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A molecular and morphological investigation of species boundaries and phylogenetic relationships in Australian free-tailed bats *Mormopterus* (Chiroptera : Molossidae)

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Abstract. The taxonomic uncertainty surrounding several prominent genera of Australian microbat has been a long-standing impediment to research and conservation efforts on these groups. The free-tail bat genus *Mormopterus* is perhaps the most significant example, with a long history of acknowledged species-level confusion. This study uses a combined molecular and morphological approach to conduct a comprehensive assessment of species and subgeneric boundaries, between-species phylogenetic affinities and within-species phylogeographic structure in Australian members of *Mormopterus*. Phylogenetic analyses based on 759 base pairs of the *NADH Dehydrogenase* subunit 2 mitochondrial gene were concordant with species boundaries delineated using an expanded allozyme dataset and by phallic morphology, and also revealed strong phylogeographic structure within two species. The levels of divergence evident in the molecular and morphological analyses led us to recognise three subgenera within Australia: *Micronomus*, *Setirostris* subgen. nov. and *Ozimops* subgen. nov. Within *Ozimops* we recognise seven Australian species, three of which are new, and none are conspecific with Indo-Papuan species. The family Molossidae now comprises eleven species across three subgenera in Australia, making it the continent's second most speciose family of bats.

Additional keywords: cryptic species, morphometrics, mtDNA barcoding, subgenera.

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Introduction

The order Chiroptera (bats) is highly diverse worldwide and contains about one fifth of all mammalian species, with ~1200 species now described (Simmons 2005). Bats are also a significant component of Australia's terrestrial mammalian fauna (roughly 23%), where they are currently represented by 70 extant species in 25 genera, spread across eight of the world's 19 bat families (Churchill 2008). Despite this prominence, several key taxonomic issues remain unresolved, including the need for formal recognition of known cryptic species, delineation of suspected cryptic taxa, clarification of the taxonomic affinities of Australian and extralimital populations of what are apparently the same species, and elucidation of higher-level systematic relationships. A rigorous systematic framework for Australian bats is both overdue and necessary to underpin research and conservation, especially given that over 10% of species are currently listed nationally as threatened (http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted = fauna August 2013).

The family Molossidae is currently represented in Australia by three genera, the polytypic *Mormopterus* Peters, and the two monotypic genera *Austronomus* Troughton and *Chaerephon* Dobson. *Mormopterus*, as currently defined in Simmons (2005), is represented worldwide by three species groups, one in Madagascar, Mascarene Islands and Sumatra (four species in total), another in the Neotropics (three species), and the third group comprising an unresolved complex in the Indo-Australian region. These three groups are likely to be polyphyletic (Lamb *et al*. 2011) and the Indo-Australian group has previously been recognised as a separate genus, namely *Micronomus* (Troughton 1944). Australian *Mormopterus* comprises a distinctive group of small, free-tailed bats found throughout the Australian mainland, with representatives in most major habitat types (Van Dyck and Strahan 2008). *Mormopterus* taxa occur in

moderate abundance over much of the continent and are an often surveyed component of the microbat fauna. However, the genus is widely acknowledged to be in taxonomic disarray (Adams *et al*. 1988; Churchill 2008; Van Dyck and Strahan 2008).

The taxonomic history of Australian *Mormopterus* until 1989 is thoroughly reviewed in Mahoney and Walton (1988) and in Allison (1989). Both reviews concluded by tentatively recognising three species in Australia, *M. norfolkensis*, *M. planiceps*, and *M. beccarii*, and both made it clear that this was an interim arrangement and that cryptic species were likely to be present. Significant reviews or comments on the species-level taxonomy of Australian *Mormopterus* before this time include those of Dobson (1876), Troughton (1926, 1941), Iredale and Troughton (1934), Tate (1941, 1952), Hill (1961, 1983), Felten (1964), Ride (1970), Hall and Richards (1979), Freeman (1981), Koopman (1984), Legendre (1984) and Peterson (1985).

Around the time of the 1988/89 reviews an allozyme study by Adams *et al*. (1988) on Australian Molossidae was published, and it provided a new taxonomic hypothesis that recognised a minimum of six *Mormopterus* species (referred to in the paper as Species 1 through Species 6; for convenience, we hereinafter use this nomenclature without citing Adams *et al*. (1988) on each occasion). In addition, two of the proposed species (Species 4 and Species 5), each comprised two genetically distinct, eastern and western allopatric populations of uncertain taxonomic status. Adams *et al*. (1988) declined to equate any of their candidate species to existing named forms other than to say that Species 3 and Species 4 together '... appear to correspond to *planiceps*'. Importantly, tissues from typical *M. norfolkensis* specimens were not available to the Adams *et al*. (1988) study, implying the likely presence of a seventh candidate species in the genus. The taxa delineated by Adams *et al*. (1988) were quickly and widely adopted as operational taxonomic units by Australian bat researchers and were thereafter referred to under a range of formal and informal names. This remained the *de facto* situation for Australian *Mormopterus* until Reardon *et al*. (2008) clarified the taxonomic status of *Mormopterus norfolkensis* (Gray, 1839) in Australia and described a new species *M. eleryi* Reardon & McKenzie 2008 (equivalent to Species 6). The taxonomic resolution of the remaining group Species 1–5, referred to as the '*planiceps–beccarii–loriae* complex' in Reardon *et al*. (2008) and hereinafter as the '*planiceps* complex', is the subject of this paper.

Herein we present a molecular and morphological assessment of the '*planiceps* complex'. This study has the 3-fold aims of (1) formally stabilising species boundaries in this complex, (2) providing a solid phylogenetic framework for the genus as a null hypothesis for future investigations, and (3) documenting cases of strong phylogeographic structure within each species. Although this study has focussed on the resolution of the systematics of Australian members of *Mormopterus*, we are mindful that this group is clearly allied to taxa in the Indo-Papuan region. Having examined many of the available New Guinean and Indonesian specimens, including type material, it is clear to us that the taxonomic situation in that region is complex and a satisfactory resolution will require further assessment of additional key specimens. We do show, however, that the named forms from that region (namely, *beccarii*, *astrolabiensis* and *loriae*) are taxonomically distinct from the Australian species described herein.

Materials and methods

Allozyme analyses

An allozyme study of 65 previously uncharacterised tissues, representing the key morphotypes and geographic regions covered by all new vouchers or specimens collected since 1988, were genotyped at a suite of 41 putative allozyme loci. The loci in question were the 40 loci surveyed by Reardon *et al*. (2008) plus the single locus encoded by the enzyme Glutathione peroxidase (GPX; E.C. number 1.11.1.9). Included in this study were 12 previously genotyped tissues from the original study of Adams *et al*. (1988), which served as reference profiles for Species 1–6 and therefore permitted us to combine all three studies into a single allozyme dataset. As for the previous allozyme studies, the Australian molossids *Austronomus australis* and *Chaerephon jobensis* were included as outgroup species. All tissues were obtained from the Australian Biological Tissues Collection (ABTC), based at the South Australian Museum. Details of all specimens included in the combined allozyme dataset are provided in the Supplementary Material.

Our laboratory methods used for allozyme electrophoresis of liver homogenates follow those detailed previously (Adams *et al*. 1988; Reardon *et al*. 2008). The data were initially analysed using the multivariate clustering technique of Principal Coordinates Analysis (PCO), which has been found previously to be ideal for identifying cohesive genetic groupings among individuals, independent of any *a priori* expectations as to taxon (Horner and Adams 2007). Stepwise PCO was undertaken on the overall pair-wise matrix of Roger's genetic distance among individuals, and on various subsets of these individuals, as fully detailed in Horner and Adams (2007). Subsequent labelling of individuals on these various PCOs according to morphotype and/or mtDNA lineage permitted us to define taxa based on concordant, diagnostic differences across all datasets examined. For the allozyme comparisons, we used the presence of multiple fixed differences (as defined in Reardon *et al*. 2008) among taxa as the best measure of taxon diagnosability. Thereafter, a Neighbour Joining (NJ) tree, including bootstrap values from 1000 pseudoreplicates, was constructed from a pair-wise matrix of unbiased Nei's Distances, according to the methodologies presented in Adams *et al*. (2013).

Mitochondrial DNA sequencing and analysis

In total, 91 tissue samples, either as frozen or alcohol-preserved liver, kidney or wing tissue, were obtained either from museum collections, or from specimens specifically collected for the project and subsequently released in the field. Tissues were selected to cover the available geographic spread in Australia of each of Species 1–5, and where available included specimens also represented in one or more of the allozyme and morphological datasets (Supplementary Material). Tissues of *M. eleryi* and *M. norfolkensis* as well as *M. loriae* and *M. beccarii astrolabiensis* from Papua New Guinea and *Mormopterus* cf. *beccarii* from Ceram, Indonesia, were also sequenced, as were

reference specimens of the three molossid outgroup taxa *Cheiromeles torquatus*, *Chaerephon jobensis*, and *Austronomus australis*. The recent phylogenetic study of world molossid genera (Ammerman *et al*. 2012) showed *Cheiromeles* as a basal lineage to all molossids and it was initially used as an outgroup to show that *Austronomus* represented a sister lineage to the Australian *Mormopterus*.

Total genomic DNA was extracted from these tissues using the Qiagen DNeasy kit and following the manufacturer's protocol. An ~760-bp region of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) gene was amplified by polymerase chain reaction (PCR) using the primers Forward 5′-CTAATTAAGCTATCGGGCCCATAC-3′ and Reverse 5′-TTC TTGGATRATTAKTCATTTKGG-3′. These primers were modified from L-5208 and H-6315 respectively from Kirchman *et al*. (2001). Each 50-μL reaction contained 0.8 μM of each primer, 0.25 mM dNTP, 1U of HotMaster *Taq* DNA polymerase (Eppendorf) or *Taq* DNA polymerase (Promega), 1 × corresponding PCR buffer (2 mM $MgSO_4$), and ~50–100 ng template DNA. The amplification protocol comprised denaturation at 94°C for 2 min, followed by 35 cycles of denaturing for 45 s at 92°C, 45 s of annealing at 50−55°C, and 60 s extension at 72°C. The reaction ended with one longer extension phase at 72°C for 5 min. PCR clean-up and sequencing was carried out by Macrogen (Seoul, S. Korea – http://dna.macrogen.com), using the same *ND2* primers for sequencing.

PCR amplifications with these *ND2* primers failed to amplify DNA from some key specimens where the only available tissue was highly degraded (Roper River, Northern Territory; Kandanji village, Papua New Guinea; Solea village, Ceram, Indonesia). We designed the following internal primers: forward 5′-GAG TCCCAGAAGTAACCCAAGG-3′, 5′-ACAAGCTCACAYT GAC-3′ and 5′-CAGGCCAATGAACTGTCA-3′ and reverse 5′-GTTTGGTTTAGTCCTCCTCA-3′, 5′-GTGGTTGTGGTG ATTAGTG-3′ and 5′-GGATTCCTTGGGTTACTTC-3′ and, using the same PCR conditions above, we were able to amplify and assemble a composite sequence of ~450–680 bp for each of these species.

Forward and reverse sequences were assembled using BioEdit ver. 7.1.11 (Hall 1999) and aligned by eye. Each sequence was translated to an amino acid sequence using MEGA ver. 5 (Tamura *et al*. 2011) and checked for the presence of stop or nonsense codons or frameshifts indicative of the presence of nuclear copies of mitochondrial DNA in the dataset (Zhang and Hewitt 1996).

Phylogenetic analyses were conducted using Bayesian inference (BI) and implemented using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). We used MrModeltest 2.2 (Nylander 2004) to identify the best-fit model of sequence evolution using the Akaike Information Criterion. This produced a general time-reversible (GTR) model (Tavaré 1986) with a proportion of invariant sites (I) and gamma distributed among-site rate variation (Yang 1996) (i.e. GTR + I + G). We ran the analysis for five million generations, sampling every 1000 generations. The average standard deviation of split frequencies reached 0.008. We used Tracer ver. 1.5 (Rambaut and Drummond 2007) to test whether the analyses had sufficient effective sample sizes (>200) for each parameter. The first one million generations were discarded as burn-in.

A matrix of uncorrected pair-wise distances (p-distance) among species and among key phylogeographic lineages within species was generated using the program MEGA ver. 5 (Tamura *et al*. 2011).

Morphological analyses

In total, 479 specimens of Australian *Mormopterus* and 51 specimens from New Guinea and Indonesia formed the basis for the mensurative component of the first part of the study to establish species boundaries and nomenclature. An additional 648 museum and field specimens were subsequently identified to species using the morphological criteria defined in the first part of the project, and these were used to supplement the distribution maps. Specimens were drawn from existing museum collections or collected specifically for this study under permit. Relevant details for all specimens used in this study are given in the Supplementary Material. Cranial photographs were taken with a Canon 450D camera mounted on a Stackshot step driver (Cognisys Inc.) and each final photograph is the combined stack of 10 images using Zerene Stacker ver. 1.04 (Zerene Systems).

Cranial and external measurements

The following 12 external and 11 cranial measures, with abbreviations in parentheses, were taken to the nearest 0.01 mm with digital calipers in combination with a binocular microscope: forearm length (FA), metacarpal digit 3 length (D3M), proximal phalanx length digit 3 (D3PP), middle phalanx digit 3 length (D3MP), metacarpal digit 4 length (D4M), proximal phalanx length digit 4 (D4PP), middle phalanx digit 4 length (D4MP), metacarpal digit 5 length (D5M), proximal phalanx length digit 5 (D5PP), middle phalanx digit 5 length (D5MP), tibia length (TL), pes length (PL), greatest skull length (GSL), condylobasal length (CBL), mastoid breadth of the skull (MB), postzygomatic breadth (PZB), postpalatal length (PPL), palate length (PaL), interorbital breadth (IOB), length from outer margins of upper canine to third molar (C1-M3), width across outer margins of upper third molars (M3-M3), width between outer margins of upper canines (C1-C1). The final cranial measure, skull height (SH) was measured using calipers that were modified by having a notch ground into one of the tangs, so that this side could be laid transversely across the pterygoid processes at the postpalatal margin while the other tang was placed at the top of skull. This measure would not be accessible with unmodified calipers without causing damage to the zygomatic arch. All univariate statistics, bivariate plots, Principal Components Analyses (PCA) and Discriminant Function Analyses (DFA) were generated using Statistica ver. 12 (StatSoft Inc.).

Phallic morphology

The glans penis is defined here as in Ryan (1991), being that portion of the penile shaft distal to the point where the inner prepuce (foreskin) adheres to the shaft; this junction is usually about one-third the length of the penis from where it joins the body. All species have a prepuce (foreskin) that covers the glans penis when the penis is flaccid, so it was necessary to manipulate the prepuce back along the penile shaft to fully expose the glans penis. This manipulation is not difficult in live animals, but is

often difficult in preserved specimens. We therefore made a single cut along the prepuce on the side of the penis to expose the glans penis for examination in some specimens. We noted that in most preserved specimens, the shape of the glans penis was compromised, typically with marked dorso-ventral flattening of the glans body as well as distortion due to dehydration. Since our descriptions were based mainly on preserved specimens, they may vary a little from those that might be observed on a live animal. The descriptions and illustrations in this study were derived from observations made under a light microscope, which placed limits on our ability to resolve some of the finer detail of the surface structures. Glans penis photographs were taken with a Canon 450D camera with a Photar microscope lens; the camera was mounted on a Stackshot step driver (Cognisys Inc.) and each final photograph is the combined stack of 50 images using Zerene Stacker ver. 1.04 (Zerene Systems).

Institution and collection acronyms

ABTC: Australian Biological Tissue Collection, South Australian Museum, Adelaide, Australia; AMS: Australian Museum, Sydney, Australia; ANWC: Australian National Wildlife Collection, Canberra, Australia; BMNH: The Natural History Museum, London, United Kingdom; DECWA: Department of Environment and Conservation, Perth, Western Australia; MSNG: Museo Civico di Storia Naturale di Genova 'Giacomo Doria', Genova, Italy; NMV: National Museum of Victoria, Melbourne, Australia; NRM: Naturhistoriska Rijkmuseet, Stockholm, Sweden; NTM: Museum and Art Gallery of the Northern Territory, Darwin, Australia; QM: Queensland Museum, Brisbane, Australia; ROM: Royal Ontario Museum, Toronto, Canada; SAMA: South Australia Museum, Adelaide, Australia; SMF: Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt-am-Main 1, Germany; UNIMAS: Universiti Malaysia Sarawak, Kota Samarahan, Sarawak; UPNG: University of Papua New Guinea Port Moresby, Papua New Guinea; USNM: National Museum of Natural History, Washington, DC, USA; WAM: Western Australia Museum, Perth, Western Australia; ZMB: Universität Humboldt, Zoologisches Museum, Berlin, Germany.

Supplementary material

We have included several tables and figures in the Supplementary Material and where these are referred to in the text, the table and figure number is prefixed by 'S'.

Results

Nomenclatural framework for this paper

Given the wide range of informal taxon names used to designate taxa in the past, and the completely new arrangement of formal names presented in this paper, we have opted for clarity by employing our final nomenclature for the new subgeneric arrangement and all seven species in the '*planiceps* complex' from this point forward. The relationship between our new taxonomic nomenclature and the names applied to each in the recent literature is detailed in Table 1. All species in this complex belong to the new subgenus *Ozimops* erected herein. The justification for our application of the names to delineated species is described in the *Systematics* section. Newly described species have been identified using the qualifier 'sp. nov.' It is also important to note that some of the species retaining existing valid names have been rediagnosed herein, and are not directly equivalent to species thus labelled in previous studies.

Allozyme analyses

The final allozyme dataset, which combined the current study with the two previous datasets generated in the same laboratory, consisted of 230 individuals (65 from the present study and 9 from Reardon *et al*. (2008) (Table S1), and 156 from Adams *et al*. (1988)) genotyped at 35–41 allozyme loci. An initial PCO on the 193 '*planiceps* complex' individuals revealed four primary genetic groups (Fig. 1), corresponding to (1) *M. ridei*/*M. lumsdenae* sp. nov., (2) *M. halli* sp. nov./*M. cobourgianus*/*M. loriae* (the latter a single tissue from PNG), (3) *M. kitcheneri* sp. nov./*M. planiceps*, and (4) *M. petersi*. Follow-up PCOs on each of these four groups (Figs 2–5) confirmed that all species found to overlap in the first two dimensions of the initial PCO were genuinely diagnosable from one another in deeper PCO dimensions. Most importantly, all species within the '*planiceps* complex' displayed multiple fixed differences from one another

Table 1. Taxonomic outcomes from this study contrasted with those used in selected recent publications

This paper	Adams *et al*. (1988); Reardon *et al*. (2008)	Recent taxonomic treatment				
		Koopman (1994)	Simmons (2005)	Van Dyck and Strahan (2008)	Churchill (2008)	Hall (2009)
lumsdenae sp. nov.	Species 1	*beccarii* unallocated subspecies	*beccarii*	*beccarii astrolabiensis*	*beccarii*	*beccarii*
ridei	Species 2	*planiceps*	*planiceps*	sp.	*ridei*	*planiceps*
petersi	Species 3	*planiceps*	*planiceps*	sp.	Species 3	*planiceps*
planiceps	Species 4 Populations P,Q & R	*planiceps*	*planiceps*	sp.	Species 4	*planiceps*
kitcheneri sp. nov.	Species 4 Population O	*planiceps*	*planiceps*	sp.	Species 4	*planiceps*
halli sp. nov.	Species 5 Populations S & T	*planiceps ridei*	*loriae*	*loriae ridei*	*ridei*	sp.
cobourgianus	Species 5 Populations U & V	*planiceps coburgiana* [sic]	*loriae*	*loriae cobourgiana*	*cobourgiana*	sp.

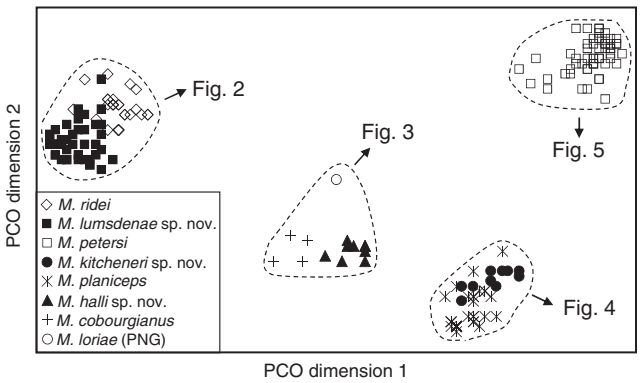

Fig. 1. Principal Coordinates Analysis of all 193 *Mormopterus* (*Ozimops* subgen. nov.) individuals. Relative PCO scores have been plotted for the first and second dimensions, which individually explained 35% and 19% respectively of the total multivariate variation present in 192 dimensions. Individuals have been labelled *post hoc* according to their ultimate taxon identification (using the symbols embedded within the figure). Follow-up PCOs on each of the four major genetic groups are presented in Figs 2–5, as indicated. The number of points shown is less than 193 because some individuals of the same taxon had identical PCO scores in the first two dimensions.

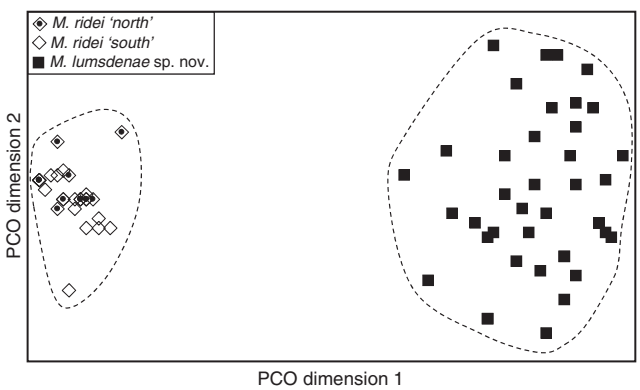

Fig. 2. Principal Coordinates Analysis of the 70 individuals belonging to the *M.* (*O.*) *ridei*/*lumsdenae* sp. nov. genetic group, as identified in the initial PCO (Fig. 1). Relative PCO scores have been plotted for the first and second dimensions, which individually explained 55% and 6% respectively of the total multivariate variation present in 69 dimensions. Individuals within *M. ridei* are also identified by known or presumed (based on geographic criteria) mtDNA lineage. General format as for Fig. 1.

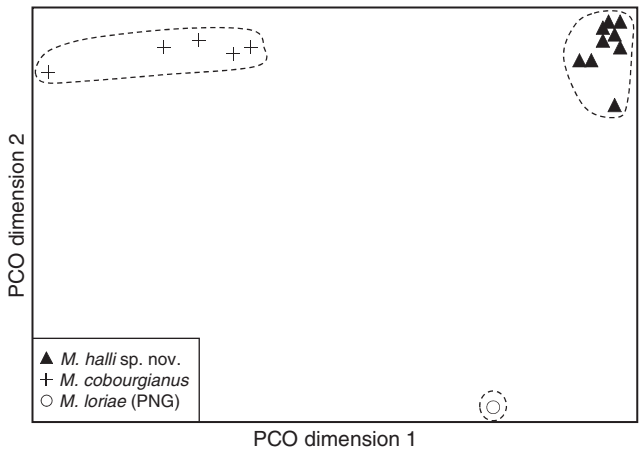

Fig. 3. Principal Coordinates Analysis of the 15 individuals belonging to the *M.* (*O*). *halli* sp. nov./*cobourgianus*/*loriae* genetic group, as identified in the initial PCO (Fig. 1). Relative PCO scores have been plotted for the first and second dimensions, which individually explained 38% and 23% respectively of the total multivariate variation present in 14 dimensions. General format as for Fig. 1.

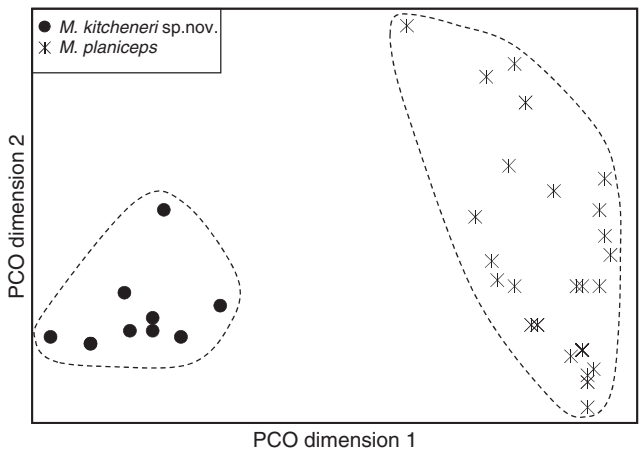

Fig. 4. Principal Coordinates Analysis of the 52 individuals belonging to the *M.* (*O.*) *kitcheneri* sp. *nov./planiceps* genetic group, as identified in the initial PCO (Fig. 1). Relative PCO scores have been plotted for the first and second dimensions, which individually explained 46% and 10% respectively of the total multivariate variation present in 51 dimensions. General format as for Fig. 1.

(minimum two fixed differences between *M. kitcheneri* sp. nov. and *M. planiceps*, maximum 11 fixed differences between *M. petersi* and *M. cobourgianus*: Table S2). The allele frequencies for all molossid species surveyed and the key diagnostic loci for the seven '*planiceps* complex' species are presented in Table S3.

The results of the NJ analysis of allozyme data from all 12 molossid species are presented in Fig. 6. As it is not possible to use either or both outgroups to root the NJ tree such that all species currently assigned to *Mormopterus* are monophyletic, the results are shown as an unrooted network. The analysis demonstrates moderate support (bootstrap = 70%) for the monophyly of all seven species within the '*planiceps* complex' and suggests that *M. eleryi* and *M. norfolkensis*, the two other species currently assigned to the genus, are only distantly related to these other seven species and to each other. Importantly, the pair-wise genetic distance values among these three basal lineages of Australian *Mormopterus* are roughly double the maximum values found within the '*planiceps* complex', being instead more comparable to those that distinguish *Mormopterus* from the two outgroup genera *Austronomus* and *Chaerephon* (Table S2).

With respect to documenting phylogeographic structure within species, neither the follow-up PCOs (Figs 2, 5) nor an examination of the raw genotypes provided any evidence that the distinct mtDNA lineages observed within two species

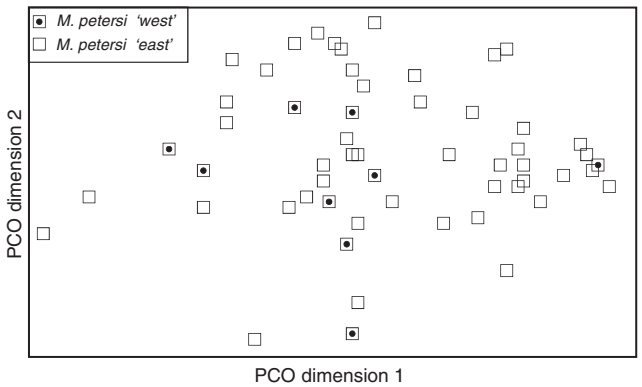

Fig. 5. Principal Coordinates Analysis of the 56 individuals of *M.* (*O.*) *petersi*, as identified in the initial PCO (Fig. 1). Relative PCO scores have been plotted for the first and second dimensions, which individually explained 16% and 12% respectively of the total multivariate variation present in 55 dimensions. Individuals are also identified by known or presumed (based on geographic criteria) mtDNA lineage. General format as for Fig. 1.

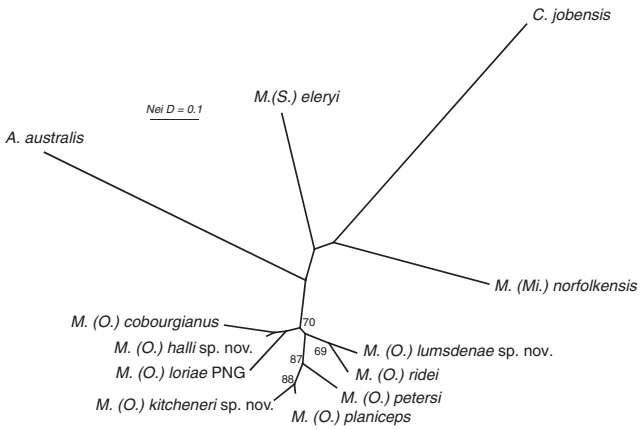

Fig. 6. Unrooted Neighbour-Joining network for all molossid species surveyed in combined allozyme dataset. Bootstrap values greater than 65% are shown for all nodes.

('north' and 'south' in *M. ridei*; 'east' and 'west' in *M. petersi*; see below and Fig. 7), displayed concordant differences in allozyme profile.

Phylogenetic analyses of the mtDNA sequence data

The final mtDNA dataset comprised 91 *Mormopterus* individuals, plus three outgroup sequences for 759 bp of *ND2* (Table S1). Sequences for all taxa have been deposited in GenBank as accession numbers KJ588277 – KJ588367. Initial phylogenetic analysis (Bayesian Inference) was conducted using all three outgroup genera, and then subsequent analyses iteratively dropped the most distant outgroup taxon, namely *Cheiromeles* and then *Chaerephon*, to arrive at the closest outgroup to maximise the number of phylogenetically informative sites for the ingroup. Each of these analyses consistently show 100% support for the monophyly of the Australian *Mormopterus* species and its closer relationship to *Austronomus*. These analyses are not presented here, but will feature in a subsequent paper evaluating the phylogenetic affinities of all Australian molossids. The final analysis presented included the single outgroup *Austronomus australis.*

The BI phylogenetic tree is presented in Fig. 7 and includes posterior probabilities from BI analyses for key nodes. Genetic distances (p-distances) between and within major clades are shown in Table S4. The deep structure in the tree defines two major lineages: one clade comprising all members of the Australian (and New Guinean) '*planiceps* complex' (supported by a posterior probability (pp) of 0.93) and a further lineage comprising *M. eleryi* and *M. norfolkensis* (supported by a pp of 0.95). The tree shows that both *M. norfolkensis* and *M. eleryi* are distant relatives of each other and of the '*planiceps* complex', differing from each other at an average p-distance of 14.1%, and from the '*planiceps* complex' at an average of 14.1%, a value only marginally lower than those that characterise the ingroup versus outgroup genera (Table S4).

Within the '*planiceps* complex' the seven Australian taxa delineated by Adams *et al*. (1988) each form well supported clades, generally with high BI posterior probabilities (pp > 0.97). The only exception was the monophyletic group comprising two clades referred to as *M. ridei*, which was supported by a pp of 0.61.

A key feature of the tree is a strongly supported clade (pp = 1) that includes the Indo-Papuan species *M. loriae* and *M. beccarii* and the Australian species *M. cobourgianus* and *M. halli* sp. nov. The tree also shows divergent clades within both *M. petersi* and *M. ridei*. Within *M. petersi* there are two strongly supported clades (pp = 0.97 and 0.98) that reflect eastern and western samples and these differ on average at 3.6% of *ND2* sites. Within *M. ridei* there are two clades (pp = 0.98 and 0.87) that represent northern and southern samples that differ on average at 3.1% of *ND2* sites.

Overall, there is an average genetic divergence between the seven '*planiceps* complex' taxa of 8.1% (range = 4.5–10.1%) with low intrataxon distances of 0.2–2.6%; however, the phylogenetic relationships among the species in the 'planiceps complex' are generally poorly resolved by the mtDNA data.

Phallic morphology

Amongst the Australian 'planiceps complex' male specimens available for the study, seven different forms of phallic morphologies were evident and these correspond to the seven groups defined by the allozyme analyses of Adams *et al*. (1988). The morphology of the glans penis for each species is illustrated in Fig. 8 and diagnostic features for each species are described in detail in the Systematics section below. Key features of the penis are illustrated in Fig. 9. Amongst the seven glans penis types, two are more similar in form, but these two and the remaining five show remarkable diversity in morphology, especially for a group of species that are otherwise morphologically conservative. The length of the penis varies between species and is itself diagnostic for some species. In most species there is a small gland on the distodorsal surface of the prepuce and it is usually accompanied by several long hairs. This feature seems to vary in degree of development within species and between species (and is therefore possibly diagnostic) although the development of this gland among species in the 'planiceps complex' almost never exceeds

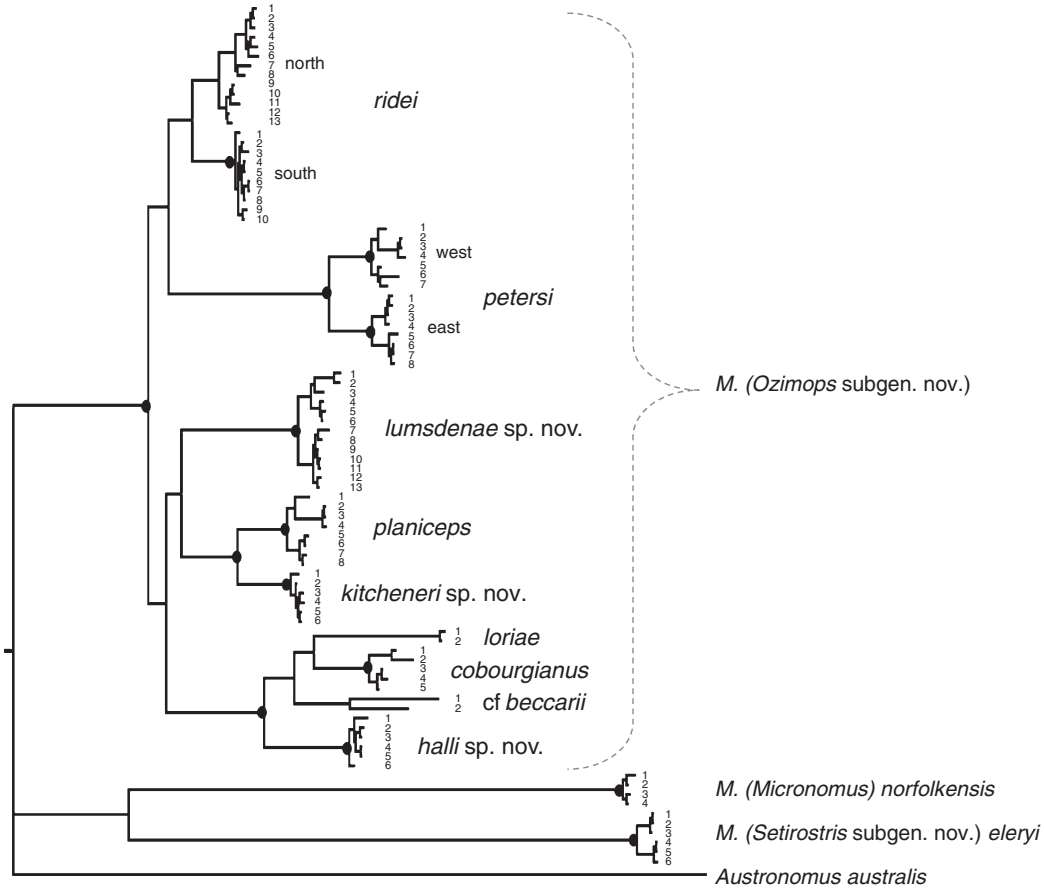

Fig. 7. Phylogenetic tree of ND2 sequence data. The tree was constructed using Bayesian Inference. Nodes with >0.9 credibility scores are marked with a dot.

the proportions of those found in *M. eleryi* and *M. norfolkensis* (Reardon *et al*. 2008).

In all species the glans penis comprises a body and head. The body is roughly cylindrical at the proximal end, but exhibits variation distally among species. In all species the body is covered in basally directed epithelial spines that vary in extent of coverage and size, depending on the species. The fine structure of the head of the glans is difficult to observe under the microscope, but it appears to be constructed of two parts, the distal bacular mound that varies in shape, and the inner head, which for some species is contained mostly within the end of the glans body. The head is smooth and without spines. The urinary meatus is a longitudinal slit on the ventral surface of the head. The head is readily observed and its relative shape, position and size provide distinguishing features. A ventral transverse opening (lip) is present in some species. Although there is considerable variation in morphology of the glans penis amongst the species of the 'planiceps complex', this variation does not extend to including the remarkable structures such as lateral serrations in *M. eleryi* and the distal claw in *M. norfolkensis.*

Summary

Species boundaries and nomenclature

There is strong concordant evidence from allozymes, mtDNA and penis morphology to confidently show that a minimum of seven species occur within the Australian 'planiceps complex'. In addition, the combinations of allozyme, mtDNA data and morphology (elaborated in the Systematics section below) support the species-level distinction between all Australian forms and *M. loriae* from southern Papua New Guinea, and *M. beccarii beccarii* from the type locality of Ambon, Indonesia, and specimens referable to *M. beccarii astrolabiensis* from northern Papua New Guinea. The justification and process for matching available species names to our delineated species is detailed in the Systematics section.

Subgeneric boundaries

Although the generic status and species composition of *Mormopterus* have both been historically unsettled, *Mormopterus* has been treated as a genus in its own right by most authors since the revision of Freeman (1981). The genus, as currently recognised, comprises the following valid species: *jugularis* (Peters, 1865) (the type species), *acetabulosus* (Hermann, 1804), *norfolkensis* (Gray, 1839), *planiceps* (Peters, 1866), *beccarii* Peters, 1881, *kalinowskii* (Thomas, 1893), *loriae* (Thomas, 1897), *minutus* (Miller, 1899), *doriae* Andersen, 1907, *phrudus* (Handley, 1956), *eleryi* Reardon & McKenzie, 2008, and *francoismoutoui* Goodman *et al*., 2008 (Simmons 2005; Goodman *et al*. 2008).

Fig. 8. Photographs and illustrations of the glans penis for the seven species of *Ozimops* subgen. nov. described in paper. Photographs: left side = dorsal view; right side = lateral view except for *M. cobourgianus* and *M. halli* sp. nov., which show ventro-lateral view. Illustrations (not to relative scale) show dorso-lateral view except for *M. cobourgianus* and *M. halli* sp. nov., which show ventro-lateral view. (*a*) *M. planiceps*, (*b*) *M. petersi*, (*c*) *M. kitcheneri* sp. nov., (*d*) *M. lumsdenae* sp. nov., (*e*) *M. ridei*, (*f*) *M. cobourgianus*, and (*g*) *M. halli* sp. nov.

Some authors have recognised 'species groups' within this suite of species that largely correspond to geographic regions, namely, the *acetabulosus* group (*jugularis* (Madagascar), *acetabulosus* and *francoismoutoui* (Mascarene Islands), and *doriae* (Sumatra)), the *kalinowskii* group (*kalinowskii* and *phrudus* (western South America), and *minutus* (Cuba)) and the *norfolkensis* group (*beccarii*, *loriae*, *norfolkensis*, *planiceps* (Indo-Australia)) (Koopman 1994; Simmons 2005). More formal taxonomic distinctions for these groups have been previously proposed. Miller (1907), for the species recognised at that time and that he was able to examine, included *jugularis*, *acetabulosus*, *kalinowskii* and *minutus* in the genus *Mormopterus*, and *loriae* and *norfolkensis* in *Nyctinomus*. Iredale and Troughton (1934) considered that Australian forms were generically distinct from true *Mormopterus* and proposed (albeit invalidly) the name *Micronomus* to accommodate them. Troughton (1944) is the first valid publication of the name *Micronomus* (see note below regarding the date of publication). Churchill (2008) recognised *Micronomus norfolkensis* but used *Mormopterus* for the remaining Australian species.

Other authors have recognised *Mormopterus* and *Micronomus* as subgenera, with the former including both the *acetabulosus* and *kalinowskii* groups and the latter the *norfolkensis* group (Tate 1952; Laurie and Hill 1954; Legendre 1984; Nowak 1994; Hand *et al*. 1999). We agree that the *norfolkensis* group is, at the least, distinct from true *Mormopterus* (= the *acetabulosus* group) at the subgeneric level, a view also supported by our unpublished sequencing data. The systematic placement of the *kalinowskii* group is not fully clear but the molecular evidence of Lamb *et al*. (2011) and the inference of Goodman *et al*. (2008) suggest that

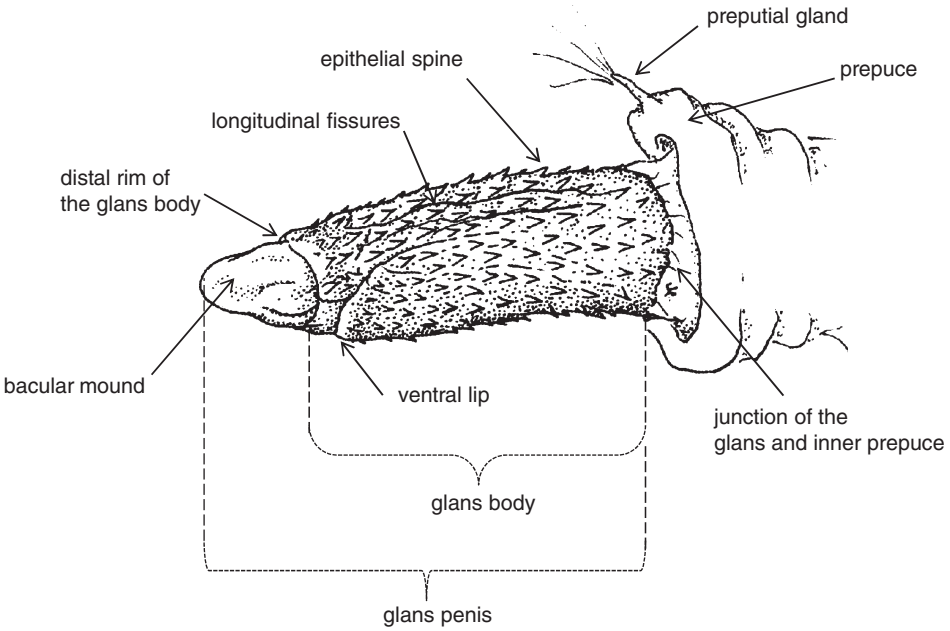

Fig. 9. Diagram of the penis morphology showing features mentioned in the text.

this group's affinities (subgeneric or generic) are likely to lie elsewhere other than with either true *Mormopterus* or its Australian exemplars.

Within the Australian *Mormopterus*, the magnitude of the genetic distances exhibited by allozymes and mtDNA between the 'planiceps complex' and *M. eleryi* and *M. norfolkensis*, and those between *M. eleryi* and *M. norfolkensis*, are close to those shown between these three groups and other molossid outgroup genera. This together with the corresponding cranial and dental differences evident between these three groups, lead us to conclude that these three groups each warrant subgeneric status.

Systematics

Family **Molossidae** Gervais, 1855

Genus ***Mormopterus*** Peters, 1865

Subgenus ***Micronomus*** Troughton, 1944

Type species: *Molossus norfolkensis* Gray, 1839

Revised diagnosis

Differs from the subgenus *Mormopterus* (*jugularis*, *acetabulosus*, *francoismoutoui* and *doriae*) by the following characters: possesses two rather than three lower incisors; has two upper premolars rather than one; lacks a gular sac that is well developed in *Mormopterus*.

Differs from *Setirostris* subgen. nov. as follows: the upper first and second molars with scallop-shaped lobes extending from the posterolingual margin of the heel with the most anterior lobe in the position typical of a hypocone (Fig. 10*a*), as opposed to a single crochet-hook shaped 'hypocone' extending from the disto-lingual edge of the heel (Fig. 10*b*); is larger in most cranial and external characters; lacks strongly developed facial bristles; has radically different glans penis structure with distal claw and no lateral serrated edge; exhibits fixed allelic differences at 20 independent allozyme loci (Tables S2, S3); mtDNA haplotypes highly divergent (average *ND2* sequence divergence >14%: Table S4).

Differs from *Ozimops* subgen. nov. as follows: skull profile more domed rather than straight; the upper first and second molars with scallop-shaped lobes extending from the posterolingual margin of the heel with the most anterior lobe in the position typical of a hypocone (Fig. 10*a*) as opposed to a semi-isolated well developed cone- or blade-shaped hypocone arising from the central body of the heel (Fig. 10*c*), and with the tip of the hypocone terminating close to the metaconule but separated via a short saddle; has radically different glans penis structure with distal claw; exhibits fixed allelic differences at a minimum of 17 independent allozyme loci (Tables S2, S3); highly divergent mtDNA haplotypes (average *ND2* sequence divergence >14%: Table S4). A detailed description of this monotypic subgenus is given in Reardon *et al*. (2008).

Note on the publication date

The years 1943 and 1944 have variously been attributed as the date of publication of the second edition of Troughton's 'Furred Animals of Australia' in which the first valid use of *Micronomus* appears. The year of publication printed in the book itself is 1943. We have followed Mahoney and Walton (1988) in accepting 1944 as the official date of publication based on confirmation by letter from the publisher to Walton.

Subgenus ***Setirostris*** Reardon, McKenzie & Adams, subgen. nov.

Type species: *Mormopterus eleryi* Reardon & McKenzie, 2008

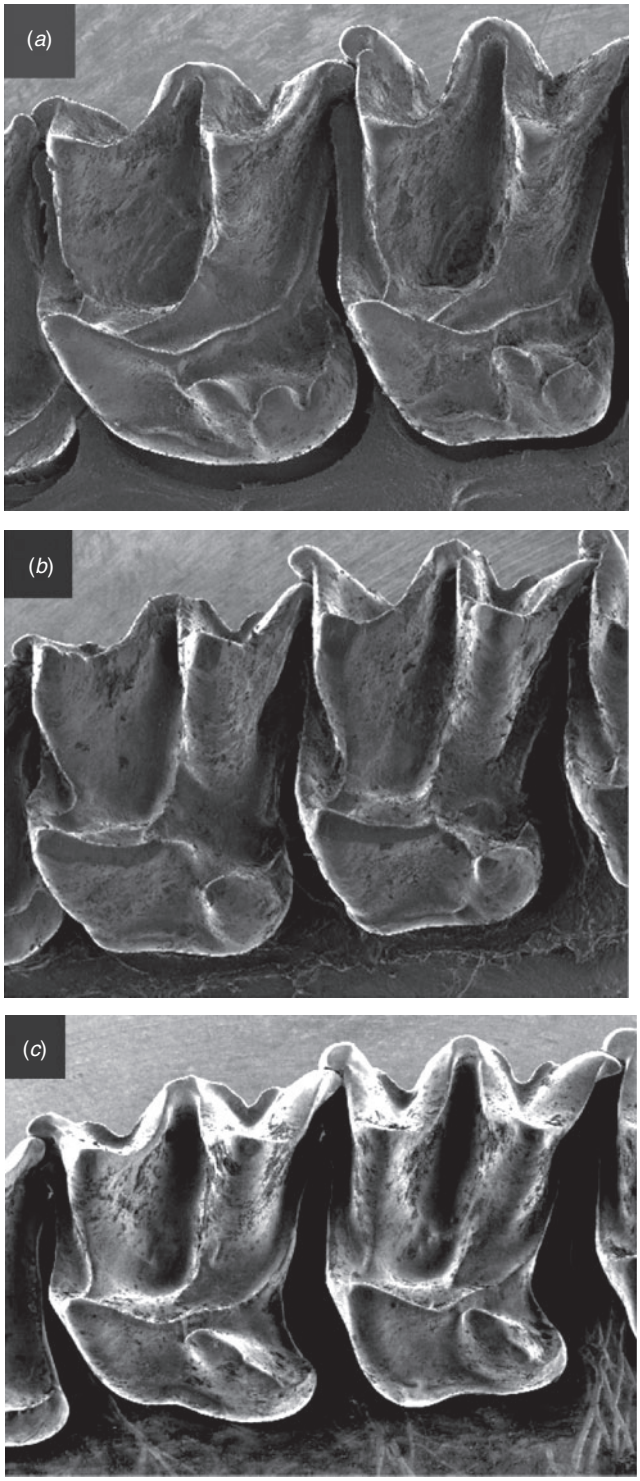

Fig. 10. Comparison of the upper molars showing differences in the heel region of the three subgenera of Australasian *Mormopterus*. (*a*) *Micronomus*, (*b*) *Setirostris*, and (*c*) *Ozimops*.

Diagnosis

Differs from the subgenus *Mormopterus* (*jugularis*, *acetabulosus*, *francoismoutoui and doriae*) by the following characters: possesses two rather than three lower incisors; has two upper premolars rather than one; lacks a gular sac that is well developed in *Mormopterus*.

Differs from the subgenus *Micronomus* as described above. Differs from *Ozimops* subgen. nov. by the following characters: skull profile more domed rather than flatter profile; upper first and second molars with a single crochet-hook-shaped 'hypocone' extending from the disto-lingual edge of the heel (Fig. 10*b*) as opposed to a semi-isolated well developed cone-shaped hypocone arising from the central body of the heel, and with the tip of the hypocone terminating close to the metaconule but separated via a short saddle (Fig. 10*c*); has radically different glans penis structure with serrated edge; fixed allelic differences at a minimum of 15 independent allozyme loci (Tables S2, S3); reciprocal monophyly (Fig. 7) for highly divergent mtDNA haplotypes (average *ND2* sequence divergence = 14%: Table S4). A detailed description of this monotypic subgenus is given in Reardon *et al*. (2008).

Etymology

From seta L. = bristle + rostrum L. = beak or snout, referring to the characteristic stout bristles on the face. Gender of name is feminine.

Subgenus ***Ozimops*** Reardon, McKenzie & Adams, subgen. nov.

Type species: *Nyctinomus planiceps* Peters, 1866

Content

Indo-Papuan forms: *M. beccarii*, *M. b. astrolabiensis* and *M. loriae*, and seven Australian species described below.

Diagnosis

Differs from the subgenus *Mormopterus* by the following characters: possesses two rather than three lower incisors; has two upper premolars rather than one; lacks a gular sac that is well developed in *Mormopterus*. Differs from the subgenera *Micronomus* and *Setirostris* by the characters described above.

General description

A group of small stout free-tailed bats (forearm length 29–41 mm and live mass 6–18 g) with dental formula 1/2, 1/1, 2/2, 3/3 = 30 although in some species, especially in *M. halli* sp. nov. the upper anterior premolar on one or both sides is occasionally lost in older animals; upper incisors convergent, simple with a small posterolingual cusp close to the cingulum; upper canine weak with cingulum roughly triangular in occlusal outline; the very small upper anterior premolar varies in shape and cingulum development, and is sometimes isolated but often compressed between the cingulum of the canine and that of the posterior premolar and sometimes pushed well out to the labial margin of the tooth row when the cingulum of the canine and of the posterior premolar are in contact; the two upper anterior molars have a tall protocone with the postprotocrista linked by a short crest to the metacingulum, although this crest may be lost with wear, the heel is moderately developed, although this is more reduced in some Indo-Papuan forms, the hypercone sometimes strongly developed as a semi-isolated cone or as a blade-like

point and linked by a crest to the postprotocrista such that the crest sometimes forms a valley or is in line with the tip of hypocone and postprotocrista (Fig. 10*c*); the posterior upper molar is reduced but with a well developed paracone and protocone and with a well developed metacone; the lower incisors with flared and bifurcated tips; the lower premolars have a well developed cingulum, and the relative widths of these two teeth to one another varies between species. In general, the dental morphology (excluding size) is similar amongst the species of *Ozimops* and any differences appear to be confounded by substantial intraspecific variation. Skulls with relatively straight profile, sagittal crests weakly developed, lambdoidal crests usually well developed and form a high lambda; the mandible with a high coronoid process (higher than the tip of the canine).

Ears triangular with tips rounded, not joined together but separated by 2–4 mm; ears held laterally at rest but upright when the animal is active; tragus broad at the base narrowing to a thicker rounded tip; antitragus varies from being scarcely indicated to a semicircular lobe and composed of thicker skin than the rest of the ear. Muzzle broad, convex, but tapering anteriorly; upper part of the rostrum generally furred with very short fine hairs and some longer vibrissae, the sides of the muzzle ranging from a sparser covering of short hairs to almost naked with some tubercles displaying vibrissae and a few short bristles, but overall the rostrum never has long thick bristles as in *M. eleryi*. The upper lip wrinkled and with short dense fringe of hairs that overhang the bottom lip. Nostrils are slightly procumbent with crenulations on the outer margins and centre line. Body fur generally short not woolly, usually uniform in colour on the head and dorsum, and lighter underneath, colour ranging from darker brown to lighter grey-brown and sometimes with yellowish tinge and typically lighter ventrally. Albino forms have been reported. Wings long and narrow, with some New Guinean forms having the skin pigment bleached. Legs short, stout. Tail emerges from posterior margin of the uropatagium.

Sexual dimorphism is not strongly developed in the Australian species (with some character exceptions), but we cannot comment on Indo-Papuan species. For the cranial measures taken, sexual dimorphism as analysed by *t*-tests is evident only in *M. lumsdenae* sp. nov., in which all measures except M3-M3 and CBL/SH are significant between sexes ($P < 0.05$); for *M. ridei* only C1-C1 has a $P < 0.05$ and *M. petersi* IOB and CC; our sample size was too small to test *M. halli* sp. nov. For 17 external characters measured, the following species and characters (in parentheses) have $P < 0.05$: *M. petersi* (D3DP, D5M), *M. kitcheneri* sp. nov. (FA, D3M, D3PP, D4M, D5M), *M. lumsdenae* sp. nov. (D3DP, D5PP) and *M. ridei* (D5MP, D5PP).

Etymology

Ozi = colloquialism for Australia (as the centre of diversity of this group) + mops = suffix for many molossid genera. Gender of name is masculine.

Mormopterus planiceps (Peters, 1866)

South-eastern free-tailed bat

Figs 8, 11, 12, 13*a*, 14, S1.

Nyctinomus planiceps Peters, 1866: 23–25.

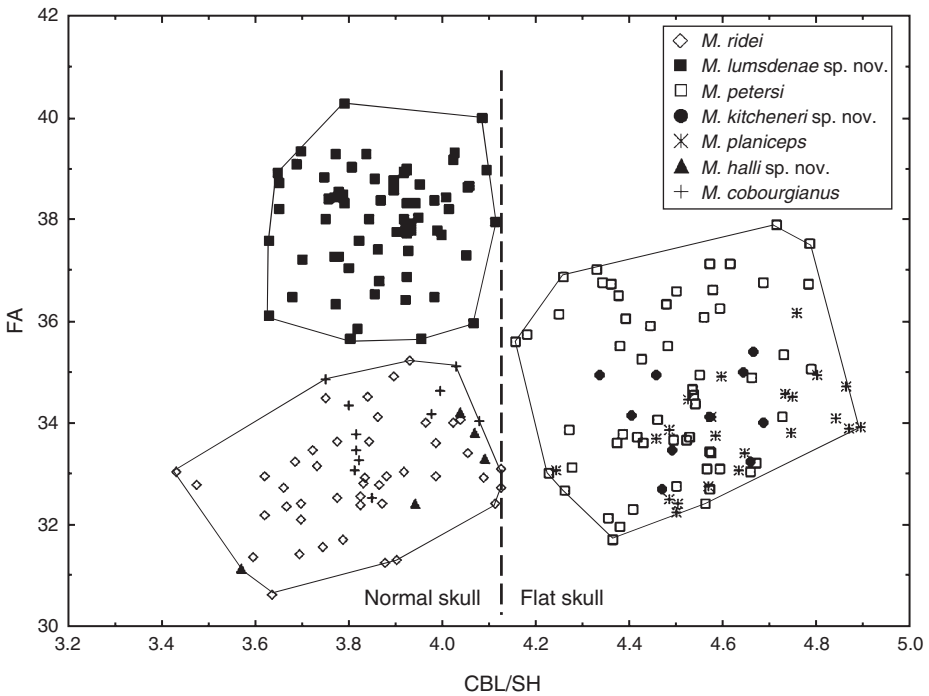

Fig. 11. Bivariate plot of 'condylobasal length divided by skull height' versus forearm length, showing the division of species based on relative flattening of skull.

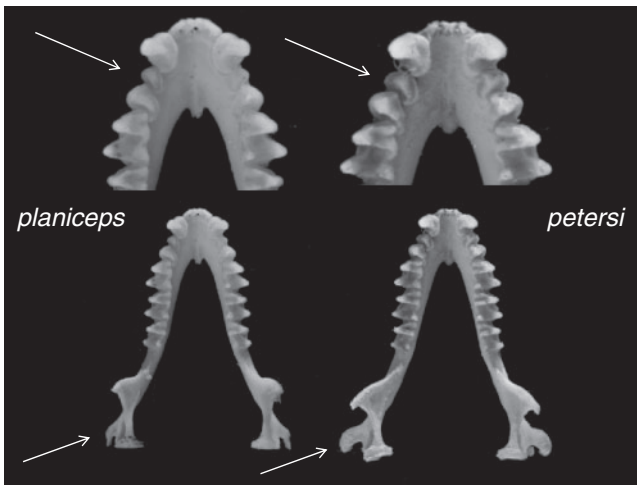

Fig. 12. Occlusal views of the dentaries of *M. planiceps* and *M. petersi* showing the differences in relative outward rotation of the angular process, and the relative sizes of the anterior versus posterior premolars.

Synopsis of taxonomic history

Dobson (1876) considered *planiceps* as a junior synonym of *norfolcensis* (= *norfolkensis*), which Peters (1881) himself appears to have agreed with by omitting reference to *planiceps* in his description of *M. beccarii.* Thomas (1906) reinstated the specific status of *planiceps* and it has remained since as a valid species.

Type details

Lectotype

SMF 4283 female, preserved in spirit, designated by Mertens (1925). Skull removed and described by Felten (1964).

Type locality

Australia; possibly New South Wales.

Felten (1964) discusses the difficulty in establishing the geographic origin of the type material. Peters records that the two female specimens upon which his description was based, were donated to the Frankfurt Museum from Becker 'aus Australien (angeblich aus Sydney)' = from Australia (allegedly from Sydney). Felten understood that the word 'angeblich', meaning 'allegedly', implied that there may have been some information suggesting Sydney rather than that being an assumption of Peters.

One of the specimen labels is marked with Ad. Becker (Sydney). Adam Becker had worked as a taxidermist with the Australian Museum (Sydney) from 1859 to 1864 (Kohlstedt 1980) and donated specimens of Australian fish and reptiles to the Frankfurt Museum during that time; he, with little doubt, is the same Becker that Peters mentions as the donor. However, although Becker worked in Sydney, this fact alone does not provide any certainty on the location of where the specimens were collected. Iredale and Troughton (1934) noted that the type locality of *M. planiceps* is Western Australia, but provided no argument as to why. This conjecture can be easily dismissed, given that *planiceps* is an eastern Australian form.

Justification for assigning the name planiceps *to this taxon*

The first described Australian species in this complex is *planiceps* and its identity is pivotal to the allocation of all other available names. Having delineated seven species in the '*planiceps* complex' our primary task was to determine to which of the seven groups the lectotype of *planiceps* belonged. Had the lectotype been male, or had our attempts to obtain an *ND2* sequence from it been successful, this would have been straightforward.

Peters described *Nyctinomus planiceps* based on the external morphology of two female specimens drawn from five specimens 'perhaps from Sydney' donated to the SMF by A. Becker. One of these two female specimens was subsequently donated to the Berlin Museum by Dr Ruppell (Peters 1866). The lectotype (SMF 4283) was designated by Mertens (1925) and the Berlin specimen was designated a paralectotype (ZMB 3101) by Turni and Kock (2008). The remainder of the collection (not types) includes two males (SMF 12065–6) and a female (SMF 12067).

Felten (1964) was the first to describe the skull of *planiceps* and, in doing so, observed that some Australian *Mormopterus* species, including *planiceps*, had particularly flattened skulls and this could be shown by plotting the skull height (measured at the posterior margin of the palate) against the skull length. Although Koopman (1984) was less convinced by this, our measurements suggest that Felten's observation is a very useful primary way to divide species. Using condylobasal length (CBL) divided by skull height (SH) we show that three of the seven species (*planiceps*, *petersi* and *kitcheneri* sp. nov.) are flat-skulled and clearly separated from *lumsdenae* sp. nov., *ridei*, *cobourgianus* and *halli* sp. nov. CBL/SH values from all flat-skull species combined have a mean of 4.54 (4.15–4.90), s.d. = 0.17, $n = 111$ while the Australian 'normal skull' species have a mean of 3.84 (3.40–4.13) s.d. = 0.15, $n = 172$. A plot of CBL/SH against FA for the seven species is given in Fig. 11. All Indonesian and New Guinean specimens available for measurement ($n = 21$) have a CBL/SH of less than 3.87 (that is, normal skulls).

To establish which of the two eastern Australian flat-skulled species is allied to the *planiceps* lectotype, we performed a two-group DFA using a combination of external and cranial measures from *petersi* (excluding the larger Northern Territory forms, explained later) and *planiceps*, but not including the measurements from the types. We then conducted an *a posteriori* classification of the lectotype using cranial and then external measurements kindly provided by D. Kock, as well as using external measurements from the original description by Peters (although he did not indicate which of the two female syntypes were measured so it is equally likely it was from the paralectotype). Our set of cranial measures poorly resolves *planiceps* and *petersi* and the posterior classification of the lectotype was equivocal. However, the two sets of external measures (FA, D3M, D3PP, D3MP, D4M, D4PP, D4MP, D5M, D5PP and D5MP) show a 99.9% probability of the lectotype aligning with Species 4 east and 100% for the type that Peters measured (Wilks' Lambda = 0.30, approximate $F_{10,81} = 18.86$, $P = 0.0000$).

In addition, we observe that there is a difference in the degree of the outward rotation of the angular process of the mandible

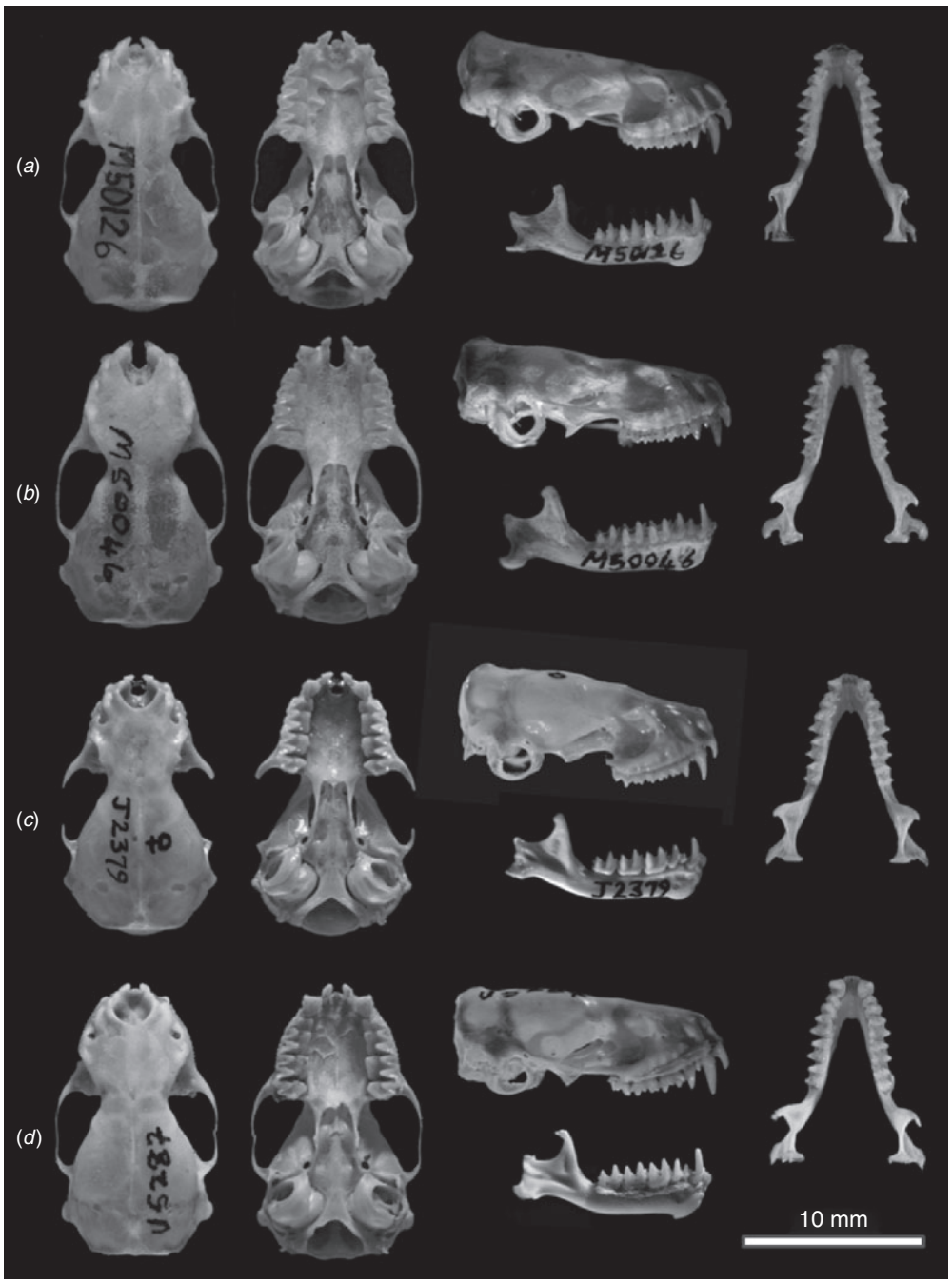

Fig. 13. Skull and dentary photographs. (*a*) *M. planiceps* WAM M50126; (*b*) *M. petersi* WAM M50046; (*c*) *M. ridei* QM J2379; (*d*) *M. cobourgianus* NTM U5287; (*e*) *M. kitcheneri* sp. nov. holotype WAM M60848; (*f*) *M. lumsdenae* sp. nov. holotype QM JM15323; (*g*) *M. halli* sp. nov. holotype QM JM 19625.

between *planiceps* and *petersi* (Fig. 12) and photographs provided of the lectotype clearly show that it matches the range for *planiceps*. Finally, the relative width of the anterior to the posterior lower premolar differs between *planiceps* (<0.75) and *petersi* (>0.75), with the lectotype having an average from both sides of the mandible of 0.66 and thus falling well within the range for *planiceps*. In Peters' original description he noted that the first premolar is about half as big as the second.

We are therefore confident on the basis of this evidence that the *planiceps* lectotype (SMF 4283) is allied to the species characterised by males having an exceptionally long penis, and this is consistent with the two long-penis males in the original

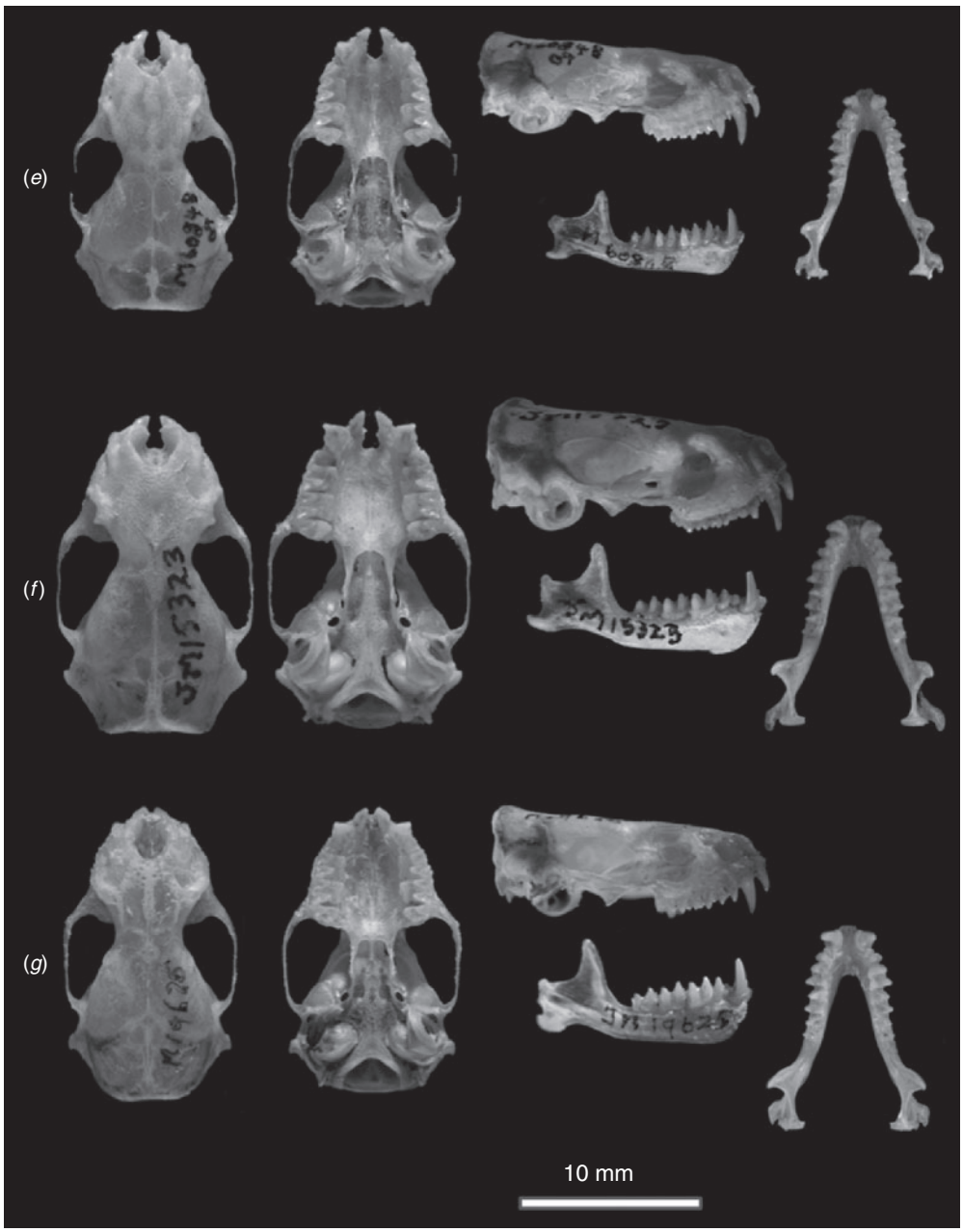

Fig. 13. (*continued*)

consignment of specimens that included the female lectotype and paralectotype.

Referred specimens

See Tables S1, S5, S6.

Diagnosis

Distinguishable from all other species in the subgenus by having an exceptionally long penis that is greater than 7.5 mm in length. Differs from all species except *kitcheneri* sp. nov. and *petersi* by having an unusually flattened skull (Fig. 11). Otherwise similar in appearance to all other species with mostly overlapping external and cranial measurements other than with *lumsdenae* sp. nov., from which it differs by being smaller in most measures (Tables S7, S8). Distinguished from all Australian forms and *loriae* by having a unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 2 to 10 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pairwise genetic distances of 0.045–0.095 (Table S4).

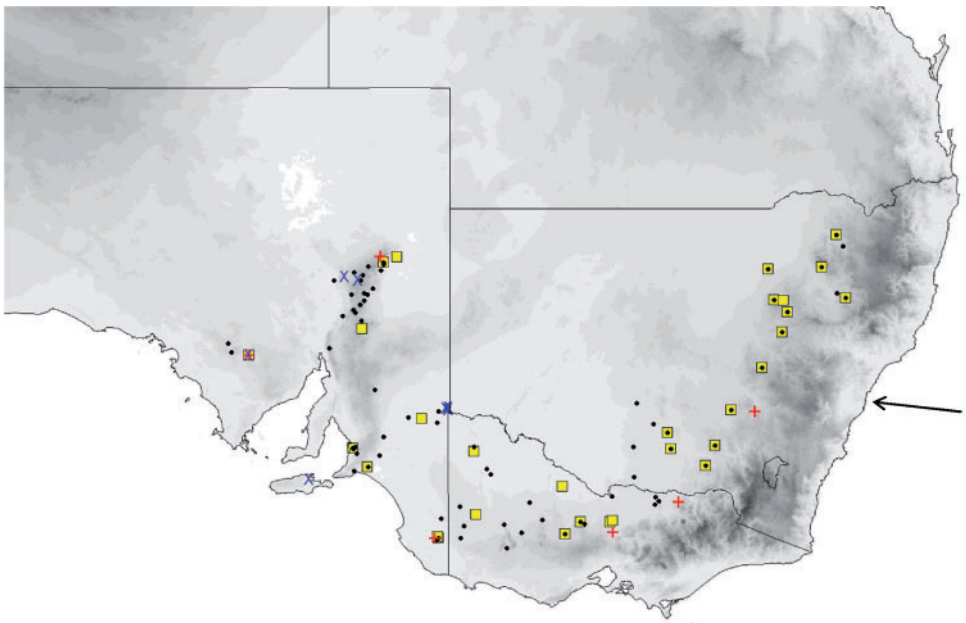

Fig. 14. Locations of specimens used in this study for *Mormopterus planiceps*. Measured = □; mtDNA = +; allozymes = X; other museum specimens identified on phallic morphology or previous allozyme studies = ●. Type locality (arrowed) given as 'near Sydney?'

Revised description and contrasts with sympatric species

Sympatric species: *M. petersi*, *M. ridei* and possibly *M. lumsdenae* sp. nov.

External. A small species with a forearm range of 32.2–36.1 mm and mass of 6.5–12.0 g with features typical of the description for the subgenus. Head and dorsal fur uniform in colour, but varies between individuals from grey-brown to light brown. Ventral fur is lighter, usually pale brown (hairs white based, light brown mid-shaft and lighter tips). Similar in appearance to *petersi* but usually darker in fur colour, and with slightly smaller width across the nostrils. DFA using wing bone measures as described earlier may allow confident discrimination for some individuals. Similar to lighter-fur-coloured *ridei*, but with larger width across the nostrils, and slightly longer ears, and longer rostrum length. Is smaller than *lumsdenae* sp. nov. on most external measures.

The phallus is by far the longest in the genus (9–11 mm) and is described in detail in Krutzsch and Crichton (1987). The glans penis averages nearly 9 mm and is highly distinctive in shape (Fig. 8). The glans is long and slender and divided into two parts roughly equal in length. Krutzsch and Crichton (1987) describe these two parts as the primary glans (dorsal) and secondary glans (ventral) and these are demarcated by a large lateral opening on the ventral side. The head of the glans (bacular mound) is broad and rounded posteriorly but quickly tapers to a blunt point that is ventrally inflected. The glans body has longitudinal fissures and ridges extend along its length, some originating lateroventrally and stretching to the dorsal base. The glans body has proximally directed epithelial spines. The great length of the phallus would immediately allow unequivocal identification of this species.

Cranial (Fig. 13*a*). We have not examined the lectotype but have Felten's (1964) description and skull drawing of it, as well as a series of photographs of the skull and dentary kindly provided by the Senckenberg Museum. The lectotype skull observations fit well within the range of variation we observe in our sample, but with the benefit of now possessing a large series of identified specimens, we are able to observe more variation in some of the characters than Felten observed. While the skull profile is indeed almost straight, many specimens have small depressions and inflations. In most specimens the lambdoidal crests are well developed, arising from near the postoccipital process and continue in the same size till converging together and with the sagittal crest forming elevated raised triangular-shaped raised lambda. However in some specimens the lambdoidal crests fade near their confluence and in place of a raised lambda, that part of the skull is simply a rounded continuum of the supraoccipital onto the parietals. The sagittal crest is absent but for where it forms the lambda. The orbital rim varies in the degree of strength in development, with some specimens showing a pronounced ridge while in others there is no ridge. The sphenorbital pits are shallow, but often scarcely indicated. Teeth generally as described for the subgenus.

Similar to *petersi* but distinguishable by a less outward rotated angular process and a smaller ratio of the widths of the lower anterior to posterior premolar. Similar to *ridei* with GSL and CBL averaging slightly larger but with strong overlap in range, but distinguished by much larger CBL/SH. Differs from *lumsdenae* sp. nov. by being overall less robust and by being smaller on most cranial measures but larger CBL/SH (Table S8).

Distribution and habitat

The distribution map (Fig. 14) is based solely on specimens that we have examined and identified from morphology and/or from molecular methods. From these records, *planiceps* has a

distribution that follows along the western slopes of the Great Dividing Range in New South Wales to most of Victoria and into southern South Australia to the Flinders Ranges and the Gawler Ranges in a band that has 300–700 mm annual rainfall. We have no museum records from Queensland or from east of the Great Dividing Range although there are reports of occurrences from there. This species is known to roost in tree hollows and thus far is not recorded from caves. It is also often reported roosting in the roofs and walls of buildings. Across its distribution area it occurs in mallee, mulga, box iron bark, river red gum.

Remarks

The name *wilcoxii* (Krefft 1873) appears to be a valid and available name in the context of this study. The species name first appeared in Krefft (1864) as *Molossus wilcoxii* and was subsequently used in Krefft (1871), but both were invalid acts because neither was accompanied by a description. Krefft (1873) is the first valid use of the name because it is accompanied by a brief description. Dobson (1876) synonymised *wilcoxii* (and *planiceps*) with *norfolcensis* (= *norfolkensis*), citing Krefft (1871) and it has remained a junior synonym since. The history of *wilcoxii* is partly discussed in Allison (1989), although curiously Allison considered *wilcoxii* a *nomen nudum* despite citing Krefft (1873), perhaps because he was influenced by Hill (1961), who only referred to Krefft (1871) and therefore rightly treated the name *wilcoxii* as a *nomen nudum*. Mahoney and Walton (1988) imply that *wilcoxii* Krefft (1873) is a valid name by listing it as a synonym of *norfolkensis* (ignoring Felten 1964) but agreeing with Hill (1961). Further, they note: 'syntypes, not found in the AM [= Australian Museum], whereabouts unknown'.

The valid description in 1873 does not designate a type or specific museum specimens and thus we must consider that all the specimens upon which Krefft based his description, that is, those referred to in his described distribution 'first discovered. on the Clarence River and occurs as far as Rockhampton' comprise the syntypes. However, we do not know which specimens, or how many, but, given the designated localities, it is likely that the series contains more than one species.

Although no candidate syntypes specimens are yet known from Australian collections, we do know of two *Mormopterus* specimens currently held in European collections and donated by Krefft, one in the BMNH (BM 64.8.14.1) and one in the ZMB (ZMB 3521). Significantly, the BMNH specimen was catalogued into the collection in 1864 as indicated by the registration number and therefore is most likely a member of the original series upon which Krefft named *wilcoxii.* This is also the specimen that Dobson referred to in synonymising *wilcoxii* with *norfolkensis*. Subsequently, this specimen was identified as a *planiceps* by Felten (1964), with Thomas (1906) having earlier resurrected *planiceps* from *norfolkensis*. Felten (1964) suggested that this could be the original *wilcoxii* specimen. This may be true although it is a female and Krefft's first invalid use of *wilcoxii* in 1864 is based on a male from the Clarence River, New South Wales.

Felten (1964) describes BMNH 64.8.14.1 as flat-skulled, which, in eastern Australia and under our species concept, ensures that it must either represent *planiceps* or *petersi*. We have not personally examined this specimen, but using Dobson's (1878) measures for FA, D3M, D3PP, D4M, D4PP, D4MP, D5M and D5PP, the *a posteriori* classification using DFA places it in *planiceps* with a 98.1% probability (Wilks' Lambda = 0.381, approximate $F_{81,16} = 23.583$, $P < 0.0000$). Paula Jenkins of the BMNH also kindly examined the specimen and confirmed that the specimen matches Fig. 12. with respect to the radial displacement of the angular process and the relative widths of the anterior versus posterior premolars.

In view of the potential for other specimens to be discovered that might be considered syntypes of *wilcoxii*, and the potential for those to comprise more than one species, one of which could displace a proposed junior synonym, it seems prudent for us to take action on this matter in the interest of future stability of the taxonomy presented in this study. **We consider BMNH 64.8.14.1 as a genuine syntype of *wilcoxii* and hereby designate it as the lectotype, and in consequence, we treat *wilcoxii* (Krefft 1873) as a junior synonym of *M. planiceps.*** We have not examined the Berlin Museum specimen and its identity remains to be determined.

Mormopterus petersi (Leche, 1884)

Inland free-tailed bat

Figs 8, 11, 12, 13*b*, 15, S2.

Nyctinomus petersi Leche, 1884: 49–50, fig. 1a, b

Synopsis of taxonomic history

Thomas (1906) considered *petersi* as a junior synonym of *planiceps* and it has been treated as such to the present but for brief periods when it was recognised as a valid species by Wood Jones (1925) and later Peterson (1985).

Type details

Lectotype

NRM A59/1983809.3137 male (young adult) preserved in spirit with skull *in situ.* External measures are given in Table S7.

Type locality

Probably South Australia. One of the type specimens has 'Adelaide' written on the label according to Tate (1952); however, *petersi* has not otherwise been recorded from Adelaide.

Notes on the syntypes

Although Leche did not explicitly state how many specimens formed the basis of his description, four specimens are held to comprise the original syntypes according to Mahoney and Walton (1988). We have examined the three specimens held in NRM and found that at least two species are represented based on penis morphology. Leche's description is therefore based on a species composite. We have chosen to designate NRM A59/1983809.3137 as the lectotype since, although it is a young male, the penis morphology clearly defines the species. Specimen NRM A59/1983809.3138, male spirit, skull not extracted, is a *M. planiceps* (based on penis morphology). NRM A59/1983809.3136 female, spirit (skull extracted but lost),

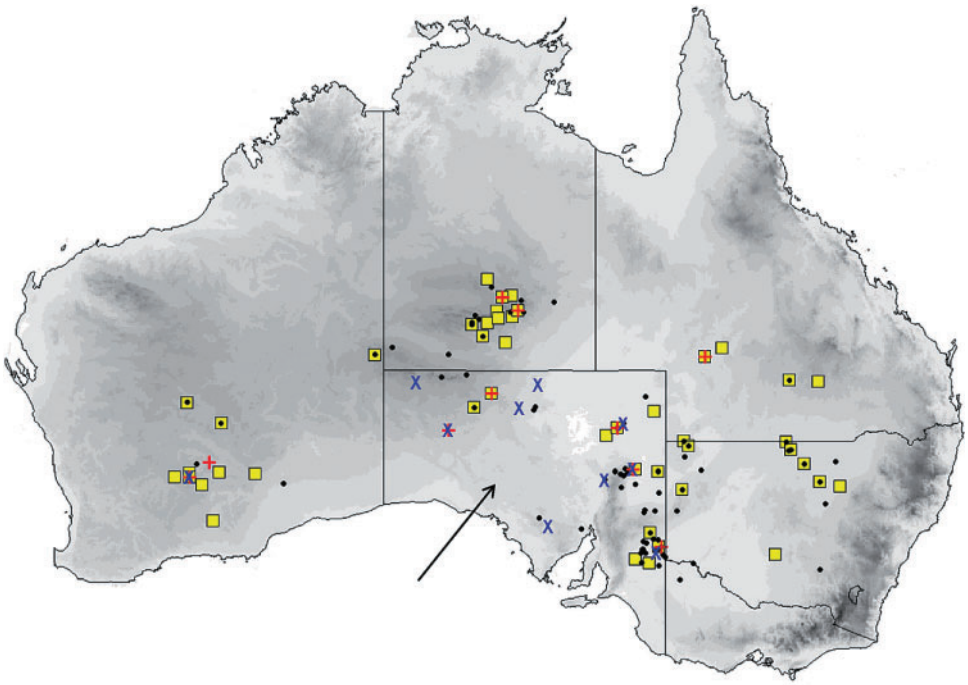

Fig. 15. Locations of specimens used in this study for *Mormopterus petersi.* Measured = □; mtDNA = +; allozymes = X; other museum specimens identified on phallic morphology or previous allozyme studies = ●. Type locality (arrowed) given as 'South Australia'.

has been measured by us and has a posterior probability of 99.9% of being a *petersi* according to the same DFA described in the *planiceps* account above. A DFA (the same ran in the *wilcoxii* account above) based on a reduced number of variables to match the available measures for the last syntype specimen BMNH 90.8.1.12 female (spirit and skull), resulted in a posterior probability of 93.7% that this specimen is a *planiceps*.

Referred specimens

See Table S1, S5, S6.

Diagnosis

Distinguishable from all other species in the subgenus except *lumsdenae* sp. nov. by having a penis that is cylindrical for its entire length with a small bacular mound emanating from within the anterior rim of the glans body. Differs from all species except *planiceps* and *kitcheneri* sp. nov. by having an unusually flattened skull. Otherwise similar in appearance to all other species with mostly overlapping external and cranial measurements other than with *lumsdenae* sp. nov., from which it differs by being smaller in most measures (Tables S7, S8). Distinguished from all Australian forms and *loriae* by having a unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 4 to 11 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pairwise genetic distances from 0.075 to 0.094 (Table S4).

Revised description and contrasts with sympatric species

Sympatric species: *M. planiceps*, *M. kitcheneri* sp. nov., *M. ridei*, and possibly *M. lumsdenae* sp. nov.

External. A small species with forearm range 31.9–38.2 mm and mass 7.5–11.8 g. There is a clinal increase in size of most wing (and cranial) measures from south to north. The external appearance is as described for *planiceps* except that the fur is sometimes shorter and the colour lighter brown than in *planiceps*, although inconsistently so. Not easily distinguished from *kitcheneri* sp. nov., although DFA on wing element measures generally distinguish *petersi* from *kitcheneri* sp. nov. and *planiceps*. The smaller southern forms of *petersi* that co-occur with the lighter forms of *ridei* are similar in appearance. The large Northern Territory forms of *petersi* approach the size of *lumsdenae* sp. nov. but in this region they do not appear to occur together. In south-eastern Queensland these two species may occur together but are separable by the smaller external measures of *petersi*.

The phallus is short, averaging around 5 mm, with the glans penis averaging 2.4 mm in length. The preputial gland is a small bump accompanied by some short hairs. The glans is cylindrical along its length in the live animal but typically there is dorsoventral flattening in many of the preserved specimens. The anterior rim of the glans body is almost circular surrounding the bacular mound, although in some specimens that ventral extremity of the rim extends slightly further than the dorsal extremity. The bacular mound is round and its anterior extent hardly protrudes beyond the anterior rim. The bacular mound is not attached to the very edge of the rim, but is instead attached via an inner head within the glans body. The glans body has a

series of longitudinal ridges and fissures running from the anterior rim to near the junction of the prepuce and penis; these ridges are covered with small epithelial spines. There is a small depression in the mid body of the dorsal surface of the glans body.

The glans penis of *petersi* is most similar in size and form to that of *lumsdenae* sp. nov., but *lumsdenae* sp. nov. has a considerably larger bacular mound that protrudes much further than it does in *petersi*. In *lumsdenae* sp. nov. there is a single central dorsal ridge that bifurcates slightly just before the rim, but this ridge extends back along the length of the glans body. In *petersi* there is a fissure on the centre line of the dorsal glans body, and the ridges either side diverge from one another at about a glans width's length back from the rim and surround a central mound or depression.

Cranial (Fig. 13*b*). The skull is as described for *planiceps* but with the following differences: the lower part of the ramus of the mandible is outwardly displaced such that the inner margin of the angular process sits well outside the line of the outer edge of the condyle when viewed from above (Fig. 12). In addition, the relative width of the first to the second lower premolar is greater than 0.75.

Distribution and habitat

The distribution map (Fig. 15) is based solely on specimens that we have examined and identified from morphology and/or from molecular methods. Distribution is largely arid to semiarid regions in the southern half of the continent. There appears to be a genuine disjunction in distribution between Western Australian records and those in central and eastern Australia. Natural roosts are in tree hollows but this species is sometimes found in buildings (Richards *et al*. 2008).

Remarks

The mtDNA data also show a marked difference between eastern and western populations, with the 3.6% average sequence divergence approaching a magnitude that might indicate species-level differences. At present these two populations appear to be allopatric and we can find no concordant morphological or allozymic support for recognising these populations at a higher taxonomic level. However, we flag this as a possibility for future investigation, especially if additional specimens can be obtained from the geographic zone of potential overlap.

Mormopterus kitcheneri McKenzie, Reardon & Adams, sp. nov.

South-western free-tailed bat

Figs 8, 11, 12, 13*e*, 16, S3.

Type details

Holotype

WAM M60848, adult male, body in spirit, skull removed. Holotype measures are given in Tables S7 and S8.

Type locality

20 km north-west of Balladonia, Western Australia. 32.252°S, 123.431°E. Mist-netted over roadside dam on 12 November 2007. Collectors: Terry Reardon, Michael Pennay, April Reside and Annette Scanlon.

Paratypes

WAM M60849, adult female, body in spirit, skull *in situ*, collected at the same locality and date as the holotype; SAMA

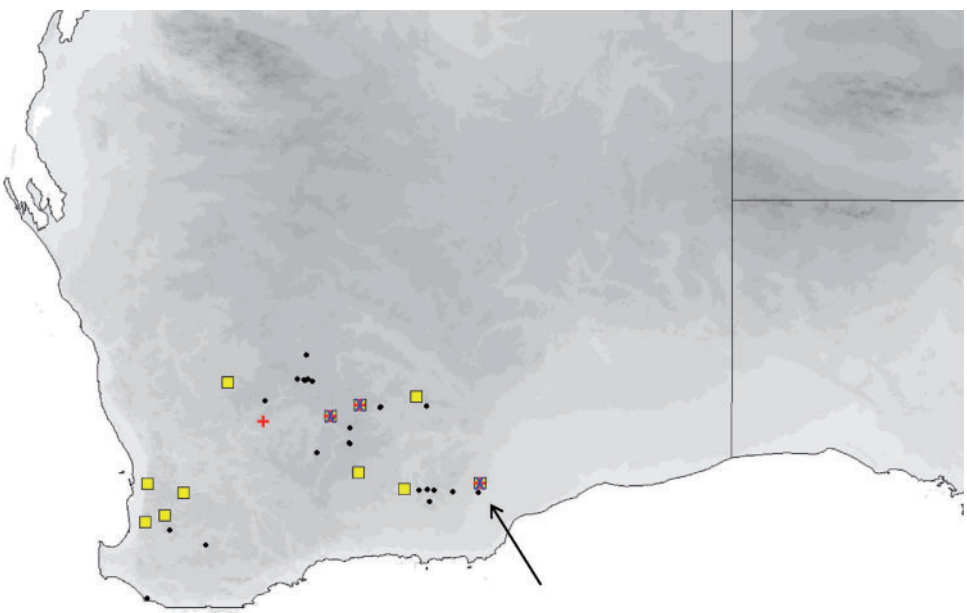

Fig. 16. Locations of specimens used in this study for *Mormopterus kitcheneri* sp. nov. Measured = □; mtDNA = +; allozymes = ×; other museum specimens identified on phallic morphology or previous allozyme studies = ●. Type locality (arrowed): Balladonia, Western Australia.

M25843 adult male, Johnnies Dam, Jaurdi, WA, 30.77°S, 120.13°E; WAM M60855 adult female, Almond Dam, Credo, WA, 30.52°S, 120.779°E.

Referred specimens

See Tables S1, S5, S6.

Diagnosis

Distinguishable from all other species in the subgenus by having a penis that is shorter than 7.5 mm but with a pointed bacular mound (Fig. 8). Differs from all species except *planiceps* and *petersi* by having an unusually flattened skull (Fig. 11). Otherwise similar in appearance to all other species with mostly overlapping external and cranial measurements, other than with *lumsdenae* sp. nov., from which it differs by being smaller in most measures (Tables S7, S8). Distinguished from all Australian forms and *loriae* by having a unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 2 to 10 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pair-wise genetic distances from 0.045 to 0.094 (Table S4).

Description and contrasts with sympatric species

Sympatric species: *M. petersi.*

External. A small species with forearm length 32.6–35.4 mm and body mass 7.5–10.5 g, and appearance as described for *planiceps*. The fur colour tends to be grey-brown, dorsally and lighter ventrally, but variable in length. DFA using wing measurements should distinguish *kitcheneri* and Western Australian *petersi*.

The phallus is ~6 mm in length and the glans averages 5 mm and is mostly cylindrical in shape, with a slight tapering at the distal end. The bacular mound is distinctive by being sharply tapered to a dorsally inflected point. The dorsal surface of the bacular mound is joined as a continuous extension of the upper central glans body. The ventral surface of the mound emerges from within the cavity of the glans body and the ventral anterior rim of the body forms a lip. The body has longitudinal ridges and fissures running the length of the entire glans body. The ridges have rows of proximally directed epithelial spines. The length of the penis and the pointed shape of the glans will enable easy identification from the sympatric *petersi.*

Cranial (Fig. 13*e*). As described in *planiceps*, but averaging slightly larger in all measures (Tables S7, S8). The angular process of the mandible is as described for *planiceps* (Fig. 12), therefore differs from *petersi* in the same manner.

Distribution and habitat

The distribution map (Fig. 16) is based solely on specimens that we have examined and identified from morphology and/or from molecular methods. Sympatric with *petersi* in Avon and Coolgardie regions of Western Australia. Found in mesic and semiarid woodlands throughout south-western Australia, and forages in semiopen and open air spaces. Roosts in tree hollows.

Etymology

This species is named in honour of Dr Darrell Kitchener for his prolific contribution to elucidating the systematics of Indo-Australian mammals, especially bats.

Mormopterus lumsdenae Reardon, McKenzie & Adams, sp. nov.

Northern free-tailed bat

Figs 8, 11, 13*f*, 17, 18, S4.

Type details

Holotype

QM JM15323, adult male, body in spirit, skull removed, tissue in alcohol, SAMA ABTC81358. Holotype measurements are given in Tables S7, S8.

Type locality

Roadside dam, Peninsula Developmental Road, ~16 km north of Coen, Queensland, 14.809°S, 143.146°E. Collectors: Harry Hines, Keith McDonald and Jeanette Covacevich on 13 September 2002.

Paratypes

QM JM15324, adult male, body in spirit, skull *in situ*, collected at the same locality and date as the *holotype*; SAMA M25848, M25849, adult females, Bourne Creek overflow, Qld, 13.75°S, 143.076°E; SAMA25850, M2585, adult males, 4 km east of Petford, Qld, 17.35S°, 144.904°E; WAM M50042, adult male, M50077, adult female, Laura, Qld, 15.53°S, 144.45°E.

Referred specimens

See Tables S1, S5, S6.

Diagnosis

Distinguishable from all other species in the subgenus by having a penis that is cylindrical along its entire length but with a large bulbous bacular mound (Fig. 8). Is the largest species in the subgenus and averages larger in most external and cranial measurements (Tables S7, S8). Distinguished from all Australian forms and *loriae* by having unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 3 to 9 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pairwise genetic distances from 0.067 to 0.102 (Table S4). Differs from *beccarii* as described in the Remarks section.

Description and contrasts with sympatric species

Sympatric species: *M. ridei*, *M. cobourgianus*, *M. halli* sp. nov. and possibly *M. petersi*.

External. The largest species of the subgenus (forearm 35.2–40.4 mm, mass 11–19.5 g). Robust looking, with all external measures except D5MP averaging much greater than for other species; in contrast, D5MP is larger in *cobourgianus* and *halli* sp. nov. Females have a long clitoral projection. Dorsal fur rich brown and lighter ventrally.

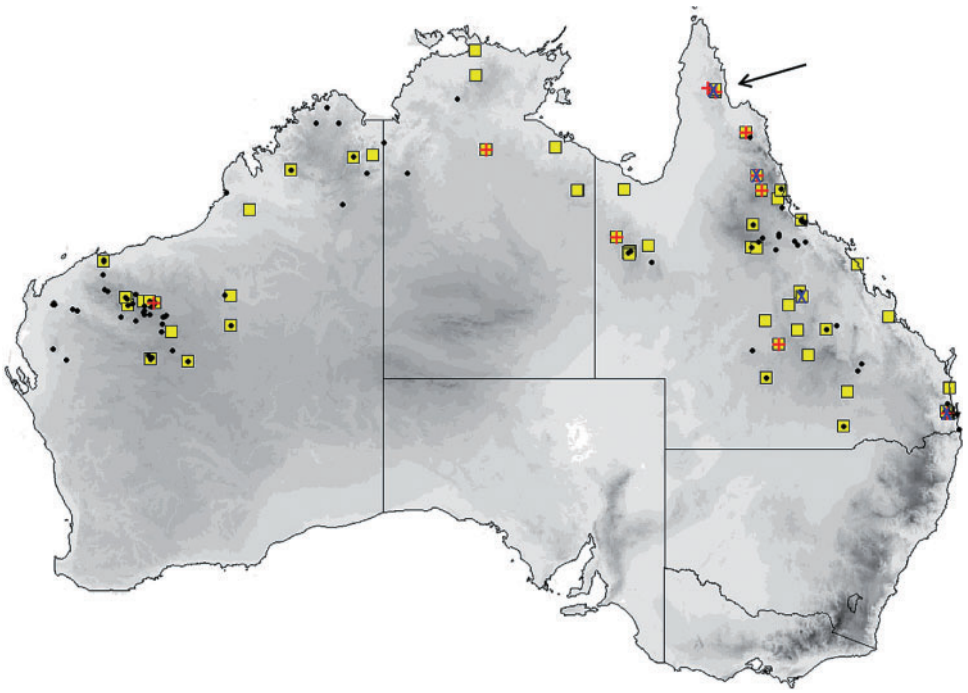

Fig. 17. Locations of specimens used in this study for *Mormopterus lumsdenae* sp. nov. Measured = ■; mtDNA = +; allozymes = ×; other museum specimens identified on phallic morphology or previous allozyme studies = ●. Type locality (arrowed): 16 km north of Coen, Queensland.

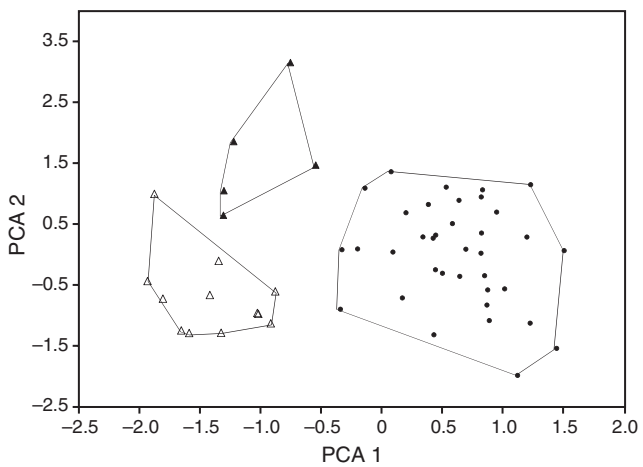

Fig. 18. Principal Components Analysis based on four cranial and six external measures. *M. lumsdenae* sp. nov. = solid circles; *M. beccarii beccarii* = open triangles; *M. beccarii astrolabiensis* = solid triangles.

The phallus is short, averaging near 4 mm, and often has a well developed elongated preputial gland. The glans penis averages 2.6 mm in length and is cylindrical for its length; the distal rim with the dorsal extremity reaching less distance than the ventral rim. The bacular mound is bulbous and usually extends well beyond the dorsal margin of the distal rim of the glans body and at least to the ventral margin of the rim. As in the case of *petersi*, the bacular mound is not contiguous with the distal dorsal surface of the glans body but emanates from slightly within the glans body and is attached as described for *petersi*. The lateral ridges with epithelial spines and fissures extend from the distal rim to just before the junction of the glans and inner preputial skin. The glans is most similar to that of *petersi* but the bacular mound is much larger.

Cranial (Fig. 13*f*). Robust skull with most cranial measures averaging, and sometimes absolutely, much greater than all other Australian *Ozimops* species. The skull has a low sagittal crest running from the lambda to the interorbital constriction. The lambdoidal crests are well developed and the lambda itself rises as a large prominence onto the skull. The preorbital ridge is moderately enlarged. The skull is readily distinguished from that of *petersi* by a much smaller CBL/SH. Most skull dimensions are absolutely larger than for *cobourgianus* and, on average, from *halli* sp. nov. (Table S8).

Etymology

This species is named in honour of Dr Lindy Lumsden for her contribution to the study of Australian bat ecology, for her mentoring of students and for her advocacy for conservation of bats through public engagement.

Distribution and habitat

The distribution map (Fig. 17) is based on specimens that we have examined and identified from morphology and/or from molecular methods. The species is confined to the northern half of the continent within 600 km of the coast, encompassing annual rainfalls from 200 mm to over 1500 mm. The southern Northern

Territory distribution given in Milne and Pavey (2011) is based on previously misidentified museum specimens that have been reidentified in this study as the very large form of *petersi*. Across this distribution it is found in drier shrublands and grasslands to rainforest. It occurs in arid and semiarid areas of Western Australia north of 26°S, where it favours woodland patches and riparian zones (McKenzie and Bullen 2009). Roosts in tree hollows and buildings.

Remarks

The first application of the name *beccarii* Peters, 1881 to this large northern Australian species appears in Winter and Allison (1980) and has been in subsequent use till now. Hill (1983) ascribed Australian forms to the subspecies *astrolabiensis* Meyer, 1899, but suggested that a new subspecies might be erected to account for the size difference he observed between Papuan and Australian forms. Peterson (1985) suggested that the Australian large *Mormopterus* was distantly related to *beccarii* but closer to *astrolabiensis*, which he considered a full species. Koopman (1994) also suggested that the Australian form had not been allocated yet to a subspecies of *beccarii*.

The type locality of *beccarii* is Ambon Island in Indonesia, and of *astrolabiensis* is Bongu, Papua New Guinea. The holotype of *astrolabiensis* was lost during allied bombing during World War II. We have examined both the holotype of *beccarii* (MCG CE44447) and have measures for a large series from the type locality (kindly provided by Judith Eger, ROM). We have also measured a series of specimens from northern Papua New Guinea from the putative distribution of *beccarii astrolabiensis*, including a specimen collected 30 km from the type locality. The glans penis morphology of *beccarii beccarii* and *beccarii astrolabiensis* differs radically from that of *lumsdenae*. Both *beccarii* and *astrolabiensis* have a long tapering glans penis that is clothed with large broad-based epithelial spines, and both have a ventral transverse lip, whereas the glans penis of *lumsdenae* is shorter and not tapered, the spines are fine and there is no ventral transverse lip. We also conducted a PCA analysis based on four external and seven cranial measures for available specimens from Ambon, northern Papua New Guinea, and *lumsdenae* (Fig. 18), which shows clear delineation between the three taxa. The factor loadings for the 10 measures are presented in Table 2. No frozen tissues of *beccarii beccarii* or *beccarii astrolabiensis* were available for inclusion in the allozyme study, but our *ND2* sequencing of a specimen of *astrolabiensis* and a specimen from near the type locality of *beccarii beccarii* showed that they belonged to clades distant from *lumsdenae*. While the species-level systematics of Indo-Papuan *Mormopterus* remains unclear, it is certain that *lumsdenae* is not allied with either *beccarii* or *astrolabiensis*. *lumsdenae* is readily differentiated from *loriae* from Papua New Guinea by its greater size in most measures, allozyme and *ND2* divergence and glans penis morphology.

Mormopterus ridei (Felten, 1964)

Eastern free-tailed bat

Figs 8, 13*c*, 19, 20, S5.

Tadarida loriae ridei Felten, 1964: 6–8, figs 3, 4

Table 2. Factor loadings for four cranial and six external measures from PCA on *M. lumsdenae* sp. nov., *M. beccarii* (from type locality) and *M. b. astrolabiensis*

Measure	Factor 1	Factor 2
GSL	–0.034583	0.921420
M3-M3	0.067330	0.888389
C1-M3	0.196626	0.892842
C1-C1	0.343101	0.879606
D3M	0.936676	0.220520
D3PP	0.870482	0.131208
D4M	0.957485	0.153927
D4PP	0.928567	0.172604
D5M	0.937042	0.040890
D5PP	0.945731	0.068111
Explained variation	5.348678	3.334765
Proportion of total	0.534868	0.333476

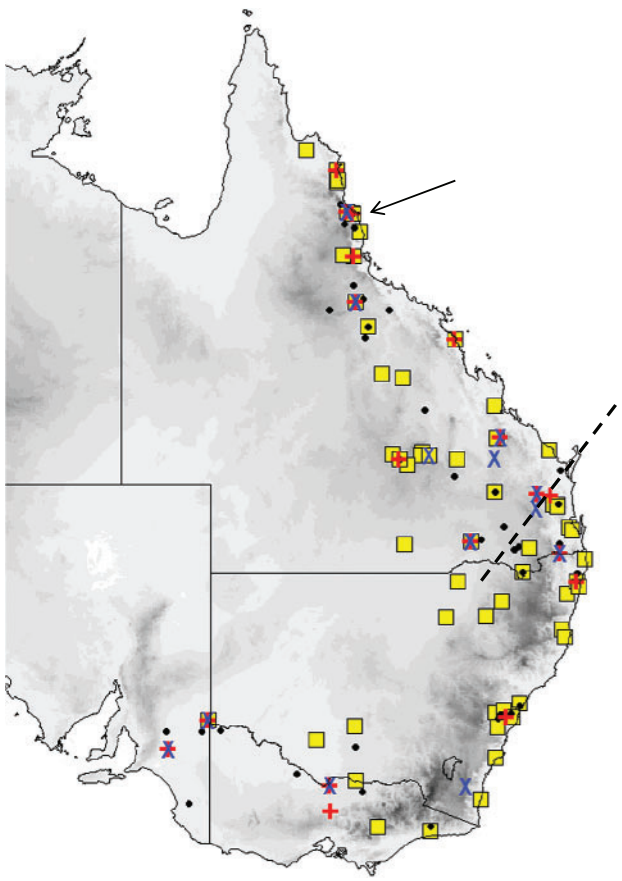

Fig. 19. Locations of specimens used in this study for *Mormopterus ridei*. Measured = □; mtDNA = +; allozymes = X; other museum specimens identified on phallic morphology or previous allozyme studies = ●. Type locality (arrowed): Cairns, Queensland. Division of north and south clades indicated by dashed line.

Synopsis of taxonomic history

Felten's concept of *ridei* as a subspecies has persisted for most of its short history although it has been treated as a subspecies of

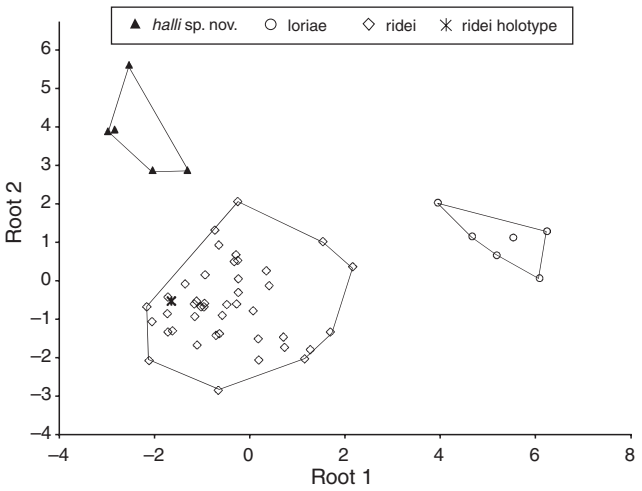

Fig. 20. Graph showing the DFA based on three cranial and nine external measures of *ridei*, *loriae* and *halli* sp. nov. to show the position of the holotype of *ridei.* Discriminant functions were derived without including the *ridei* holotype.

planiceps rather than *loriae* by some authors (Koopman 1984; Mahoney and Walton 1988). In an opinion that has been mostly ignored, Peterson (1985) considered all small Australian species including *ridei* to be synonymous with, or races of, *petersi*. Churchill (2008) recognised *ridei* as a species in its own right.

Type details

Holotype

SMF 17652 adult female, skin in spirit, skull removed.

Type locality

Cairns, Queensland.

Paratypes

SMF 17651 (male), SMF17653–5 (females) all drawn from the same house roof.

Referred specimens

See Tables S1, S5, S6.

Diagnosis

Distinguishable from all other species in the subgenus by having a glans penis that is short, cylindrical and tapered at the tip, with dorsal glans body contiguous with the bacular mound and the glans body covered in small epithelial spines (Fig. 8). Distinguished from all Australian forms and *M. loriae* by having a unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 3 to 10 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pair-wise genetic distances from 0.061 to 0.088 (Table S4).

Redescription and contrasts with sympatric species

Sympatric species: *M. planiceps*, *M. petersi*, *M. lumsdenae*, and probably *M. halli* sp. nov.

External. A small, compact-looking species with forearm 30–35 mm and mass 5–11.2 g. Averages slightly smaller on several external characters from sympatric species, but typically with considerable overlap with most other species except with *lumsdenae*, which is much larger. Fur colour quite variable, with some forms being lighter brown-grey, similar to *planiceps* and *petersi*, but typically darker brown dorsally and lighter underneath (although these differences in colour are not correlated with the two intraspecific mtDNA subclades) (Fig. 7). Where it occurs together with *petersi* and *planiceps* it is difficult to distinguish on external characters. The ears and the length of the rostrum are slightly smaller than in *planiceps* and *petersi*. Average values for external characters much smaller than for *halli* sp. nov.

The penis length averages ~4 mm. The glans body is cylindrical for its length but tapers at the tip. The glans body has a series of ridges with small epithelial spines and fissures that run the length of the body. The bacular mound is round and small and dorsally is contiguous with the central part of the dorsal glans body (thus differing from *petersi* and *lumsdenae*, in which the bacular mound emanates from within the body of the glans). The anterior edge of the ventral glans body is not attached to the bacular mound but forms an opening to the body of the glans body. The ventral part of the bacular mound emanates from within the cavity of the glans body. The glans is distinctive in that it has a bullet-shaped tip compared with the blunted shape of *petersi* and should be easily distinguished on live animals.

Cranial (Fig. 13*c*). Skull averages shorter than in *planiceps* and *petersi* and differs clearly by the much smaller CBL/SH. Weak to no sagittal crest, well developed lambdoidal crests, although the lambda varies considerably, with some specimens having almost no visible indication through to those with prominent triangular-shaped elevation. The skull measures average much smaller than in *lumsdenae* but absolutely so in GSL and CBL (Table S8). Averages much smaller than in *halli* sp. nov. but reliably distinguished on DFA using all cranial measures. Also differs from *halli* sp. nov. by having a less crowded upper tooth-row with the small upper premolar always present and in line with the tooth-row.

We tested both external and cranial measures for correlation to latitude and hence the north versus south mtDNA boundary, but failed to find support for any correlation. Based on our few sequenced samples in south-eastern Queensland, the current boundaries of the north and south mtDNA clades (Wrattens State Forest and Cherbourg State Forest) are only 45 km apart and at about the same latitude.

Distribution and habitat

The distribution map (Fig. 19) is based on specimens that we have examined and identified from morphology and/or from molecular methods. *M. ridei* occurs in eastern Australia in the higher-than-500-mm annual rainfall zone, but also occurs in the lower-rainfall areas of South Australia, Victoria and southern central New South Wales but always associated with rivers and swamps. In South Australia it occurs along most of the length of the Murray River but has not yet been recorded very far from the river or its associated streams. Habitat ranges from wet tropical forest to swamplands, river red gum–lined streams and open

woodland. Roosts in eucalypt hollows and in buildings (Hoye *et al*. 2008).

Remarks

Felten (1964) described *ridei* as a subspecies of *loriae* and for most of its short history it has been treated as such. Since Adams *et al*. (1988), the name *ridei* has usually been associated with Species 5 populations 'S & T' from far northern Queensland. However, the type locality for *ridei* is Cairns, which falls better within the distribution of Species 2, rather than Species 5. Had Felten (1964) chosen a male for the holotype, it would have been a simple task to associate *ridei* with Species 2 on the basis of glans penis morphology. To test which of the three possible candidate species, Species 2 (our *ridei*), Species 5 populations S & T (*halli* sp. nov.) and also *loriae* from Papua New Guinea, matched the *ridei* holotype, we ran a DFA using CBL, MB, C1-C1, FA, D3M, D3PP, D3MP, D4M, D4PP, D4MP, D5M, D5PP. There was very strong discrimination between these three taxa (Wilks' Lambda = 0.069, approximate $F_{22,80} = 10.16$, $P < 0.0000$) and there was a 100% posterior probability of the holotype belonging to *ridei* (Fig. 20).

Mormopterus cobourgianus (Johnson, 1959)

North-western free-tailed bat

Figs 8, 13*d*, 21, S6.

Tadarida loriae cobourgiana Johnson, 1959: 185–186

Synopsis of taxonomic history

Johnson's concept of *cobourgiana* as a subspecies has persisted for most of its short history, although it has been treated as a subspecies of *planiceps* rather than of *loriae* by some authors (Koopman 1984; Mahoney and Walton 1988). In an opinion that has been mostly ignored, Peterson (1985) considered all small Australian species including *cobourgiana* as synonymous with, or races of, *petersi*. Churchill (2008) recognised *cobourgiana* as a species in its own right.

Type details

Holotype

USNM 284243 adult female, skin with skull removed.

Type locality

Black Rock Point, on north shore of Van Diemen Gulf, 15 miles SE of Cape Don lighthouse, Cobourg Peninsula, Northern Territory, 11.43°S, 131.93°E.

Referred specimens

See Tables S1, S5, S6.

Diagnosis

Distinguishable from all other species in the subgenus by having a glans penis with large epithelial spines covering the glans body from the base of the glans to the bacular mound (Fig. 8). Distinguished from all Australian forms and *loriae* by having a unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 4 to 11 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pair-wise genetic distances from 0.065 to 0.102 (Table S4).

Redescription and contrasts with sympatric species

Marginally sympatric with *M. lumsdenae.*

External. A small species with forearm 32.0–35.1 mm and live mass 6.8–10.5 g. Head and dorsal fur cream based with light orange brown and sometimes frosting of grey brown. Ventral fur cream, sometimes yellowy cream. The ventral fur extends well onto the wing to a line extending from the mid humerus to the knee. Upper lip fringe is light creamy yellow. Northern Territory forms ($n = 3$) are slightly darker above and below. Sympatric

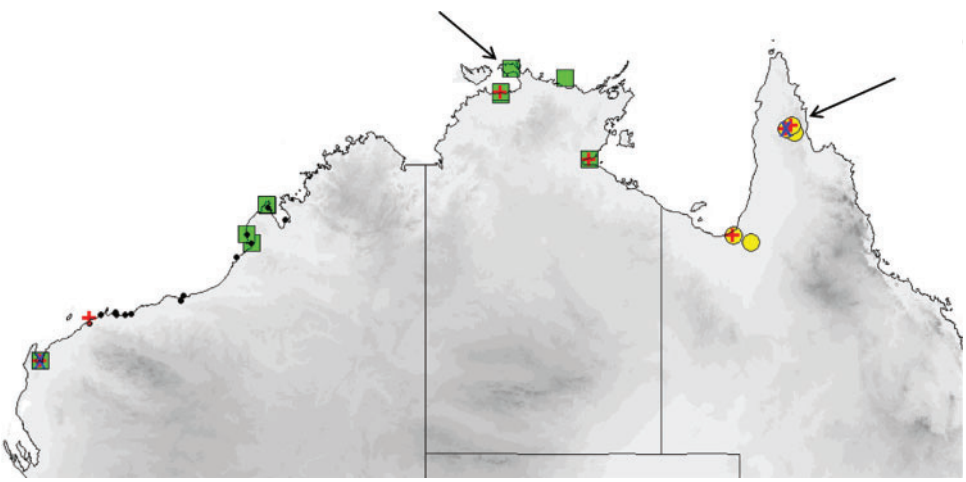

Fig. 21. Locations of specimens used in this study for *Mormopterus cobourgianus* and *M. halli.* Measured = ■ (*cobourgianus*) and ● (*halli*); mtDNA = +; allozymes = ×; other museum specimens identified on phallic morphology or previous allozyme studies = ●. Type locality of *M. cobourgianus* (arrowed): Cobourg Peninsula, Northern Territory. Type locality of *M. halli* sp. nov. (arrowed) near Coen, Queensland.

only with *lumsdenae*, from which it is readily distinguished by being much smaller on most external measures. Ears triangular with relatively straight leading edge and rounded tips. The bottom of the ear ends in a semicircular antitragus. An unusual feature of this species (and of *halli* sp. nov.) is the relatively long D5MP, even though the other wing elements are of similar length to, or smaller than, those of *lumsdenae.*

The penis is sparsely covered by long hairs and a small preputial gland with 10 or so long hairs. The glans penis has a cylindrical body but with a tapering end where it joins the glans head. A broad transverse lip is present on the ventral side close the head. The entire glans body back from the margin with the glans head is covered with large epithelial spines. There is a central longitudinal fissure both ventrally and dorsally. The head has no spines and comprises two sections, the more distal globular bacular mound and the inner head. The glans penis morphology easily distinguishes *cobourgianus* from other Australian species.

Cranial (Fig. 13*d*). Small slender skull with no sagittal crest. Upper anterior premolar, while small and compressed between the canine and posterior premolar, is taller than the cingulum of the canine and readily visible. The width of the lower first premolar is ~80% the size of the second premolar. Readily distinguished from *lumsdenae* by smaller averages on all cranial measures and by some measures being always smaller (Table S8).

Distribution and habitat

The distribution map (Fig. 21) is based on specimens that we have examined and identified from morphology and/or from molecular methods. *M. cobourgianus* occurs coastally from Exmouth to western Gulf of Carpentaria. However, the Western Australian and Northern Territory populations appear disjunct, with no records yet from the northern and eastern Kimberley coast or islands, despite this area being well surveyed (McKenzie and Bullen 2012). Associated with mangrove communities in Western Australia (McKenzie and Bullen 2009, 2012) but also woodland in the Northern Territory (Milne *et al*. 2008). Roosts in tree hollows. Although we have found no evidence yet that the allopatric populations in Western Australia and Northern Territory are taxonomically distinct, a more detailed examination might be worthwhile as there is some divergence in *ND2* haplotypes. Only six specimens are currently known from the Northern Territory.

Mormopterus halli Reardon, McKenzie & Adams, sp. nov.

Cape York free-tailed bat

Figs 8, 13*g*, 21, S7.

Type details

Holotype

QM JM19625, adult male, body in spirit and skull extracted. Liver tissue deposited in SAMA ABTC 94541. Holotype measurements are given in Tables S7, S8.

Type locality

Ironbark Dam, Oyala Thumotang National Park, Queensland, 13.625°S, 142.801°E. Collectors: Terry Reardon, Stanley Flavel, Luke Hogan and Annette Scanlon, 7 November 2006.

Paratypes

QM JM19624, JM19627, JM19628, adult females, and QM JM19636, adult male, all collected on the same night at the same locality as the holotype; WAM M50138, M50139, adult females, Archer Bend, Qld, 13.5°S, 143.0°E; WAM M50069, adult male, Normanton, Qld, 17.67°S, 140.76°E; AMS M13280, adult female, 42 km SE of Normanton, Qld, 17.93°S, 141.433°E.

Diagnosis

Distinguishable from all other species in the subgenus by having a short tapering glans penis with a ventral transverse lip at about half the length of the glans body, and with large epithelial spines that cover the glans body dorsally from the head to the base and ventrally from the lip to the base (Fig. 8) Distinguished from all Australian forms and *loriae* by having a unique combination of allozyme alleles (Table S3) and with the number of fixed differences from other species ranging from 4 to 7 (Table S2); also forms a monophyletic assemblage of *ND2* haplotypes and differs from other species in average unweighted pair-wise genetic distances from 0.067 to 0.101 (Table S4).

Description and contrasts with sympatric species

Sympatric species: *M. lumsdenae* and probably *M. ridei.*

External. A small stout species with forearm length 31–35 mm and live mass ~9 g. Head, body and wings as described for the subgenus but with the following additional observations: dorsal fur variable from rich brown to orange brown and only weakly contrasting with lighter ventral fur; yellowish tinge to the fur on the side of the neck. Skin on ears, wings, and muzzle very dark brown; ears with half round antitragus. Similar in appearance and colouration to *lumsdenae* but averages smaller on most wing element measures, and absolutely smaller on FA and D3M lengths (Table S7). Likely to be sympatric with *ridei* and, apart from glans penis morphology, may be difficult to distinguish on external characters. However C1-C1 is easy to measure on a live animal and is close to unequivocally distinguishing these two species (Table S8).

Penis with sparse short hairs and preputial gland is short with five or so long hairs. Glans penis body ~5 mm in length. The glans penis is cylindrical but tapering a little distally to a relatively long head. The dorsal body is covered with large epithelial spines extending to its junction with globular shaped head. The ventral body is composed of two sections of approximately equal lengths, and divided by a broad transverse lip, the ends of which reach half way up the sides of the glans body. The proximal section of the ventral body is covered with large epithelial spines but the section distal to the lip has no spines and is characterised by a series of transverse folds until it ultimately joins the glans head. A longitudinal slot marking the urinary meatus is situated ventrally in the glans head, just proximally from the tip of the bacular mound.

Cranial (Fig. 13*g*). The skull is large and robust, averaging larger than all species other than *lumsdenae.* Lambdoidal crest

strongly developed but weak sagittal crest. The mandibular body is tall and thick at the anterior end. Tooth-row crowded and the upper anterior premolar is very small and, when present, is often pushed out the line of the row between the cingulum of the second premolar and the canine. In some specimens either one or both little upper premolars are missing. Differs from both *ridei* and *lumsdenae* as outlined in the accounts of those species.

Distribution and habitat

The distribution map (Fig. 21) is based on specimens that we have examined and identified from morphology and/or from molecular methods. Thus far *halli* is known from only 11 specimens and has been collected from two disparate locations: central Cape York Peninsula and near Normanton in the Gulf Country. All specimens have been captured by mist nets and all over, or very near to, fresh water. The small number of specimens especially on Cape York Peninsula probably does not reflect that the species is uncommon or geographically restricted, but more that previous survey effort in that region has focussed on rainforest and riparian habitats along major river courses rather than in the woodland habitat of *halli* (Reardon *et al*. 2010). Survey efficiency for this species will be improved when its echolocation call is characterised. Natural roosts are unknown although likely to be tree hollows.

Etymology

This species is named in honour of Dr Leslie Hall for his life-long contribution to the conservation of Australasian bats through his research, mentoring of students and public engagement.

Discussion

This revision provides the first solid working hypothesis for the species boundaries, nomenclature and higher taxonomic structure in Australian *Mormopterus*. After years of confusion with extralimital species, we have shown that Australia does not share *Mormopterus* species with the Indo-Papuan region and therefore Australia is home to nine endemic species. These nine species are readily referrable to three distinctive basal groups, which we have conservatively designated herein as subgenera.

Despite the molecular and morphological scope of this study, several knowledge gaps remain in Australian *Mormopterus*. In particular, the geographic distribution limits for most of the Australian species of the new subgenus *Ozimops* are far from fully understood. *halli* and Northern Territory *cobourgianus* are currently known from only a handful of localities, and whether these are truly rare species or just rarely collected remains to be determined. Given that our maps are based only on records unequivocally identified from glans penis morphology or molecular methods, we expect that knowledge gaps regarding the distribution and abundance of each species are likely to be gradually filled as the species boundaries outlined herein become understood by field workers.

Traditional biogeographic barriers are consistent with the apparent allopatry of closely related pairs of species and intraspecies clades, namely the Gulf of Carpentaria for *cobourgianus* and *halli*, and the Nullarbor for the closely related species *planiceps* and *kitcheneri* plus the east and west clades of *petersi.* In all three cases it is possible that further collecting will demonstrate geographic adjacency or overlap between the pairs of species/clades. Interestingly, the distributional boundaries of the north and south *ND2* clades of *ridei*, based on our limited sampling, meet in the Macleay–McPherson Overlap (Burbidge 1960).

Significance of mtDNA clades within species

The discovery of significantly divergent mtDNA clades within both *ridei* and *petersi* (and to a lesser degree between Western Australian and Northern Territory clades of *cobourgianus*) warrant more detailed genetic and morphological investigation, particularly to resolve whether these clades should reflect taxonomic distinction. The lack of supportive allozyme or morphological differences for these clades is somewhat surprising, given that the magnitude of these *ND2* divergences approaches that between other allozymically distinctive species (e.g. the p-distance between *kitcheneri* and *planiceps* is 0.045 versus 0.042 for the east and west clades of *petersi*). Nevertheless, mtDNA gene trees are commonly discordant with their underlying population/species trees (Funk and Omland 2003), and numerous possible explanations have been proposed to account for such discrepancies (Toews and Brelsford 2012).

The species *kitcheneri* and *planiceps* are sister species on the basis of the mtDNA phylogeny (Fig. 7), with the former species distributed in south-west Western Australia and the latter from the Eyre Peninsular to eastern Australia, with each species apparently absent from the Nullarbor plain. These two species are also distinguished on the basis of two fixed differences at allozyme loci and major differences in glans penis morphology. This result contrasts with that obtained for the east and west clades of *petersi*, which show no clear allozyme and morphological distinction. These two *petersi* clades are similarly found on either side of the Nullarbor plain, though the distribution of *petersi* also extends into parts of central Australia, suggesting that it may be more arid-adapted than *kitcheneri* or *planiceps*. Nevertheless, the similar geographic and matrilineal genetic pattern displayed by the two species/populations on either side of the Nullarbor suggests that their differentiation may have resulted from similar evolutionary/environmental forces. Interestingly, a similarly high level of *ND2* divergence (p-distance = 0.049) was found among populations of the bird species *Melithreptus lunatus* located on either side of the Nullarbor plain, and this was estimated to equate to a population fragmentation time of between 594 000 and 3.4 million years ago (Dolman and Joseph 2012). This period coincides with a period of increasing aridity on the Australian continent that commenced during the Plio-Pleistocene and intensified during Milankovitch cycles of the Pleistocene, when the Nullarbor plain is likely to have become a significant barrier to gene flow of mesic-adapted animals in open forest and woodland habitats (Fujioka *et al*. 2005; Byrne *et al*. 2008; Dolman and Joseph 2012). Currently, our data are too limited to provide robust date estimates for the divergence of the bat populations, but additional comparative phylogeographic studies of bat species distributed across southern Australia would be of considerable interest, and may potentially reveal similar patterns of population differentiation.

The lack of supporting morphological differences associated with the *ND2* clade divergence in *petersi* may also reflect the general conservative nature of the morphology among the species, and perhaps the limits of examining finer features of the genitalia under the microscope alone. The absence of nuclear gene divergence within *petersi*, in contrast to the mtDNA divergence, could alternatively reflect features of the biology of the species, such as sex-biased dispersal and/or female philopatry. For example, male-biased dispersal was suggested as an explanation for the incongruence between patterns of gene flow inferred from mitochondrial and nuclear DNA markers in the ghost bat *Macroderma gigas* (Worthington-Wilmer *et al*. 1999). However, this finding is not strictly analogous, first because microsatellite nuclear markers (likely more sensitive than allozymes for detecting sex-biased dispersal) were used in the latter study, and second because ghost bat mtDNA clades were correlated with defined distributions around maternity caves, whereas *Ozimops* species are not cave dwellers and are not obviously confined by roosting opportunity.

Comparisons of the new taxonomy with fossils

Fossil remains of molossid bats in Australia are rare, with only four sets of material thus far described (Hand 1990; Hand *et al*. 1997, 1999; Martinez 2010). While various preliminary taxonomic assessments have been made of this material, a key impediment to identifying and interpreting this fossil material has been the lack of a solid taxonomic framework for extant Australian *Mormopterus* (Martinez 2010). Our taxonomic revision of the extant taxa now provides a strong basis for developing a more robust understanding of intra- and interspecies variation in dental and cranial morphology.

Field identification

The shape features and size of the glans penis varies considerably between species and is both one of the clearest field diagnostic characters to identify species from a live animal, as well as being easily observed under a hand lens or microscope with minimal retraction of the prepuce. However, identification of female *Mormopterus* remains difficult for some sets of sympatric species. We are hoping that with a more robust taxonomic framework in place, field biologists will uncover reliable diagnostic characters, especially those more easily and consistently observed in live animals rather than preserved specimens. This situation is similar to that in another Australian bat genus, *Vespadelus*, in which the male genitalia are highly distinctive but diagnostic characters in females for distinguishing some species are elusive (Churchill 2008). Until diagnostic characters are available for distinguishing these species, we recommend that skin biopsies be collected to enable confirmation of the species using genetic analyses.

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