius* **sp. nov.**, particularly given the typically long lag time between discovery and formal description of species. Consequently, our morphological diagnosis of *C. orarius* **sp. nov.** should be tested and expanded using additional material and characters. In particular, to establish whether the secondary cusp on I^1 is invariably present in this species. Van Deusen & Koopman (1971) concluded that it was present in the great majority of PNG specimens but hard to evaluate in some, particularly those with worn dentition. They remarked that the secondary cusp was absent in only one skull examined. Their table 2 lists a further two specimens in alcohol with skulls in situ (AMNH 193796 and 193798) for which they also scored the secondary cusp as absent. Clearly, if the latter specimens are found to be *C. orarius* **sp. nov.** then the secondary cusp is not invariably present, or those specimens are not that species.

Our molecular analysis was also limited by meagre sampling for most taxa. Interspecific relationships within *Chalinolobus* remain unclear and the relationships of *C. orarius* **sp. nov.** are unresolved. Our phylogenetic analysis is the first assessment of interspecific relationships within the genus based on sequencing data. Although tissue samples and/or sequencing data were available for all seven currently recognised species of the genus, samples were not available for *C. n. nigrogriseus*, a key taxon for comparison with *C. orarius* **sp. nov.** The presence of two divergent lineages within *Chalinolobus* is a significant insight to emerge from our analysis. This consists of a highly divergent "*C. morio*" (showing up to 4.5% sd amongst haplotypes) which forms a separate well supported clade, but the relationships of remaining species is unresolved in our analysis. The low sequence divergence of 2.2% between samples of *C. picatus* and *C. dwyeri* was unexpected for these morphologically distinctive species.

The majority of our estimates of elevation for PNG *Chalinolobus* records are below ca. 50 m. The highest elevation site was "Saraga" which defaulted to 150 m, the maximum possible elevation for that suburb but most land within that suburb is below c. 100 m. Consequently, we propose a conservative maximum elevation of 150 m to define the occurrence of the genus in PNG. This refines previous suggestions that the genus occurs below 300 m in PNG (Ziegler 1982; Bonaccorso 1998). These records are associated with the broad categories of savannah and woodland with mosaics of grasslands and various swamp vegetation categories. Our results indicate that the vegetation classes associated with *Chalinolobus* records have a limited and disjunct coastal distribution in southern PNG, implying a limited distribution of the genus in low elevation coastal regions.

Our results broadly support Lavery & Flannery (2023), who suggest that PNG *Chalinolobus* occur in areas of sparser understoreys, inferred from suspected habitat of Australian *C. nigrogriseus*. However, whereas those authors list riparian woodlands, tall open forests, grasslands and floodplains, we found limited occurrence of tall open forests within 5 km of locality records. We found a striking associate of records with savannah, present in the vicinity of all sites except Bandaber (Western Province), and Fergusson Island for which the collecting locality is unknown. However, open habitat including savannah elements are mapped for the lowlands of Fergusson (Paijmans 1975). The association of records with savannah does not seem to have been previously noted and requires further assessment. Half of the records are from the National Capital District, an area largely mapped as Savannah by Paijmans (1975). However, a record from Waigani sewerage works on the edge of the extensive Waigani swamp but mapped as Savannah, illustrates the limitations of mapping at a scale of 1: 1000000. The relevance of gallery forest to the distribution of the genus also needs to be investigated but was not mapped by Paijmans.

Past determinations of a low conservation threat status for New Guinean *Chalinolobus* (as *C. nigrogriseus*) were possibly at least partly an inference based on an IUCN Red List category of Least Concern assigned to Australian populations of *C. nigrogriseus* (Hutson *et al.* 2020). In the absence of adequate survey data, several factors should be considered in future evaluations of the status of *C. orarius* **sp. nov.** that do not invite complacency that the species is currently secure. The species is known from relatively few collection events, even if we assume that all past records of New Guinean *Chalinolobus* are this species. The great majority of records originate prior to 1986 and to our knowledge the Serki specimen reported here is one of the few if not the only record this century, perhaps due to the lack of surveys. Populations are probably declining, inferred from the declining habitat quality in its lowland savannah woodland distribution, and the genus is likely to have a disjunct coastal distribution. This species most likely relies on hollows in old trees as roost sites. Potentially significant threats could include loss of hollow-bearing trees from increased fire frequency and intensity, firewood collection, and habitat clearing and modification from increased human populations.

To our knowledge, new information has not been published about PNG *Chalinolobus* so far this century. Bat surveys relying on capture techniques (mist-nets and harp traps) are urgently needed to evaluate the distribution and status of *C. orarius* **sp. nov.** A sole reliance on bat call surveys is premature until call identification criteria are resolved because the species is likely to be confused with species of Bent-wing Bats *Miniopterus*, Broad-nosed Bats *Scotorepens* and Pipistrelles *Pipistrellus* which are thought to have similar call characteristics (Kale *et al.* 2018).

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Appendix: Specimens measured

Measurements from the following specimens were included in numerical analyses. Published measurements were also included as indicated. Asterisk indicates specimens used in PCAs. Most specimens used in summary statistics had missing values.

C. gouldii northern (n = 29): **WA.** M.22062, M.22066, M.22067, M.22078–80, M.22085, M.22088*, M.22089–91. McKenzie & Youngson (1983): WAM M22833* (FW942), WAM M22837* (FW983). **NT.** NHMUK BM6.3.9.2*, 6.3.9.3, 6.3.9.4*, 6.3.9.5*, 7.1.4.4* (type series of *C. g. venatoris*). USNM 237954 (from Johnson 1964). **QLD.** AM M.22070, M.22071, M.8515*–17*. Tate (1942): AMNH 107764, 107765, 107800, 109274–275.

C. gouldii southern (n = 85): **NSW**. AM: M.3656*, M.4524*–26*, M.5073*, M.8239, M.8292, M.8473*, M.8614*, M.9131, M.11519*, M.14553, M.17958–61, M.19201, M.20379–80, M.23962, M.25366–77, M.25677, M.26477–79, M.26492–93, M.26529, M.26681, M.26783–84, M.26787, M.26789–91, M.28778–79, M.28785, M.28817, M.28832–33, M.28938–39, M.28959, M.28974, M.29039, M.29058, M.31040, M.32030, M.32035, M.32036*, M.32037, M.32040, M.32047, M.32060, M.36078, M.36159, M.36162, M.36913, M.49991, M.55562*. Tate (1942): USNM 221242. **QLD.** (8) M.16073–79, M.23567, M.23568*. **NT.** Johnson (1964): USNM 284187–88. **SA.** AM M.4867. **WA.** (8) M.39783, M.39790, M.39796, M.39819–21, M.39842–43. **VIC.** AM M.51371*–72*.

C. nigrogriseus (n = 43): **QLD**., M.8519, M.8521, M.13275–M.13278, M.13284, M.13312–M.13315, M.16101–M.16105, M.35501, M.51095*. Van Deusen & Koopman (1971): AMNH 160243*, 154661*–154663*, 155230*, 155234*, 194250*, USNM 238619, NHMUK BM15.3.5.11*, BM56.10.28.3* (holotype). **NSW.** AM: M.25437, M.26598, M.29059, M.31079, M.31090, M.31093, M.33378, M.33489. M.36022, M.50019, M.50020*. Van Deusen & Koopman (1971): AMNH 194250, MV C5162*–63*, C5164.

Chalinolobus sp. indet. Papua New Guinea (n = 28): Van Deusen & Koopman (1971): AMNH 160337*, 193791*–193800*. NHMUK BM69.330*–331* (Anja Divlyan, pers. comm.). NHMUK BM70.2001–2005 (FA only, Glenn Hoye, pers. comm.). BPBM 109602–611 (WT, A. Engilis, Jnr. pers. comm.).

Adult bats measured (FA, WT) and released

C. gouldii southern (n = 200, 97 males, 103 females): **New South Wales**. Plagyan State Forest, northern branch of Teatree Creek, 30° 25.5183’S, 150° 13.4037’E (1 male, 1 female, 6 Dec 2001, David Milledge (DM)). Melville Range Nature Reserve, 31° 6.1388’S, 150° 36.8841’E (1 male, 2 females, 20 Dec 2001, DM). Dowe State Forest, 1km S of Bullock Yoke Gully. 30° 48.3031’S, 150° 29.8724’E (3 females, 26 Nov 2003, DM). Melville Range Nature Reserve, 31° 6.3034’S, 150° 37.0058’E (2 females, 20 Dec 2001, DM). Mehi State Forest. Junction of Cameron-Mehi and Munro Roads. 29° 57.2649’S, 150° 45.0070’E (2 males, 3 Dec 2001, HP). Mt Kaputar National Park 30° 3.8111’S, 150° 5.5526’E (2 males, 16 Dec 2000, DM). Warialda State Forest, near Yellow George Waterholes. 29° 39.2213’S, 150° 35.0393’E (2 males, 22 Oct 2001, DM). Severn State Forest, beginning of Fishermans track. 29° 7.4855’S, 150° 59.0055’E (2 males, 16 Jan 2002, DM). Plagyan State Forest, southern branch Teatree Creek Road 30° 26.2120’S, 150° 12.9469’E (2 males, 6 Dec 2001, DM). Goonoowigal Travelling Stock Reserve. Old Armidale Rd, 6.3 km SE of Inverell-Bundarra Rd. 29° 49.5392’S, 151° 9.5312’E (2 males, 2 females, 11 Dec 2002, DM). Mehi State Forest northern section 29° 53.9380’S, 150° 44.4830’E (3 males, 4 Dec 2001, HP). Hell Hole Creek, ca. 3.5 km S of Rocky Creek. 30° 4.0526’S, 150° 18.7749’E (3 males, 22 Mar 2002, HP). Arakoola Nature Reserve, 29° 18.7273’S, 150° 49.5189’E (3 males, 1 female, 7 Nov 2001, HP). On Horton River upstream of Horton Falls Road crossing. 30° 20.1796’S, 150° 18.8481’E (3 males, 3 females, 6 Mar 2002, DM). Ridge between Horton River and Cut Road Creek. 30° 20.7353’S, 150° 18.7649’E (7 males, 5 females, 6 Mar 2002, DM). Horton Falls area, on Porcupine Creek. 30° 21.5397’S, 150° 20.3616’E (8 males, 8 females, 5 Mar 2002, Phil Spark). Andersons Tank (27 males, 30 females), see Parnaby *et al.* (2020). **Victoria.** Otway Ranges (21 males, 35 females), see Parnaby *et al.* (2020). Wyperfield National Park (6 males, 8 females, 1980, HP). **Western Australia.** Dryandra Woodlands (2 males, 3 females), see Parnaby *et al.* (2020).

C. gouldii northern (n = 52, 4 males, 48 females): **Western Australia.** Mt Bruce Well and Marillana Station (2 males, 37 females), see Parnaby *et al.* (2020). **Northern Territory**. MacArthur (1 male, 5 females), see Parnaby *et al.* (2020). **Queensland.** Gregory Station (1 female), Georgetown (1 male, 5 females) see Parnaby *et al.* (2020).

C. nigrogriseus (n = 64, 46 males, 18 females): **QLD**. Listed in Parnaby *et al.* (2020, p. 139), a total of 43 males, 10 females. **NSW**. Banyabba Creek, Banyabba Nature Reserve, 29° 20.5385’ S, 152° 56.2947’ E (1 male, 20 Dec 1996, DM). McRae’s Knob, Pine Brush State Forest, 29° 35.9121’S, 153° 10.0409’E (1 male, 24 Jan 1997, DM). Minyumai Indigenous Protected Area, Tabbimoble collected by DM: 29° 12.3716’S, 153° 19.6616’ E (1 male, 14 Oct 2013), 29° 9.9357’S, 153° 22.9493’E (1 female, 9 Dec 2014), 29° 12.3974’S, 153° 19.7296’E (1 female, 21 May 2016). Six females from Bunjalung National Park listed by Parnaby *et al.* (2020).