



INSTITUTO DE BIOCÊNCIAS
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**RELAÇÕES FILOGENÉTICAS DE *PUFFINUS (SENSU LATO)* E
CALONECTRIS (AVES: PROCELLARIIFORMES), COM BASE EM
CARACTERES OSTEOLÓGICOS**

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

PORTO ALEGRE

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

Área de concentração: Biologia Comparada

Orientador: Dr. Caio José Carlos

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Aprovada em ____ de _____ de _____.

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DEDICATÓRIA

Em tempos tão difíceis, dedico esta dissertação a todos que lutam incansavelmente por um País mais justo; aos alunos, aos professores e aos que compartilham da ideia de que só a educação, gratuita e de qualidade, pode transformar nossa sociedade.

E, àqueles que insistem em agir contra o povo:

“Apesar de você(s) amanhã há de ser outro dia.”

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“E uma das condições necessárias a pensar
certo é não estarmos demasiado certos
de nossas certezas.”

Paulo Freire,
in Pedagogia da Autonomia

APRESENTAÇÃO

A presente dissertação de mestrado é apresentada conforme Resolução N°37/2018, deste Programa de Pós-Graduação em Biologia Animal (PPG-BAN) da Universidade Federal do Rio Grande do Sul, que institui procedimentos e normas para apresentação e avaliação da Dissertação de Mestrado e da Tese de Doutorado. O texto principal desta dissertação está estruturado sob a forma de um artigo científico, redigido em língua inglesa, visando à submissão ao *Zoological Journal of the Linnean Society* (Qualis A1), periódico com grande reputação na área de sistemática filogenética, aberto à publicação de manuscritos extensos e bem-ilustrados. O presente trabalho está de acordo com as “normas aos autores” do referido periódico, disponíveis no endereço eletrônico fornecido no item Referências Bibliográficas do capítulo introdutório e no Anexo 1. De acordo com o Artigo 43º do Regimento do PPG-BAN, o artigo, que compõe a parte central desta dissertação, está acompanhado de dois capítulos extras. O primeiro, a introdução geral, contém uma revisão sobre o problema abordado pelo presente trabalho, e traz os objetivos e os principais resultados obtidos, estes sob a forma de um cladograma das relações filogenéticas entre os táxons estudados. O segundo, após o texto principal, apresenta as principais conclusões. Ambos capítulos introdutório e conclusivo estão redigidos em língua portuguesa.

RESUMO

Os *shearwaters*, petréis de pequeno e médio porte, são espécies de aves marinhas de hábito pelágico, e estão entre os grupos mais diversificados de Procellariiformes. A família Procellariidae, altamente especializada no ambiente marinho, inclui, entre outros, os gêneros *Calonectris*, *Ardenna* e *Puffinus* (*sensu stricto*), cuja sistemática é particularmente complexa. Apesar das primeiras classificações gradistas, todas as hipóteses atualmente disponíveis das relações filogenéticas para este grupo são baseadas na mesma evidência molecular, *i.e.*, citocromo *b* de DNA mitocondrial. Este trabalho apresenta a primeira hipótese filogenética baseada na evidência morfológica, a partir da análise de 104 caracteres osteológicos (23 contínuos e 81 discretos). Foram analisadas 20 espécies viventes de *shearwaters*, representando 62,5% de todas as espécies atualmente reconhecidas. A hipótese final aqui apresentada é o consenso estrito das árvores mais estáveis produzidas pela análise de parcimônia com pesagem implícita. *Calonectris* foi recuperado como monofilético (RBS = 75), apresentando a seguinte topologia (*C. edwardsii* (*C. leucomelas* (*C. diomedea* + *C. borealis*))). Todas as outras espécies foram incluídas em um único clado bem suportado (RBS = 76), *Puffinus* (*sensu lato*), com as seguintes relações: (*Ardenna pacifica* (*A. bulleri* (*A. creatopus* (*A. carneipes* (*A. gravis* ((*A. grisea* + *A. tenuirostris*) (*Puffinus nativitatis* (*P. puffinus* (*P. mauretanicus* (*P. opisthomelas* (*P. gavia* (*P. huttoni* (*P. yelkouan* (*P. lherminieri* + *P. assimilis*)))))))))))). O monofiletismo de *Ardenna*, como sugerido por todas as hipóteses baseadas na evidência molecular, não foi recuperado. A hipótese final, de apenas dois gêneros irmãos para os *shearwaters*, é consistente com classificações anteriores baseadas na evidência osteológica e com algumas análises moleculares.

Palavras-chave: cladística, morfologia comparada, osteologia, petréis, Procellariidae, aves marinhas, sistemática.

ABSTRACT

Shearwaters are small to medium-sized, pelagic seabirds, and are among the most diverse group of Procellariiformes. Procellariidae, an assemblage that have become highly successful and specialized in the marine environment, includes, among others, genera *Calonectris*, *Ardenna* and *Puffinus* (*sensu stricto*), which systematics is particularly complex. Despite earlier classifications, all available hypothesis of phylogenetic relationships for this group are based on the same molecular evidence, *i.e.*, mtDNA cytochrome *b* gene. Here we present the first morphology-based phylogenetic hypothesis for the group, using 104 osteological characters (23 continuous and 81 discrete) scored for 20 extant species of shearwaters, representing 62.5% of all species currently recognized. Both equally and implied weighting were used for phylogenetic analyses, and the final hypothesis presented herein is the strict consensus of the most stable trees produced by the latter. *Calonectris* was recovered as monophyletic (RBS = 75), with the topology (*C. edwardsii* (*C. leucomelas* (*C. diomedea* + *C. borealis*))). All other members of shearwaters were included in a single, well-supported monophyletic grouping (RBS = 76): *Puffinus* (*sensu lato*), which reads (*Ardenna pacifica* (*A. bulleri* (*A. creatopus* (*A. carneipes* (*A. gravis* ((*A. grisea* + *A. tenuirostris*) (*Puffinus nativitatis* (*P. puffinus* (*P. mauretanicus* (*P. opisthomelas* (*P. gavia* (*P. huttoni* (*P. yelkouan* (*P. lherminieri* + *P. assimilis*)))))))))))). The monophyly of *Ardenna*, as suggested by all molecular-based hypotheses, was not recovered. Instead, its members appeared within the larger *Puffinus* (*sensu lato*). The final hypothesis, of only two sister genera for the shearwaters, is consistent with earlier classifications based on osteological evidence, and with some molecular analyses.

Additional Keywords: cladistics, comparative morphology, osteology, petrels, Procellariidae, seabirds, systematics.

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INTRODUÇÃO GERAL

Anatomia e morfologia, apesar de relegadas frente aos métodos moleculares, foram e seguem sendo importantes ferramentas de pesquisa para o estudo da sistemática filogenética (Hillis, 1987; Wiens, 2004; Assis, 2009; Assis & Carvalho, 2010; Bybee *et al.*, 2010). No que se refere à ornitologia, o século XX foi marcado pela falsa impressão de esgotamento em relação ao estudo da anatomia das aves, e pela demora na aderência ao método cladista, proposto por Hennig (1966), para a classificação desses organismos (Raposo, 2001). De maneira semelhante, o século XXI tem sido caracterizado pela diminuição na utilização da evidência morfológica no contexto das análises filogenéticas e pela enxurrada de análises baseadas em sequências de DNA (Livezey & Zusi, 2007). Como Mayr (2008) observou, existe uma crença de que dados morfológicos são inferiores aos moleculares no que diz respeito à reconstrução das relações filogenéticas; ainda assim, o mesmo autor afirma que “sistematas que se utilizam de dados morfológicos são mais frequentemente induzidos ao erro, por conta de caracteres homoplásticos, se comparados aqueles que estudam sequências moleculares” (Mayr, 2008: 6, tradução nossa). Outros autores compartilham dessa concepção, afirmando que, por exemplo, “os dados moleculares não são tão influenciados pela ecologia e hábitos dos organismos e [...] são mais apropriados para a inferência filogenética” (Torres & van Tuinen, 2013: 6, tradução nossa).

Apesar da tendência em se pensar que as reconstruções filogenéticas moleculares são o futuro da sistemática ornitológica, ainda há muito o que se pesquisar. Como Livezey & Zusi (2006: 440, tradução nossa) observaram, “apesar das aparências, a caracterização morfológica das aves para reconstrução filogenética ainda permanece na sua infância.” Seguindo essa mesma linha, nos últimos anos, vários estudos com base em caracteres morfológicos foram realizados visando à proposição de hipóteses de

relacionamento filogenético em diferentes grupos de aves (*e.g.* Mayr & Clarke, 2003; James, 2004; Chu *et al.*, 2009; Smith, 2010; Maurício *et al.*, 2012). Entre eles, o mais abrangente é o de Livezey & Zusi (2006, 2007), acerca das relações filogenéticas das aves modernas (Neornithes), cuja matriz inclui 2.954 caracteres e 150 táxons terminais.

Dentre todo o debate referente à classificação atual das aves, a parte que diz respeito ao “clado das aves aquáticas” (Natatores *sensu* Livezey & Zusi, 2007; Aequornithes *sensu* Mayr, 2011) é particularmente interessante, pois constitui-se de um misto de concordâncias e discordâncias entre as abordagens morfológica e molecular. A Ordem Procellariiformes, pertencente a este grupo, inclui os petréis e albatrozes, com ampla distribuição em todos os oceanos (Warham, 1990). Esse clado abrange 147 espécies separadas em quatro famílias, *i.e.*, Oceanitidae, Diomedidae, Hydrobatidae e Procellariidae (Gill & Donsker, 2019). Apesar do ainda existente debate sobre a taxonomia do grupo, Procellariidae é a família mais diversa e numerosa de todas, incluindo 16 gêneros e 99 espécies de petréis, pardelas e bobos (Onley & Scofield, 2007; Gill & Donsker, 2019).

A designação *Puffinus (sensu lato)*, deste trabalho, engloba todas as espécies pertencentes a dois gêneros atualmente aceitos, *i.e.*, *Ardenna* Reichenbach, 1853 e *Puffinus* Brisson, 1760 (aqui apresentado como *Puffinus sensu stricto*) (Gill & Donsker, 2019). As espécies do gênero *Ardenna*, de modo geral, se reproduzem em ilhas do Hemisfério Sul, principalmente no Oceano Pacífico, enquanto as do gênero *Puffinus (sensu stricto)* habitam todos os oceanos, reproduzindo-se, principalmente, em latitudes tropicais do Oceano Atlântico e do Mar Mediterrâneo (Onley & Scofield, 2007; Remsen, 2019). *Calonectris* Mathews & Iredale, 1915, por sua vez, também apresenta uma ampla distribuição nos Oceanos Pacífico e Atlântico, mas reproduz-se,

principalmente, na porção norte dos mares subtropicais (Warham, 1990; Onley & Scofield, 2007).

A classificação de *Puffinus (sensu lato)* e *Calonectris* sempre gerou controvérsia entre diferentes autores, mesmo antes da utilização do método cladista para inferência filogenética (e.g. Alexander *et al.*, 1965; Cracraft, 1981; Austin, 1996; Penhallurick & Wink, 2004). Os membros atuais de *Calonectris* foram, anteriormente, incluídos em *Puffinus (sensu lato)*, e o gênero levou quase 50 anos, após a sua proposição, para ser amplamente aceito. Essa divisão inicial em dois gêneros foi sustentada por Alexander *et al.* (1965), em um acordo assinado por quinze autores. Buscando uma maior estabilidade na classificação dos Procellariiformes, o acordo levou em conta trabalhos, à época recentes, acerca da morfologia do grupo, como o abrangente estudo anátomo-morfológico de Kuroda (1954). Com vistas à taxonomia e à classificação dessas aves, esse autor utilizou-se de caracteres osteológicos, morfométricos e do *integumentum communis* para descrever minuciosamente algumas espécies conhecidas para cada um dos gêneros estudados. *Puffinus (sensu lato)* e *Calonectris*, na visão de Kuroda (1954), eram dois grupos distintos, sendo o primeiro subdividido em cinco subgêneros, *i.e.*, *Thyellodroma*, *Hemipuffinus*, *Ardenna*, *Neonectris* (estes quatro representantes do atual *Ardenna*), e *Puffinus* (que corresponde ao gênero atual de mesmo nome).

Além de Kuroda (1954), Wragg (1985) também analisou alguns aspectos osteológicos para propor uma classificação para o grupo, mas não realizou, por assim dizer, uma análise filogenética propriamente dita. Atualmente, todas as hipóteses de relacionamento filogenético disponíveis para *Puffinus (sensu lato)* e *Calonectris* são baseadas em estudos moleculares, a partir de uma mesma evidência molecular, *i.e.*, o gene citocromo *b* do DNA mitocondrial (e.g. Austin, 1996; Heidrich *et al.*, 1998; Penhallurick & Wink, 2004). Essas mesmas propostas levaram, em um segundo

momento, à uma nova divisão de *Puffinus (sensu lato)*, com o ressurgimento de *Ardenna* para incluir algumas espécies do sul dos Oceanos Atlântico e Pacífico (Remsen *et al.*, 2019; Gill & Donsker, 2019). Apesar de bastante similares entre si, as hipóteses moleculares ainda apresentam muitas divergências, tanto nas relações entre os três gêneros reconhecidos atualmente (*i.e.*, *Calonectris*, *Ardenna* e *Puffinus (sensu stricto)*), quanto nas relações interespecíficas, especialmente em relação aos membros de *Puffinus (sensu stricto)* (*e.g.* Heidrich *et al.*, 1998; Austin *et al.*, 2004; Penhallurick & Wink, 2004; Welch *et al.*, 2014).

As recentes filogenias baseadas nas técnicas moleculares são, de modo geral, congruentes com a classificação proposta por Kuroda (1954) (apesar do método de sistemática gradista utilizada por esse autor), mas apresentam algumas diferenças importantes. Apesar do estudo de Kuroda (1954), que, de forma detalhada e ricamente ilustrada, analisou diversos caracteres fenotípicos, não há uma proposta de relações filogenéticas para *Puffinus (sensu lato)* e *Calonectris* que seja baseada na evidência morfológica. Nesse sentido, o presente estudo tem como objetivo gerar uma nova hipótese das relações filogenéticas para *Puffinus (sensu lato)* e *Calonectris*, com base em caracteres osteológicos, a partir da revisão do material descritivo de Kuroda (1954), dos caracteres já existentes na literatura, e de análises de material osteológico pertencente aos gêneros estudados.

Esta análise inclui 22 táxons terminais, sendo o grupo de estudo composto por quatro espécies de *Calonectris* e 16 de *Puffinus (sensu lato)*. As espécies representantes do grupo externo foram *Daption capense* (Linnaeus, 1758) e *Fulmarus glacialisoides* (Smith, A, 1840), esta última servindo para enraizamento dos cladogramas. Um total de 104 caracteres osteológicos (*i.e.*, esqueleto craniano e pós-craniano) foram incluídos nas

análises, todos descritos seguindo a lógica de Sereno (2007). A matriz utilizada para a análise cladística está dividida em caracteres contínuos (*i.e.*, 23) e discretos (*i.e.*, 81).

Neste trabalho, empregaram-se análises de parcimônia com pesos iguais e com pesos (ou ajustes) implícitos, esta última segundo Goloboff (1993, 1995) e Goloboff *et al.* (2008a). Nesta segunda abordagem, o método procura por cladogramas que maximizem uma função de ajuste dos caracteres; havendo conflito entre caracteres, este é resolvido em favor dos caracteres menos homoplásticos, o que geralmente resulta em cladogramas mais bem resolvidos (Goloboff, 1993, 1995; Goloboff *et al.*, 2008a). Essa função de ajuste atinge seu valor máximo quando o caráter não apresenta passos extras (*i.e.*, não é homoplástico). A severidade do ajuste “contra” a homoplasia é dada por uma constante, K , e a utilização de diferentes valores de K pode produzir diferentes cladogramas (Goloboff, 1993; 1995). A escolha desses valores, visando à diminuição da subjetividade da mesma, foi realizada de acordo com o método proposto por Mirande (2009). A estratégia básica de buscas por cladogramas foi heurística, e todas as análises foram realizadas no programa TNT versão 1.5 (Goloboff & Catalano, 2016). A hipótese final deste trabalho é o consenso estrito dos cladogramas mais estáveis, gerados a partir da análise com pesos implícitos (Mirande, 2009). O grau de suporte dos clados não refutados foi estimado a partir das medidas de Suporte de Goodman-Bremer (Grant & Kluge, 2008), para a análise com pesos iguais, e de Suporte Relativo de Bremer (Goloboff & Farris, 2001), para a análise com pesos implícitos. O método de pesagem implícita é aqui aplicado, não apenas no sentido de buscar uma melhor resolução dos cladogramas, mas, principalmente, para enfatizar o sinal filogenético daqueles caracteres menos homoplásticos, que exibem maior congruência com outros caracteres e com o próprio cladograma (Goloboff, 1993; Mirande, 2009).

A análise com pesos iguais resultou em duas árvores mais parcimoniosas (número de passos = 228,583, CI = 0,788, RI = 0,242), mas o consenso estrito dessas árvores, apesar de muito similar aos resultados obtidos com a análise de pesos implícitos, carece de resolução para alguns dos clados menos inclusivos (Figura 1). A análise com pesos implícitos, por sua vez, produziu um único cladograma para cada um dos 21 valores de *K* utilizados. Os cladogramas obtidos com os valores de *K*9, *K*10 e *K*11 foram considerados os mais estáveis, e o consenso estrito entre esses cladogramas (número de passos = 229,005, CI = 0,461, RI = 0,804) é a hipótese final deste trabalho (Figura 2).

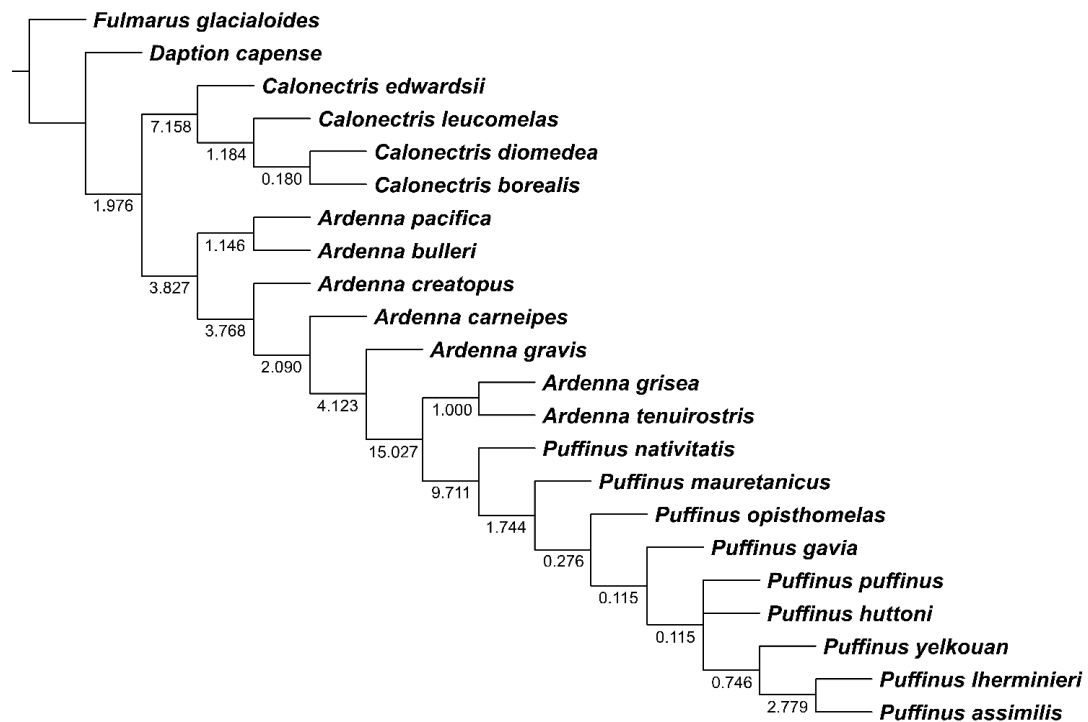


Figura 1. Consenso estrito entre as duas árvores mais parcimoniosas sob pesos iguais (número de passos = 228,583, CI = 0,788, RI = 0,242). Os números abaixo dos nós são os valores de Suporte de Goodman-Bremer.

As relações filogenéticas apresentadas neste trabalho são, de modo geral, bastante congruentes com as classificações baseadas na evidência osteológica (e.g. Kuroda, 1954; Wragg, 1985). De forma semelhante, as espécies incluídas na análise se dividem em dois clados bem suportados, representando os gêneros *Calonectris* e *Puffinus* (*sensu*

lato). As análises moleculares mais atuais, por outro lado, indicam a divisão de *Puffinus* (*sensu lato*) em *Ardenna* e *Puffinus* (*sensu stricto*), mas divergem em pontos essenciais para a classificação do grupo. *Calonectris*, aqui apresentado como grupo irmão de (*Puffinus* (*sensu lato*)) aparece, em algumas propostas, entre os dois gêneros atualmente reconhecidos, na posição de grupo irmão de *Puffinus* (*sensu stricto*). Nesse caso, *Ardenna* é indicado como grupo irmão de (*Calonectris* + *Puffinus* (*sensu stricto*)), o que tornaria *Puffinus* (*sensu lato*) um grupamento parafilético (e.g. Heidrich *et al.*, 1998; Penhallurick & Wink, 2004; Pyle *et al.*, 2011), hipótese não suportada pelos resultados aqui encontrados.

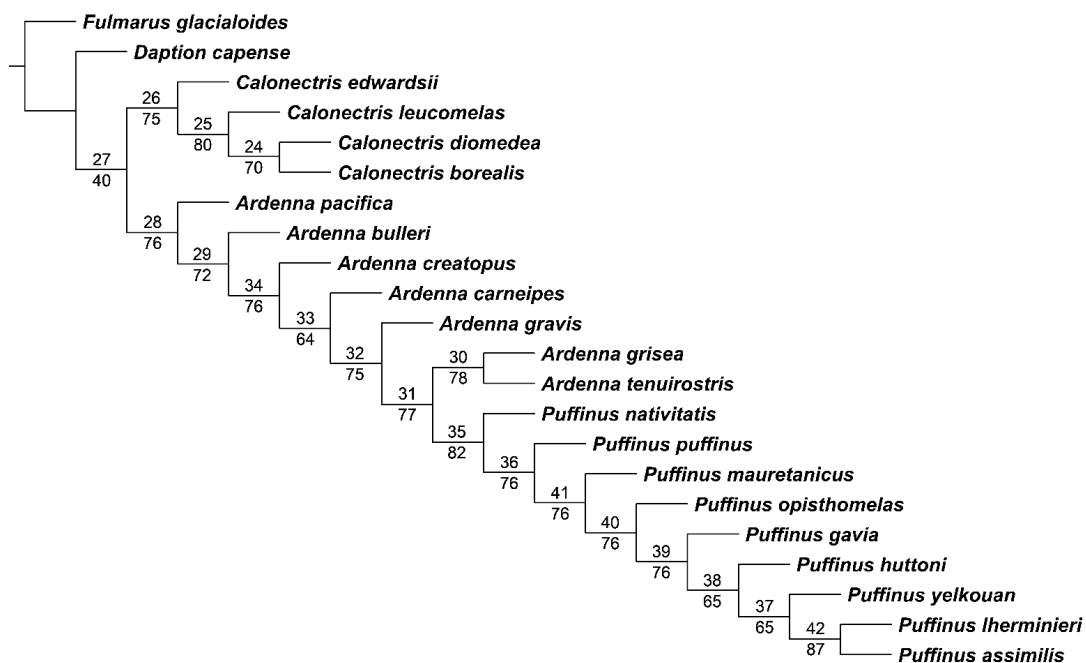


Figura 2. Consenso estrito entre as árvores mais estáveis sob pesos implícitos (a partir de K9, K10 e K11; número de passos = 229,005, CI = 0,461, RI = 0,804). O número de cada nó é mostrado acima do mesmo, e corresponde à numeração do TNT. Os números abaixo dos nós são os valores de Suporte Relativo de Bremer.

Para *Calonectris*, a análise encontrou a seguinte relação: (*C. edwardsii* (*C. leucomelas* (*C. diomedea* + *C. borealis*))). Este trabalho representa a primeira proposta de relações filogenéticas, baseada em caracteres osteológicos, a incluir as quatro

espécies atualmente reconhecidas para esse gênero. No que se refere a *Puffinus* (*sensu lato*), a hipótese final deste trabalho recuperou apenas dois dos cinco subgêneros propostos por Kuroda (1954), *i.e.*, *Neonectris* (*i.e.*, *A. grisea* + *A. tenuirostris*) e *Puffinus* (*i.e.*, *Puffinus* (*sensu stricto*)).

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**Phylogenetic relationships of shearwaters *Puffinus (sensu lato)* and *Calonectris*
(Aves: Procellariiformes) based on osteological characters**

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ABSTRACT. Shearwaters are among the most diverse groups of Procellariiformes, and the systematics of genera *Calonectris*, *Ardenna* and *Puffinus (sensu stricto)* is particularly complex. Here we present the first morphology-based phylogenetic hypothesis for the group, using 104 osteological characters (23 continuous and 81 discrete) scored for 20 extant species of shearwaters, representing 62.5% of species currently recognized. Both equal and implied weighting were used for phylogenetic analyses, and the final hypothesis presented herein is the strict consensus of the most stable trees produced by the latter. *Calonectris* was recovered as monophyletic (RBS = 75), with the topology (*C. edwardsii* (*C. leucomelas* (*C. diomedea* + *C. borealis*))). All other members of shearwaters were included in a single, monophyletic grouping: *Puffinus (sensu lato)* (RBS = 76), which reads (*Ardenna pacifica* (*A. bulleri* (*A. creatopus* (*A. carneipes* (*A. gravis* ((*A. grisea* + *A. tenuirostris*) (*Puffinus nativitatis* (*P. puffinus* (*P. mauretanicus* (*P. opisthomelas* (*P. gavia* (*P. huttoni* (*P. yelkouan* (*P. lherminieri* + *P. assimilis*)))))))))))). The monophyly of *Ardenna*, as suggested by all molecular-based hypotheses, was not recovered. The final hypothesis, of only two sister

genera for the shearwaters, is consistent with earlier classifications based on osteological evidence, and with some molecular analyses.

Additional Keywords: cladistics, comparative morphology, osteology, petrels, Procellariidae, seabirds, systematics.

INTRODUCTION

Shearwaters are small to medium-sized, pelagic seabirds and are among the most diverse groups of Procellariiformes, both morphologically and behaviourally (Warham, 1990; Onley & Scofield, 2007). They are included in Procellariidae, an assemblage that has become highly successful and specialized in the marine environment, but whose systematics is particularly complex and, therefore, frequently subject to revisions (Carboneras & Bonan, 2019). For shearwaters, three genera are recognized in most current treatments (*e.g.* Christidis & Boles, 2008; Gill & Donsker, 2019; Remsen *et al.* 2019): *Calonectris* Mathews & Iredale, 1915, containing four species; *Ardenna* Reichenbach, 1853, including seven species; and *Puffinus* Brisson, 1760, comprising all other 21 species of shearwaters (Gill & Donsker, 2019). Species included in *Calonectris*, the more aerial shearwaters, present a wide distribution in the Pacific and Atlantic Oceans, but breed mainly in the northern subtropical zone (Warham, 1990; Onley & Scofield, 2007). The larger species that breed in cold-water islands in the Southern Hemisphere, mainly in the Pacific, are included in *Ardenna*, whereas the smaller, efficient divers of the genus *Puffinus* are more widespread in tropical latitudes and breed in the Atlantic and Mediterranean (Warham, 1990; Onley & Scofield, 2007; Remsen *et al.*, 2019).

Although current evidence supports the hypothesis of a monophyletic shearwater assemblage (*e.g.* Penhallurick & Wink, 2004; Welch *et al.*, 2014), relationships among

species have always been a matter of debate. The genus *Puffinus* was erected by Brisson (1760, 1: 56; 6: 129–131) and the type species, by tautonomy, is *Procellaria puffinus* Brünnich, 1764 (*vide* Peters, 1931). By the first years of the 20th century, *Puffinus* remained the only widely accepted shearwater genus (*e.g.* Salvin, 1896; Coues, 1897; Godman, 1907–1910). In 1915, Mathews & Iredale proposed *Calonectris* for *Puffinus leucomelas* (Temminck, 1836) and *Puffinus kuhli* (Boie, 1836) (= *Calonectris diomedea* (Scopoli, 1769)), recognizing it along with *Puffinus* (for *P. puffinus*, *P. opisthomelas* Coues, 1864, *P. newelli* Henshaw, 1900, and *P. nativitatis* Streets, 1877) and six other genera: *Ardenna* (revived to include *P. gravis* (O'Reilly, 1818) and *P. creatopus* Coues, 1864); *Reinholdia* Mathews, 1912 (for *P. reinholdi* Mathews, 1912 (= *Puffinus gavia* (Forster, JR, 1844))); *Alphapuffinus* Mathews, 1914 (for *P. assimilis* Gould, 1838, *P. lherminieri* Lesson, R, 1839, and *P. persicus* Hume, 1872); *Hemipuffinus* Iredale, 1913 (for *P. carneipes* Gould, 1844); *Thyellodroma* Stejneger, 1888 (for *P. pacificus* (Gmelin, JF, 1789), *P. cuneatus* Salvin, 1888 (= *P. pacificus*) and *P. bulleri* Salvin, 1888); and *Neonectris* Mathews, 1913 (for *P. tenuirostris* (Temminck, 1836) and *P. griseus* (Gmelin, JF, 1789)). Nevertheless, their proposal received little attention and only a few authors accepted their classification, such as Oberholser (1917), who recognised the genera *Calonectris*, *Ardenna*, *Thyellodroma* and *Puffinus* for the North American species. Then, “when ‘splitting’ taxonomy was in vogue” (Alexander *et al.*, 1965: 402), Mathews (1934) adopted a new classification in his checklist of Procellariiformes, and divided the shearwaters among even more genera: ten, adding *Paranectris* Iredale, 1930 for *P. griseus*, and *Microzalias* Mathews & Iredale, 1915 for *P. nativitatis*. Most authors, however, continued to recognise only *Puffinus* as a valid genus, although some divided it into subgenera (*e.g.* Peters, 1931; Murphy, 1936). Mathews (1948) proposed another change to shearwaters systematics, lumping of all

species under the genus *Procellaria* Linnaeus, 1758. His proposal was followed, for example, by the British Ornithologist's Union committee (BOU, 1952) for its "Check-list of the Birds of Great Britain and Ireland".

The increasing confusion about the classification of not only the shearwaters, but the Procellariiformes generally, prompted Alexander *et al.* (1965) to put forward a new classification in an attempt to bring stability to the group. Fifteen authors came together and rejected the two extreme approaches, *i.e.*, the splitting and lumping of Mathews (1934, 1948), and their recommendations became the standard classification used by most subsequent authors (Christidis & Boles, 2008). For them, *Calonectris* presented enough structural differences to be recognised as a distinct genus from *Puffinus*, based in part on Kuroda (1954). Nonetheless, some authors continued to acknowledge genera from older classifications; *e.g.* Wolters (1975–1982), who also accepted *Thyellodroma* (for *P. pacificus* and *P. bulleri*) and *Ardenna* (for *P. gravis* and *P. carneipes*–*P. creatopus*).

Important contributions to the osteology of Procellariiformes were made during the 19th century (*e.g.* Forbes, 1882; Gadow, 1891; Pycraft, 1899). Detailed descriptions of eight shearwater species were given by Mayaud (1932, 1934), in the first major contribution to the comparative osteology of the shearwaters. Kuroda (1954), in an extremely detailed and richly illustrated study, examined morphological and ecological aspects of this group. Based on the osteological characters, which he stated were "very markedly demarcated by two extremely contrasted types with intermediate types between them" (Kuroda, 1954: 99), he divided the shearwaters in two main genera, *Calonectris* and *Puffinus*, the latter comprising several subgroups – a gradistic proposal that clearly indicated the habits of the species. The first extreme type, represented by *C. leucomelas* and *C. diomedea* (Scopoli, 1769), had a structurally lighter skeleton,

reflecting its highly gliding, non-aquatic life. The intermediate forms, adapted to both aerial and aquatic habits, were placed in *Puffinus*, which included subgroups ‘*Thyellodroma*’ (for *P. pacificus* and *P. bulleri*), ‘*Hemipuffinus*’ (for *P. carneipes* and *P. creatopus*), ‘*Ardenna*’ (for *P. gravis*), and ‘*Neonectris*’ (for *P. griseus*, *P. tenuirostris* and *P. nativitatis*) (currently, except for *P. nativitatis*, considered to be part of the genus *Ardenna*). All smaller shearwaters, with a heavier structure extremely adapted for aquatic life, were included in the other extreme, the *Puffinus* subgroup. Following Kuroda (1954), Wragg (1985) analysed osteological material and found a similar result – although with a conflicting placement of *P. nativitatis*, which appeared to him to be more closely related to members of the subgenus *Puffinus* than to *Neonectris* species. Despite saying that “comparative osteology was used to elucidate phylogenetic relationships within the shearwaters, and data was analysed from a cladistic point of view” (Wragg, 1985: 3), the author did not perform strict cladistic analysis; rather, he grouped species based on occurrence of the same character states.

Austin (1996) provided the first molecular study to specifically address phylogenetic relationships within *Puffinus*. Through examination of DNA sequences from a 307-bp fragment of the mitochondrial cytochrome *b* gene, he found two distinct monophyletic groups. The first consisted of all species from Kuroda’s ‘*Thyellodroma*’, ‘*Hemipuffinus*’, ‘*Ardenna*’ and ‘*Neonectris*’ subgroups – except for *P. nativitatis*, which, as found in Wragg (1985), was placed in the second clade, together with all other species from the ‘*Puffinus*’ subgroup. Likewise, Heidrich *et al.* (1998) assessed phylogenetic relationships in shearwaters from the Mediterranean and North Atlantic, based on the same gene. Results were similar, but *Calonectris*, not included in Austin (1996), was sister to the ‘*Puffinus*’ subgroup. This same relationship was presented by Nunn & Stanley (1998) in their analyses of complete cytochrome *b* gene.

Penhallurick & Wink (2004), based on further DNA analysis, proposed that the two clades first identified by Austin (1996) be afforded generic rank, subdividing *Puffinus* (*sensu lato*) into *Ardenna* and *Puffinus* (*sensu stricto*). They argued that the two lineages of *Puffinus* (*sensu lato*) were not sister taxa and differed substantially, therefore proposing that *Puffinus* (*sensu lato*) is a paraphyletic grouping and that all three shearwater clades should be considered separate genera. Austin *et al.* (2004) reached the same conclusion, but could not resolve the relationships among the three genera. More recent studies (*e.g.* Ramirez *et al.*, 2010; Pyle *et al.*, 2011; Welch *et al.*, 2014; Tennyson & Shepherd, 2017; Kawakami *et al.*, 2018) have found similar results, which is not surprising as all studies were based on the same molecular evidence, the cytochrome *b* gene; nonetheless, the studies differ in their reconstructions of both inter and intrageneric relationships.

Classification of birds has traditionally been based on morphological characters, but, in recent years, avian systematics has been characterized by a diminished reliance on morphological cladistics and an increased reliance on analyses based on DNA sequences; the genetic results have sometimes conflicted with traditional, pre-cladistic classifications (Livezey & Zusi, 2007). For shearwaters, the molecular hypotheses were congruent to those pre-cladistic classifications based on morphological evidence (*e.g.* Kuroda, 1954; Wragg, 1985) in several ways, although direct comparisons cannot be made as no morphology-based hypothesis of phylogenetic relationships is available so far. The idea of comparing hypotheses constructed with different kinds of evidence to test a particular relationship is, as discussed by Santos & Capellari (2009), rather similar to Hennig's (1968) principle of reciprocal illumination, wherein two sorts of data are complementary to each other and have the potential to enlighten one another. To this

end, we analysed osteological and morphometric characters and, here, present the first morphology-based cladistic analysis of the shearwaters.

MATERIAL AND METHODS

TAXON SAMPLING AND SURVEY

Cladistic analyses included 20 extant species of shearwaters, representing 62.5% of all species currently recognized (Gill & Donsker 2019). The ingroup is composed of *Calonectris leucomelas* (Temminck, 1836); *C. diomedea* (Scopoli, 1769); *C. borealis* (Cory, 1881); *C. edwardsii* (Oustalet, 1883); *Ardenna pacifica* (Gmelin, JF, 1789); *A. bulleri* (Salvin, 1888); *A. grisea* (Gmelin, JF, 1789); *A. tenuirostris* (Temminck, 1836); *A. creatopus* (Coues, 1864); *A. carneipes* (Gould, 1844); *A. gravis* (O'Reilly, 1818); *Puffinus nativitatis* Streets, 1877; *P. puffinus* (Brünnich, 1764); *P. yelkouan* (Acerbi, 1827); *P. mauretanicus* Lowe, 1921; *P. opisthomelas* Coues, 1864; *P. gavia* (Forster, JR, 1844); *P. huttoni* Mathews, 1912; *P. lherminieri* Lesson, R, 1839; *P. assimilis* Gould, 1838. This taxon sampling is similar to that of Wragg (1985), as well as to that in some molecular studies (*e.g.* Austin, 1996; Heidrich *et al.*, 1998; Penhallurick & Wink, 2004), with the addition of all species of *Calonectris*. Two fulmarine petrels, *Fulmarus glacialisoides* (Smith, A, 1840) and *Daption capense* (Linnaeus, 1758), were selected as outgroups, with the former being used to root the cladograms.

Skeletons of full-grown specimens were directly examined and observed by naked eye or under an 8X magnifying glass. The material examined (Appendix 1) is housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and in the Museu de Ciências Naturais, Universidade Federal do Rio Grande do Sul, Imbé, Brazil (MUCIN). Osteological comparisons were primarily based on the descriptions in Kuroda (1954), but other anatomical descriptions were added to produce

the list of characters used for the cladistic analyses. Most discrete characters were redefined from Livezey & Zusi (2006), whereas continuous characters were based on the measurements presented by Kuroda (1954) and Wragg (1985); nonetheless, the source of each character is indicated beside its character statement.

The use of a standardized nomenclature is essential not only for descriptive anatomy, but also for cladistic inference. Therefore, all anatomical terminology is in Latin and italicized, and, unless otherwise noted, is in accordance with *Nomina Anatomica Avium* (Baumel & Witmer, 1993).

All morphological characters were described and standardized following the logic of Sereno (2007), who defines ‘character’ as a feature expressed as an independent variable, and ‘states’ as its mutually exclusive conditions. When combined, both the character and its states form the ‘character statement’, which includes four logical components (*i.e.* locator, variable, variable qualifier, and character states), and can assume two specific patterns: neomorphic or transformational. Neomorphic characters are those composed only of locators, and its character states are simply ‘present’ or ‘absent’ (with optional inclusion of ‘near-absent’), whereas transformational characters also include a variable and its qualifier and, optionally, more than two character states. This character structure stands to reduce variability in morphology-based data for phylogenetic use (Sereno, 2007).

Continuous characters were treated as such, without discretization (Goloboff *et al.* 2006). To avoid giving excessive transformation costs for those characters showing higher range of values among species (*e.g.* *radius* length ranging from 54.2 to 130.71 mm), observed ranges were rescaled (or normalized) to 0–1 intervals.

CLADISTIC ANALYSIS

The taxon/character matrix was created in Mesquite, version 3.6 (Maddison & Maddison, 2018), and phylogenetic analyses using both equal and implied weighting were performed with Tree Analysis using New Technology (TNT), version 1.5 (Goloboff & Catalano, 2016). In the implied weighting method (IW), during the cladogram search process, each character is weighted relative to its fit to a cladogram under consideration, based on a constant of concavity K (Goloboff, 1993, 1995; Goloboff *et al.*, 2008). The value of K determines the ‘severity’ of differential weighing; lower values weight stronger against homoplastic characters, whereas higher values weight less drastically against it (Goloboff, 1993, 1995). Furthermore, under IW, the optimal trees are not necessarily the shortest ones, but those with the highest sum of implied weights or total fit. To reduce the subjectivity on selecting the values of K , Mirande (2009) proposed a method wherein the values of K are calculated based on the fit attributed to an ‘average’ character, with respect to the fit of a character without homoplasy, and on the average homoplasy per character. The 21 values of K used herein are those that resulted in an ‘average’ character fit of 50, 52, 54, 56, 58, 60, 62, 64, 66, 68, 70, 72, 74, 76, 78, 80, 82, 84, 86, 88, and 90% of the fit of a non-homoplastic character. The implied weighting method is herein applied not simply to improve resolution of cladograms, but to strengthen the phylogenetic signal of those characters exhibiting higher congruence with other characters and with the cladogram itself (Goloboff, 1993; Mirande, 2009).

Heuristic searches for the most parsimonious cladograms were carried out using New Technology Search with ratchet, tree-drifting, sectorial search, and tree-fusing with default settings. All discrete characters were treated as unordered. The distribution of

ambiguous character states was examined according to both ACCTRAN and DELTRAN optimizations.

Herein, similarly to Mirande (2009), the main criterion to select among the fittest cladogram(s) obtained for each value of K was their stability; the more stable trees would be those that share a higher number of nodes with the remaining ones. The measurement used to compare the cladograms was the Subtree-Prune-and-Regraft-Distance (SPR), which consists in the minimum number of ‘SPR moves’ necessary to convert one tree into another (Goloboff, 2008). In TNT, SPR distances were calculated with 1000 replications per comparison, and the fittest trees were combined into a strict consensus cladogram.

For the equal weighting analysis, the degree of support of the non-refuted clades (*sensu* Grant & Kluge, 2008) was estimated using the Goodman-Bremer Support (Grant & Kluge, 2008), which considers the number of extra steps needed to collapse a node (Bremer, 1994). In TNT, Goodman-Bremer Support was calculated from suboptimal cladograms with up to 20 additional steps, saving up to 10,000 cladograms at each stage.

For the analysis under implied weights, the support was calculated using the Relative Bremer Support (RBS; or Relative Fit Difference), which considers the evidence supportive of, or contradictory to, a given group. It varies from 0 to 100, with the extremes indicating a completely unsupported and a completely uncontradicted group, respectively (Goloboff & Farris, 2001). The RBS was calculated in TNT from approximately 34,000 suboptimal cladograms, with suboptimal values varying from 0.001 up to 0.6 units of fit.

RESULTS

DESCRIPTION OF CHARACTERS AND THE CHARACTER MATRIX

This study included 104 osteological characters, from both cranium and postcranium, coded for 22 terminal taxa, 20 ingroup and two outgroup species. The first 23 characters are continuous (Figure 1) and the other 81 are discrete; all characters are described below, some of which with additional explanatory notes. Number of steps for each character and values for both consistency and retention indices are presented in parentheses. Multistate characters are treated as unordered. The resulting matrices used in the cladistic analysis, separated into continuous and discrete characters, are provided in Appendix 2 and 3, respectively.

Continuous characters

0. *Cranium*, total length, from *apex rostri* to *regio occipitalis*: 59.35 (0); 113.88 (1). (1.755 steps, CI = 0.409, RI = 0.603). See Wragg (1985: 86, fig. 31).
1. *Sternum*, total length, from *spina externa rostri* to *trabercula mediana*: 38.58 (0); 70.26 (1). (1.552 steps, CI = 0.485, RI = 0.511). See Kuroda (1954: 80).
2. *Sternum*, width between both sides of *processus costalis*: 22.14 (0); 53.51 (1). (1.651 steps, CI = 0.422, RI = 0.664). See Kuroda (1954: 80).
3. *Sternum*, *carina sterni*, length from *apex carinae* to *trabercula mediana*: 42.83 (0); 73.56 (1). (1.730 steps, CI = 0.506, RI = 0.634). See Kuroda (1954: 80).
4. *Clavicula* [*furcula*], distance between both *processus acromialis*: 16.64 (0); 40.12 (1). (1.323 steps, CI = 0.488, RI = 0.604). See Kuroda (1954: 82).

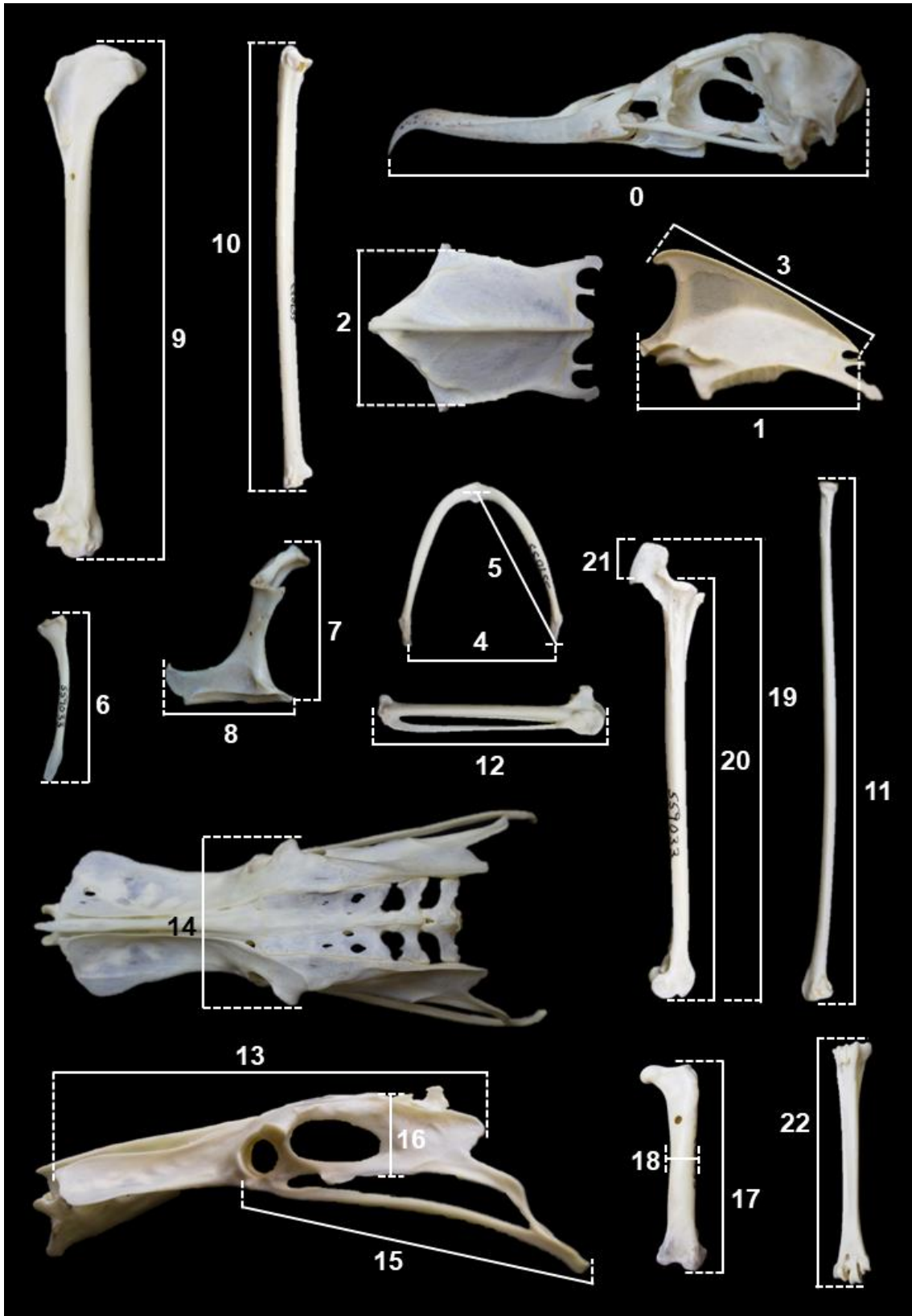


Figure 1. Measurements of both *cranium* and *postcranium* used for the analyses of the 23 continuous characters. *Calonectris leucomelas* (USNM 559033). Not to scale.

5. *Clavicula [furcula]*, length from *processus acromialis* to *extremitas omalis*: 28.54 (0); 54.42 (1). (1.624 steps, CI = 0.416, RI = 0.494). See Kuroda (1954: 82).
6. *Scapula*, total length: 28.66 (0); 57.95 (1). (1.567 steps, CI = 0.376, RI = 0.368). See Kuroda (1954: 84).
7. *Coracoideum*, length from *extremitas omalis* to *angulus medialis*: 22.44 (0); 39.48 (1). (2.212 steps, CI = 0.353, RI = 0.389). See Kuroda (1954: 83).
8. *Coracoideum*, width of root, from *processus lateralis* to *angulus medialis*: 15.05 (0); 34.84 (1). (1.495 steps, CI = 0.468, RI = 0.706). See Kuroda (1954: 83).
9. *Humerus*, total length: 63.04 (0); 156.66 (1). (1.621 steps, CI = 0.513, RI = 0.799). See Kuroda (1954: 85).
10. *Ulna*, total length: 56.3 (0); 158.04 (1). (1.581 steps, CI = 0.563, RI = 0.832). See Kuroda (1954: 86).
11. *Radius*, total length: 54.2 (0); 154.32 (1). (1.584 steps, CI = 0.564, RI = 0.836). See Kuroda (1954: 86).
12. *Carpometacarpus*, total length: 34.04 (0); 72.8 (1). (1.841 steps, CI = 0.447, RI = 0.698). See Kuroda (1954: 86).
13. *Pelvis et os coxae*, length from the anterior tip of *ala preacetabularis illi* to *spina dorsolateralis ilii*: 41.8 (0); 79.6 (1). (1.627 steps, CI = 0.462, RI = 0.525). See Kuroda (1954: 89).
14. *Pelvis et os coxae*, width between both tips of *antitrochanter*: 12.39 (0); 28.25 (1). (1.307 steps, CI = 0.662, RI = 0.834). See Kuroda (1954: 89).
15. *Pelvis et os coxae, pubis*, length from *tuberculum preacetabulare* to *apex pubis*: 30.66 (0); 64 (1). (1.848 steps, CI = 0.458, RI = 0.509). See Kuroda (1954: 89).
16. *Pelvis et os coxae*, height at *foramen ilioschiadicum*: 6.22 (0); 16.35 (1). (0.899 steps, CI = 0.725, RI = 0.910). See Kuroda (1954: 89).

17. *Femur*, total length: 23.21 (0); 53.13 (1). (1.321 steps, CI = 0.581, RI = 0.781).
See Kuroda (1954: 92).
18. *Femur*, width shaft: 2.3 (0); 4.98 (1). (1.501 steps, CI = 0.526, RI = 0.650). See Kuroda (1954: 92).
19. *Tibiotarsus*, total length: 60.4 (0); 119.75 (1). (1.929 steps, CI = 0.405, RI = 0.519). See Kuroda (1954: 92).
20. *Tibiotarsus*, length without *crista cnemialis*, from *area interarticularis* to *extremitas distalis*: 50.33 (0); 103.85 (1). (1.918 steps, CI = 0.431, RI = 0.625).
See Wragg (1985: 86, fig. 31).
21. *Tibiotarsus*, length of *crista cnemialis* (difference between char. 20 and 21): 6.63 (0); 19.86 (1). (1.215 steps, CI = 0.594, RI = 0.814). See Wragg (1985: 86, fig. 31).
22. *Tarsometatarsus*, total length: 37.12 (0); 68.88 (1). (1.904 steps, CI = 0.405, RI = 0.562). See Kuroda (1954: 93).

Discrete characters

23. *Cranium, regiones squamosalis et parietalis, fossa musculorum temporalium* (*sensu* Zusi & Livezey, 2000), dorsal extension: up to (0), or towards (1), *planum medialis cranii*. (6 steps, CI = 0.167, RI = 0.375). Figure 2.

Note: In state 0, left and right fossae meet each other dorsally in *planum medialis*, thereby forming a narrow *crista nuchalis*, whereas in state 1, they are separated from each other by a wide crest or ridge. See Kuroda (1954: 75) and Livezey & Zusi (2006: 30, char. 16).
24. *Cranium, occiput (regio occipitalis calvarii), condylus occipitalis*, position (lateral perspective): rostral to (0), or approximately aligned with (1), *processus*

paraoccipitalis ossis exoccipitalis. (1 step, CI = 1, RI = 1). Figure 3.

See Kuroda (1954: 75, plate 10) and Livezey & Zusi (2006: 31, char. 24).

25. *Cranium, os parasphenoidale, ala parasphenoidalis*, conformation: irregularly ossified, partly open *tuba* (0); laterally flared and wing-like, resulting in a small ventral aperture, almost completely ossified *tuba* (1). (3 steps, CI = 0.333, RI = 0.750). Figure 4.

See Livezey & Zusi (2006: 44, char. 124) and Cracraft (1985: 837, char. 14).

26. *Cranium, regio squamosalis, margo ventralis squamosi et processus squamosalis* (lateral perspective), dorsoventral depth: short, not covering (0), or deep, obscuring (1), *apex processus oticus quadrati*. (3 steps, CI = 0.333, RI = 0.500).

Modified from Livezey & Zusi (2006: 48, char. 145).

27. *Cranium, rostrum maxillae, facies ventralis rostri, fenestra ventrolateralis* (*sensu* Livezey & Zusi, 2006), conformation: visible (0), or obscured by (1), *margo caudalis ossis maxillaris*. (4 steps, CI = 0.250, RI = 0.667).

See Livezey & Zusi (2006: 68, char. 290).

28. *Cranium, os maxillare, facies ventralis, processus palatus maxillaris, ala caudalis* (*sensu* Livezey & Zusi, 2006), length: extends up to (0), or caudally to (1), *pons maxillarojugalis*. (3 steps, CI = 0.333, RI = 0.600).

Note: in state '0', *ala caudalis processus palatus maxillaris* is hidden when viewed from a ventral perspective, whereas in state '1' it is well visible. See Livezey & Zusi (2006: 85, char. 420).

29. *Cranium, cavum nasi, apertura nasi (nasalis) ossea* (dorsal perspective), width: narrow, opening mostly dorsal (0); wide, largely open (1). (1 step, CI = 1, RI = 1).

Note: state '0' represents smaller *apertura*, whereas state '1' comprises those species with much larger *apertura* that occupies a wider area. See Livezey & Zusi

(2006: 75, char. 334) and Smith (2010: appendix S2, char. 8).

30. *Cranium, cavum nasi, pila supranasalis* (lateral perspective), shape: essentially

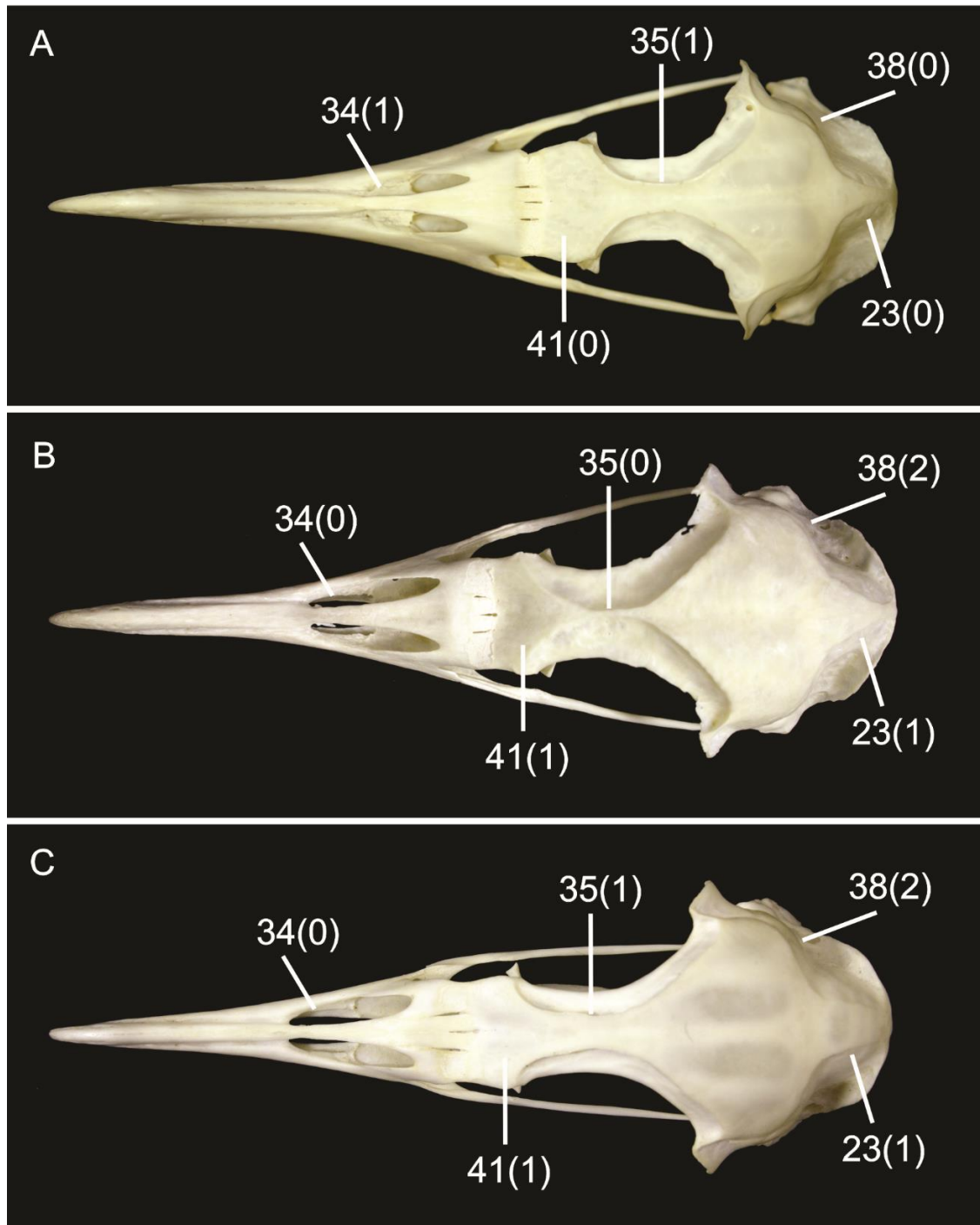


Figure 2. Dorsal view of the *cranium* of *Calonectris borealis* (A; MUCIN 393), *Ardenna grisea* (B; MUCIN 627) and *Puffinus puffinus* (C; MUCIN 745) illustrating characters 23, 34, 35, 38 and 41. Not to scale.

straight (0); convex (1) (1 step, CI = 1, RI = 1). Figure 3.

Note: *Pars rostralis pila supranasalis* is distinctly convex, in outline, in most examined species, whereas it is essentially straight (or comparably curved with *rostrum maxillae*) in some *Puffinus*. See Livezey & Zusi (2006: 76, char. 347).

31. *Cranium, os palatinum, pars choanalis, lamella dorsalis, facies dorsolateralis, recessus pneumaticus*, status: absent (0); present (1) (3 steps, CI = 0.333, RI = 0.800).

Note: The term refers to a depression on *facies dorsalis partis choanalis palatini* containing *foramina pneumatica*. See Livezey & Zusi (2006: 87, char. 434).

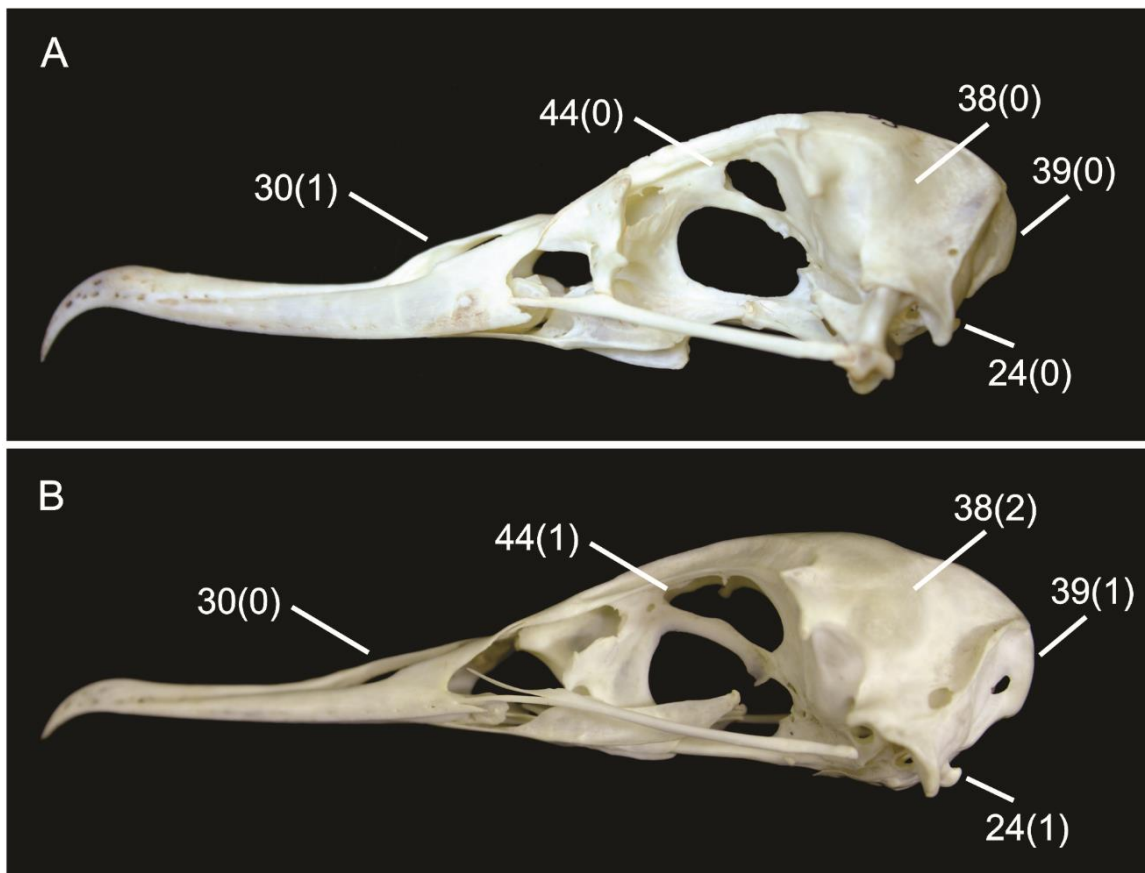


Figure 3. Lateral view of the left side of the *cranium* of *Calonectris leucomelas* (A; USNM 559033) and *Puffinus puffinus* (B; MUCIN 745) illustrating characters 24, 30, 38, 39 and 44. Not to scale.

32. *Cranium, os palatinum, pars lateralis, angulus caudolateralis*, shape: corner (0); rounded (1) (1 step, CI = 1, RI = 1). Figure 4.

Note: *Pars lateralis palatini* is caudolaterally enlarged in *Puffinus*, so that *processus pterygoideus palatini* seems reduced; therefore, they were all assigned to state '1'. See Livezey & Zusi (2006: 88, char. 454) and Mayr & Clarke (2003: 537, char. 16).

33. *Cranium, os quadratum, basis processus orbitalis, facies (ventro) medialis, foramen pneumaticum*, status: absent (0); present (1). (3 steps, CI = 0.333, RI = 0.800).

See Livezey & Zusi (2006: 96, char. 508) and Smith (2010: appendix S2, char. 31).

34. *Cranium, cavum nasi, apertura nasi (nasalis) ossea*, 'anterior lateral plates' (*sensu* Kuroda, 1954), status: absent (0); present (1). (3 steps, CI = 0.333, RI = 0.600). Figure 2 and 4.

Note: The term refers to a thin osseous *lamina* that horizontally closes *pars distalis aperturae nasalis ossea*. Present in *Calonectris* and in *Puffinus nativitatis* and *P. huttoni*. See Kuroda (1954: 75; plate 11).

35. *Cranium, os frontale, facies dorsalis, fossae glandulae nasalis*, conformation: juxtaposed to (0), narrowly separated from (1), or well separated from (2), each other. (3 steps, CI = 0.667, RI = 0.500). Figure 2.

Note: The state '0' refers to a condition wherein left and right fossae meet in *planum medialis*. In the state '1', the fossae are narrowly separated by a space about the width of *pila supranasalis*; in the state '2', fossae are well-separated from one another by a distance between *aperturae nasalis ossea*. See Kuroda (1954: 75) and Siegel-Causey (1988: 900, char. 14).

36. *Cranium, regio supraoccipitalis, crista nuchalis transversa* (caudal perspective), shape: semicircular (0); trapezoidal (1). (4 steps, CI = 0.250, RI = 0.625). New character.
37. *Cranium, os maxillare, facies ventralis, processus palatus*, length: extending up to (0), or slightly caudal to (1), to *pons maxillaro-jugalis* (5 steps, CI = 0.200, RI = 0.600). Figure 4. New character.

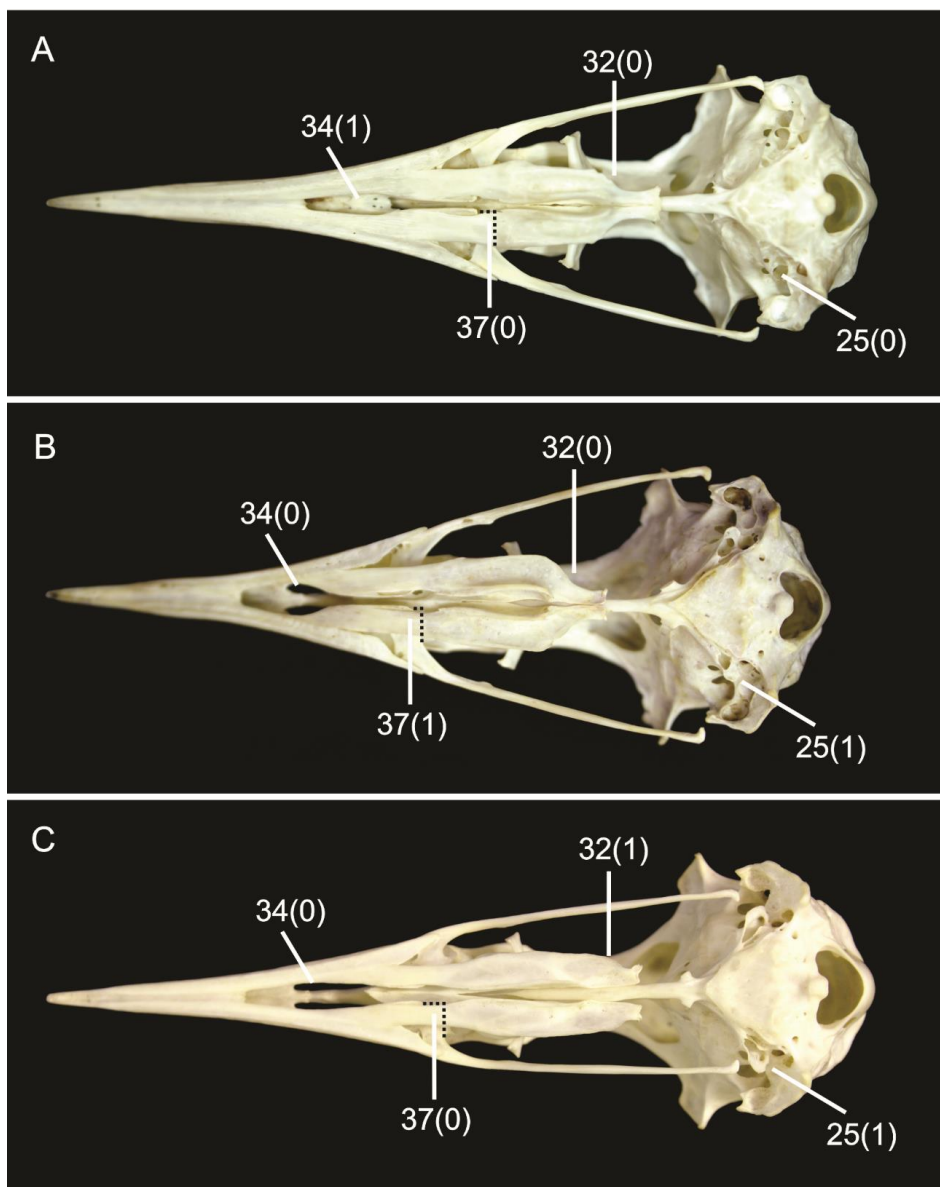


Figure 4. Ventral view of the *cranium* of *Calonectris borealis* (A; MUCIN 393), *Ardenna carneipes* (B; USNM 621658) and *Puffinus puffinus* (C; MUCIN 745) illustrating characters 25, 32, 34 and 37. Not to scale.

38. *Cranium, regio temporalis, fossa temporalis, pars rostralis*, shape: not swollen (0); rounded (1); swollen, *i.e.*, “ballon-like” (2). (2 steps, CI = 1, RI = 1). Figure 2 and 3.

See Kuroda (1954: 75), referring to “post-lateral” swelling of *os frontale*.

39. *Cranium, calvaria, prominentia cerebellaris*, shape: smoothly rounded (0); inflated and protruded (1). (2 steps, CI = 0.500, RI = 0.889). Figure 3 and 5.

See Kuroda (1954: 75) and Livezey & Zusi (2006: 32, char. 31).

40. *Cranium, calvaria, crista nuchalis transversa* (lateral perspective), height: low (0); prominent (1). (3 steps, CI = 0.333, RI = 0.800).

Note: In state 0, a low *crista nuchalis transversa* demarcates a shallow *fossa musculorum temporalium*, whereas in state 1, a marked, prominent *crista* borders *fossa m. temporalium*. See Kuroda (1954: 75), referring to prominence of “squamoso-parietal wings”.

41. *Cranium, regio frontalis, facies dorsalis, area interlacrimalis*, superficial shape: essentially planar (0); concave (1). (2 steps, CI = 0.500, RI = 0.833). Figure 2.

See Kuroda (1954: 75) and Bourdon *et al.* (2005: 169, char. 10).

42. *Cranium, regio frontalis, facies dorsalis, area interlacrimalis*, width: wide (0); narrow, *fossae glandulae nasalis* occupying most of the space (1). (2 steps, CI = 0.500, RI = 0.500).

Note: in some species, *fossae glandulae nasalis* expand anteriorly leaving a restricted, triangular shaped, *regio frontalis*. See Kuroda (1954: 75).

43. *Cranium, regio frontoparietalis* (caudal perspective), shape: planar (0); convex or rounded (1). (2 steps, CI = 0.500, RI = 0.875). Figure 5.

Note: state ‘0’ refers to a quite smooth, low roof of *cranium*, whereas state ‘1’ represents a globe-shaped roof. See Kuroda (1954: 75).

44. *Cranium, orbita, pars caudalis orbitae, fonticulus orbitocranialis*, size/shape: small, rather round (0); large, elongated and irregularly ossified anteriorly (1). (4 steps, CI = 0.250, RI = 0.500). Figure 4.

See Kuroda (1954: 75) and Olson (2008: 403; fig. 1).

45. *Cranium, os lacrimale, caput et facies articularis frontonasalis*, length: similar to (0), or longer than (1), *processus descendens*. (3 steps, CI = 0.333, RI = 0.800).

See Kuroda (1954: 75) and Livezey & Zusi (2006: 56, char. 204).

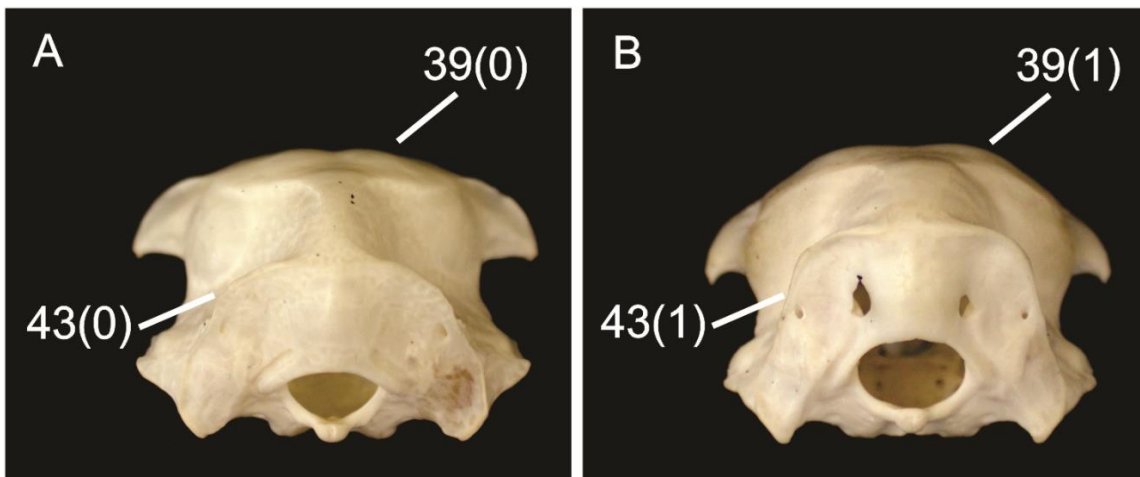


Figure 5. Posterior view of the *cranium* of *Calonectris borealis* (A; MUCIN 393) and *Puffinus puffinus* (B; MUCIN 745) illustrating characters 39 and 43. Not to scale.

46. *Cranium, os lacrimale et frontale, junctura (naso-) frontolacrimalis*, type: synarthrosis (0); syndesmosis (1). (1 step, CI = 1, RI = 1).

Note: Synarthrosis, or immovable joint, refers to both *sutura et synostosis*. See Livezey & Zusi (2006: 102, char. 564) and Mayr & Smith (2012: 872, char. 9).

47. *Cranium, os lacrimale*, general shape: bulky, thick (0); delicate, rather slender (1). (1 step, CI = 1, RI = 1).

See Kuroda (1954: 75).

48. *Cranium, mandibula, ramus mandibulae, pars intermedia, facies lateralis, fossa lateralis mandibulae*, depth: shallow, rather limited (0); deep, more extensive (1). (4 steps, CI = 0.250, RI = 0.625). Figure 6.

See Olson (2008: page 403; fig. 1), referring to “*depressio m. adductor mandibulae*”.



Figure 6. Lateral view of the left side of *ramus mandibulae* of *Calonectris borealis* (A; MUCIN 393), *Ardenna pacifica* (B; USNM 498256) and *Puffinus puffinus* (C; MUCIN 745) illustrating characters 48, 49 and 50. Not to scale.

49. *Cranium, mandibula, ramus mandibulae, pars caudalis, processus pseudocoronoideu(ei)* (*sensu* Donatelli, 1996), number: one (0); two (1). (2 steps, CI = 0.500, RI = 0.875). Figure 6. New character.

Note: Synonymy of *processus coronoideus* and *proc. m. adductoris mandibulae*.

As stated by Baumel & Witmer (1993: 73, annot. 44), “any process of *pars caudalis mandibulae* to which is attached the strong “aponeurosis” of *m. adductor mandibulae externus, pars rostralis*”.

50. *Cranium, mandibula, ramus mandibulae, pars intermedia* (lateral perspective), shape: straight (0); distinctly curved (1). (4 steps, CI = 0.250, RI = 0.625). Figure 6.

Note: curvature does not refer to that resulting from *angulus ventralis mandibulae*. State “0” refers to a condition wherein both *margo ventralis et dorsalis* are virtually straight, ascending linearly from *apex* to *angulus mandibulae*. See Livezey & Zusi (2006: 116, char. 673).

51. *Sternum, corpus sterni, facies muscularis sterni, linea intermuscularis*, vertex of “V”-shaped *linea*, position: anteriorly to (0), or at (1) *apex processus costalis*. (1). (3 steps, CI = 0.333, RI = 0.714). Figure 7.

See Livezey & Zusi (2006: 181, char. 1106; 192, char. 1203).

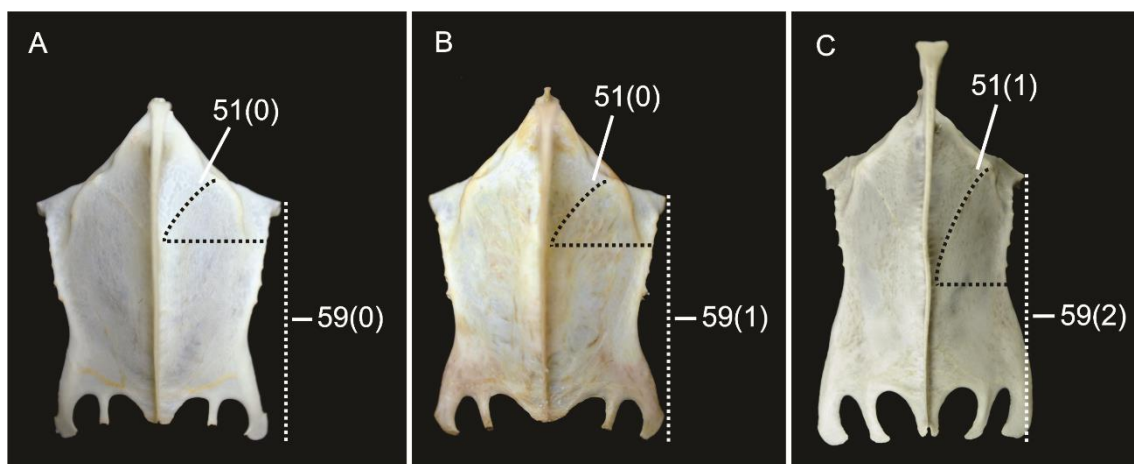


Figure 7. Ventral view of the *sternum* of *Calonectris leucomelas* (A; USNM 559033), *Ardena pacifica* (B; USNM 498256) and *Puffinus puffinus* (B; MUCIN 745) illustrating characters 51 and 59. Not to scale.

52. *Sternum, corpus sterni, facies visceralis sterni, sulcus medianus*, immediately caudal to *margo cranialis sterni, foramen pneumaticum*, status: absent (0); present (1). (5 steps, CI = 0.200, RI = 0.333). Figure 8.

Note: state “1” stands for any form of *foramen pneumaticum*, from a small aperture to deep *depression et foramen*. See Kuroda (1954: 80; plate 24) and Livezey & Zusi (2006: 181, char. 1108).

53. *Sternum, corpus sterni, facies visceralis sterni, pori pneumatici*, status: absent (0); present (1). (2 steps, CI = 0.500, RI = 0.750). Figure 8.

Note: *pori pneumatici* does not include the *foramen pneumaticum* assessed in char. 52. See Kuroda (1954: 80; plate 24) and Livezey & Zusi (2006: 182, char. 1110/1113).

54. *Sternum, corpus sterni, margo cranialis sterni, invaginatio* between *rostrum sterni et processus craniolateralis*, status: absent (0); present (1). (6 steps, CI = 0.167, RI = 0.167).

Note: *margo cranialis* is monotonically curved for all species, but in some of them, there is an invagination near *processus craniolateralis*. See Livezey & Zusi (2006: 185, char. 1144).

55. *Sternum, corpus sterni, margo cranialis sterni* (dorsal perspective), shape: triangular (0); parabolic (1). (1 step, CI = 1, RI = 1). Figure 8. New character.

Note: state “1” refers to a continuous curved *margo cranialis*, resembling a semicircle, whereas state “0” represents a somehow angled *margo*, especially near *rostrum sterni*.

56. *Sternum, corpus sterni, rostrum sterni, spina externa rostri* (lateral perspective), shape: elongate *tuberculum* (0); “fan-like” (1). (2 steps, CI = 0.500, RI = 0.833). Figure 9.

Note: “fan-like” (*sensu* Kuroda, 1954) is the shape of a dorsoventrally enlarged *spina externa*, common for most of species except *Calonectris*. See Kuroda (1954: 79; plate 22) and Livezey & Zusi (2006: 186, char. 1157).

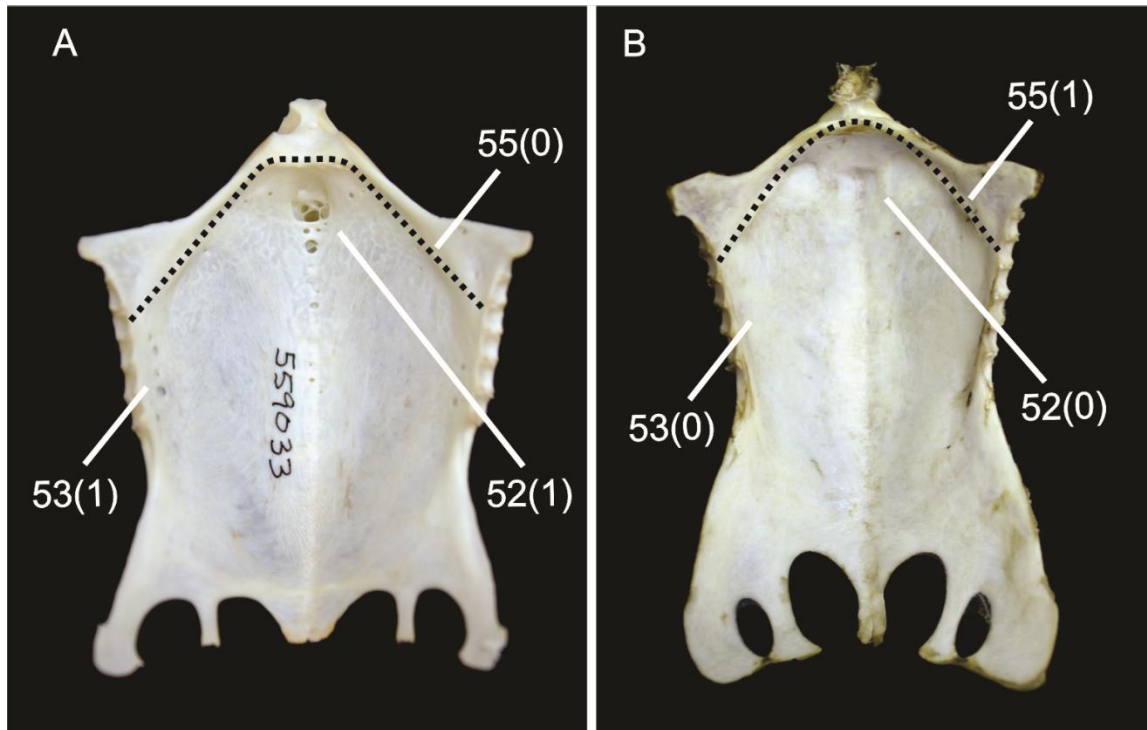


Figure 8. Dorsal view of the *sternum* of *Calonectris leucomelas* (A; USNM 559033) and *Puffinus yelkouan* (B; USNM 289433) illustrating characters 52, 53 and 55. Not to scale.

57. *Sternum, corpus sterni, rostrum sterni, spina externa rostri* (cranial perspective), dorsal extension: does not cover (0), or covers (1), *sulcus sellaris medialis*. (1 step, CI = 1, RI = 1). Figure 10.

Note: some *spina externa*, in lateral view, appear to be “higher” than others, as observed by Kuroda (1954). In this character, state “0” represents the high *spina externa*, whereas those species having stated as “1” exhibit lower *spina externa* which, from cranial perspective, covers *sulcus sellaris medialis*. See Kuroda (1954: 79)

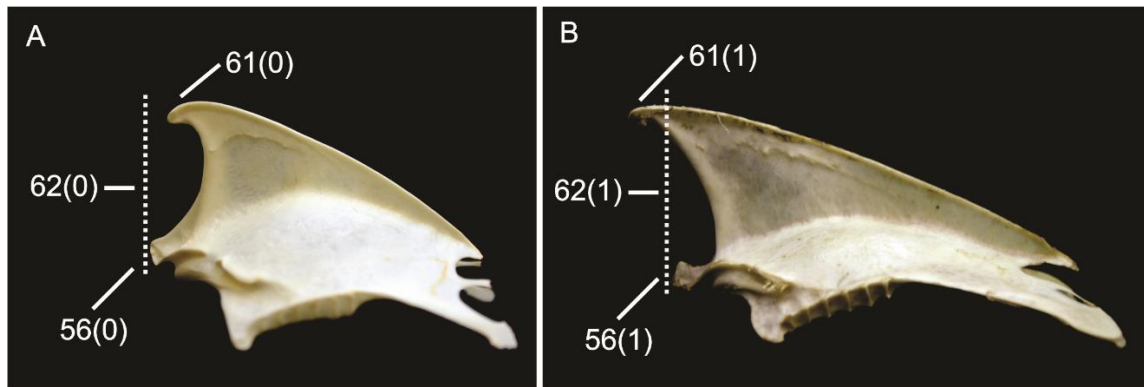


Figure 9. Lateral view of the right side of *sternum* of *Calonectris leucomelas* (A; USNM 559033) and *Puffinus yelkouan* (B; USNM 289433) illustrating characters 56, 61 and 62. Not to scale.

58. *Sternum, margo caudalis sterni, incisurae lateralis et medialis*, depth: shallow (0); deep (1). (1 step, CI = 1, RI = 1).

Note: the *sternum* is always four-notched for all species, but in some of them, the cranial extent of these notches varies. In state “0”, both *incisurae lateralis et medialis* have the same moderate cranial extension, whereas in state “1” they are also extended cranial, but *incisura medialis* is normally deeper than *incisura lateralis*. See Kuroda (1954: 79; plate 20) and Livezey & Zusi (2006: 189, char. 1183; 190, char. 1188).

59. *Sternum, margo caudalis sterni, trabecula lateralis, apex trabeculae*: position: medial (0) coplanar (1), or lateral (2), to *processus craniolateralis sterni*. (6 steps, CI = 0.333, RI = 0,636). Figure 7.

Note: as observed by Kuroda (1954), some species have long and spread “lateral posterior process”, giving the *sternum* an X-shape. *Trabecula lateralis* ends either internally, externally or in the same line when compared to the tip of *processus craniolateralis*. See Kuroda (1954: 79; plate 20).

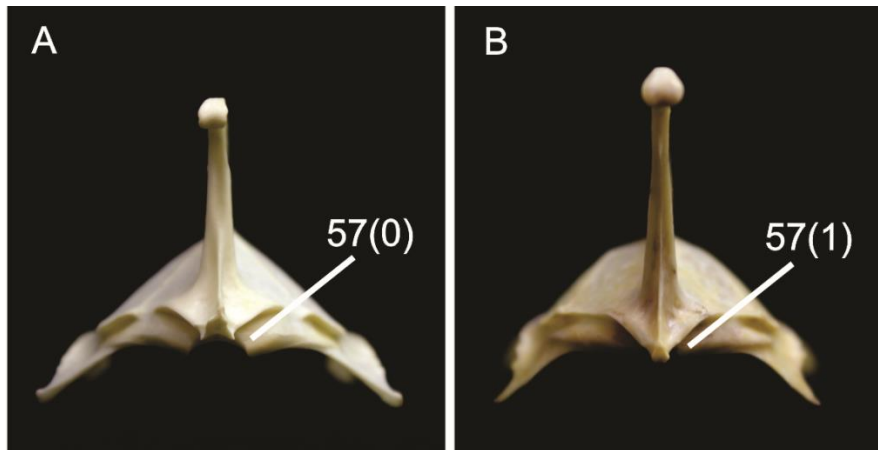


Figure 10. Cranial view of the *sternum* of *Calonectris leucomelas* (A; USNM 559033) and *Puffinus nativitatis* (B; USNM 613922) illustrating character 57. Not to scale.

60. *Sternum, margo caudalis sterni, trabercula mediana, margo aut terminus caudalis*, shape: broad, linear (0); tapered (1). (1 step, CI = 1, RI = 1).

See Livezey & Zusi (2006: 190, char. 1191).

61. *Sternum, carina sterni, apex carinae* (lateral perspective), shape: dorsocranially curved, hook-like (0); rather straight (1). (2 steps, CI = 0.500, RI = 0,889). Figure 9.

See Kuroda (1954: 79) and Livezey & Zusi (2006: 191, char. 1197).

62. *Sternum, carina sterni, apex carinae* (lateral perspective), craniocaudal position: caudal (0), or cranial (1), to *spina externa marginis cranialis sterni*. (1 step, CI = 1, RI = 1). Figure 9.

Note: a marked character for all *Puffinus* species, as discussed by Kuroda (1954), is that *apex carinae sterni* always “protrude forward beyond the vertical line drawn from the tip of *spina externa*”. See Kuroda (1954: 79; plate 22) and Livezey & Zusi (2006: 192, char. 1198).

63. *Clavicula (furcula), extremitas sternalis claviculae, scapus claviculae* (lateral perspective), curvature: moderate, constant (0); pronounced, approaching subcircular shape (1). (4 steps, CI = 0.250, RI = 0,667). Figure 11.

Note: As observed by Kuroda (1954), “the curved clavicles reflect the adaptation for aquatic life and consequently the fluttering flight, augmenting the amount of pectoral muscles”. See Kuroda (1954: 81; plate 26) and Livezey & Zusi (2006: 196, char. 1233; 197, char. 1237).



Figure 11. Lateral view of the left side of the *clavícula (furcula)* of *Calonectris borealis* (A; MUCIN 393) and *Puffinus puffinus* (B; MUCIN 745) illustrating character 63. Not to scale.

64. *Coracoideum, extremitas omalis coracoidei, processus acrocoracoideus, facies articularis clavicularis*, elongation: absent (0); present (1). (1 step, CI = 1, RI = 1). Figure 12.

Note: as described by Kuroda (1954), “the head of coracoid forms a little elongation to articulate with the clavicle”. He observed that species with the most curved clavicles, like *Ardenna grisea* and *A. tenuirostris*, are the ones with the longest *facies articularis clavicularis*. See Kuroda (1954: 82; plate 26).

65. *Coracoideum, extremitas omalis coracoidei, processus procoracoideus, apex processus*, orientation: extends primarily medially (0); extends significantly cranially (1). (4 steps, CI = 0.250, RI = 0).

Note: the orientation of *apex* is evaluated based on the anatomical position of *coracoideum*. See Smith (2010: appendix S2, char. 174).

66. *Coracoideum, extremitas omalis coracoidei, processus procoracoideus,*

size/shape: short, not very protruded (0); long, rather sharp *apex* (1). (1 step, CI = 1, RI = 1). Figure 12.

Note: Kuroda (1954) mentions that “the praecoracoidal process which articulates with the head of the scapula is also less developed in *leucomelas* and *pacificus* in comparison with that of *griseus* and *tenuirostris* [...]”. See Livezey & Zusi (2006: 205, char. 1283) and Smith (2010: appendix S2, char. 173).

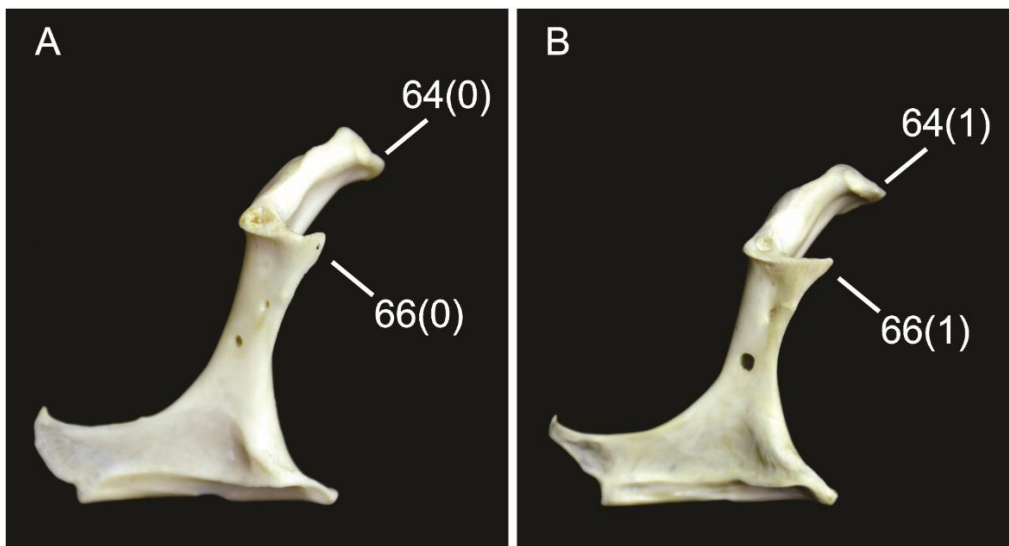


Figure 12. Dorsomedial view of the left *coracoideum* of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna tenuirostris* (B; USNM 556482) illustrating characters 64 and 66. Not to scale.

67. *Coracoideum, extremitas omalis coracoidei, processus procoracoideus, apex processus* (dorsocranial perspective), shape: straight, rather flat (0); curved inwards (0). (1 step, CI = 1, RI = 1). New character.

Note: the *apex processus procoracoideus* was found to be rather straight for *Puffinus yelkouan*, whereas for all other species it is ventrally curved.

68. *Humerus, extremitas proximalis humeri* (cranial perspective), *crista deltopectoralis*, shape: straight *margo* (0); quite curved, enlarged *margo* (1). (1 step, CI = 1, RI = 1). New character.

Note: *Puffinus* species show a small enlargement at *impressio m. pectoralis*, between *angulus et basis cristae deltopectoralis*.

69. *Humerus, corpus humeri (planum transversus)*, shape: elliptical, not compressed (0); subelliptical, cranial surface rather flat (1); compressed, flattened craniocaudally (2). (2 steps, CI = 1, RI = 1). Figure 13.

Note: as Kuroda (1954) observed, some species have “long, slender and round in transverse section” *humerus*, which is specialized for gliding flight, whereas those adapted to underwater life have the *humerus* “short, thick and flattened”. Species presenting an intermediate character are included in state “1”. See Kuroda (1954: 84; plate 28) and Livezey & Zusi (2006: 231, char. 1439).

70. *Humerus, extremitas distalis humeri, processus supracondylaris dorsalis*, size/shape: short, not so prominent, extension rather rounded (0); elongated, slimmer (1). (1 step, CI = 1, RI = 1). Figure 13.

See Kuroda (1954: 84), referring to “ectepicondylar process”, Livezey & Zusi (2006: 235, char. 1467) and Mayr & Smith (2012: 873, char. 32).

71. *Humerus, extremitas distalis humeri, facies cranialis, processus supracondylaris dorsalis*, orientation: rather straight, perpendicular (0), or proximally orientated (1), in relation to *corpus humeri*. (1 step, CI = 1, RI = 1). Figure 13.

See Livezey & Zusi (2006: 235, char. 1467).

72. *Humerus, extremitas distalis humeri, incisura intercondylaris* (distal perspective), depth: shallow (0); deep (1). (1 step, CI = 1, RI = 1). Figure 14.

Note: the notch separating the dorsal and ventral *condyli* (Baumel & Witmer, 1993: 99, annot. 193) varies in depth and can appear shallower when the *margo medialis condyli ventralis* is straight, as observed in *Calonectris*. See Livezey & Zusi (2006: 233, char. 1454).

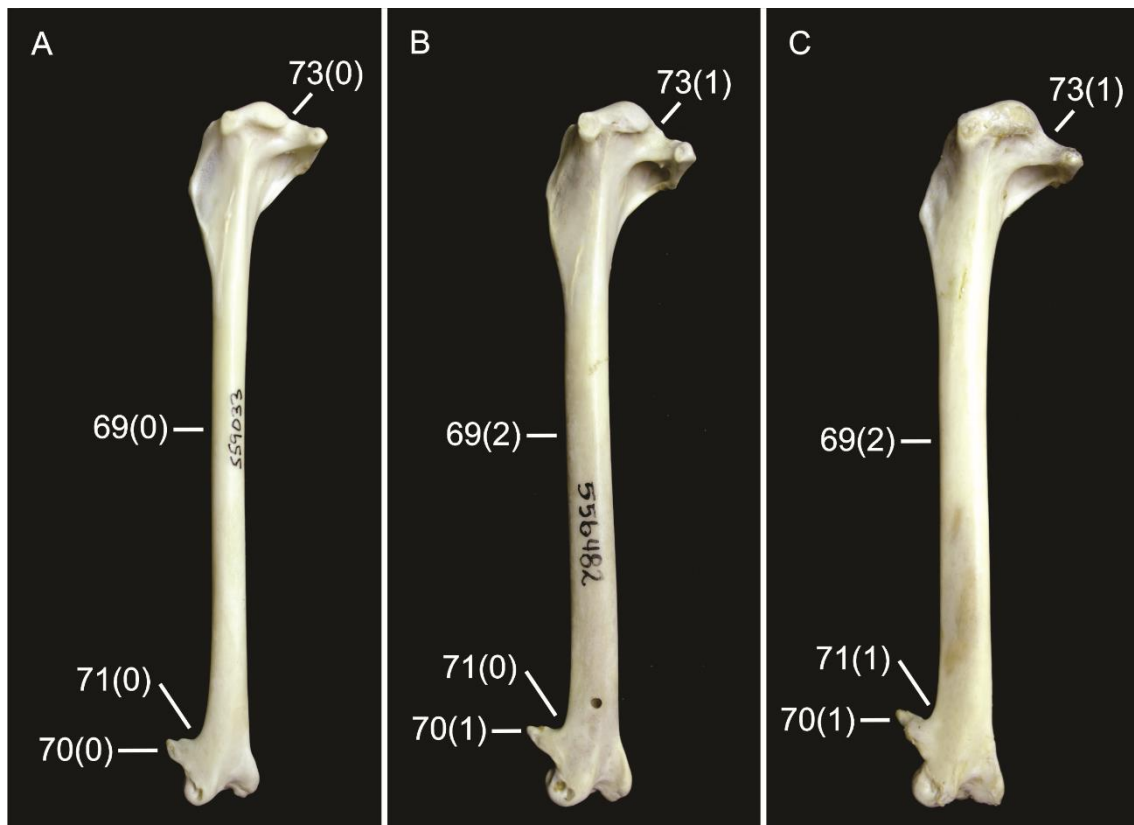


Figure 13. Caudal view of the left humerus of *Calonectris leucomelas* (A; USNM 559033), *Ardenna tenuirostris* (B; USNM 556482) and *Puffinus yelkouan* (C; USNM 289433) illustrating characters 69, 70, 71 and 73. Not to scale.

73. *Humerus, extremitas proximalis humeri, facies caudalis, tuberculum ventrale*, proximodistal position: rather lateral (0), or distal to (1), *margo distalis capiti humeri*. (3 steps, CI = 0.333, RI = 0.800). Figure 13.

See Livezey & Zusi (2006: 221, char. 1366), assessing the position of *tuberculum ventrale* in relation to *fossa pneumotricipitalis*.

74. *Ulna, extremitas proximalis ulnae* (dorsal perspective), *olecranon*, development: not so prominent, gentle slope (0); extended, steep slope (1). (3 steps, CI = 0.333, RI = 0.778). Figure 15.

See Livezey & Zusi (2006: 241, char. 1510) and Xu *et al.* (2002: char. 115) referring to length and development of *olecranon*.

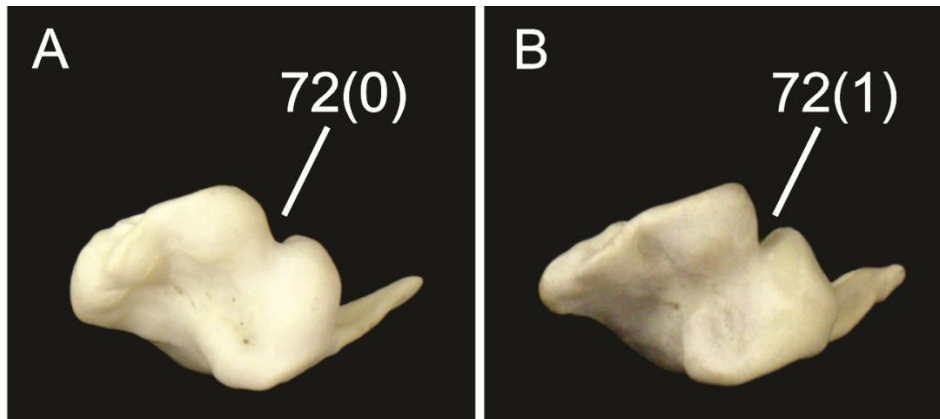


Figure 14. Distal view of the left *humerus* of *Calonectris borealis* (A; MUCIN 393) and *Puffinus puffinus* (B; MUCIN 745) illustrating character 72. Not to scale.

75. *Ulna, extremitas proximalis ulnae* (dorsal perspective), *processus cotylaris dorsalis*, general orientation: transversal (0), or distally oriented (1), in relation to *corpus ulnae*. (2 steps, CI = 0.500, RI = 0.889). Figure 15.

See Livezey & Zusi (2006: 238, char. 1492) referring to ventral orientation of *processus cotylaris dorsalis*.

76. *Ulna, extremitas proximalis ulnae* (proximal perspective), *cotyla ventralis*, shape: circular, wide and short (0); oval, narrow and elongated (1). (1 step, CI = 1, RI = 1).

Note: when compared to *cotyla dorsalis*, state “1” appears to be slimmer, more prominent than it. See Livezey & Zusi (2006: 238, char. 1491) referring to *forma* of *cotyla dorsalis*.

77. *Ulna, corpus ulnae*, shape: elliptical (0), subelliptical, *facies ventralis* rather flattened (1), rather flattened (2). (2 steps, CI = 1, RI = 1).

See Kuroda (1954: 86) and Livezey & Zusi (2006: 242, char. 1516/1518), referring to “craniocaudal compression of *corpus ulnae*”.

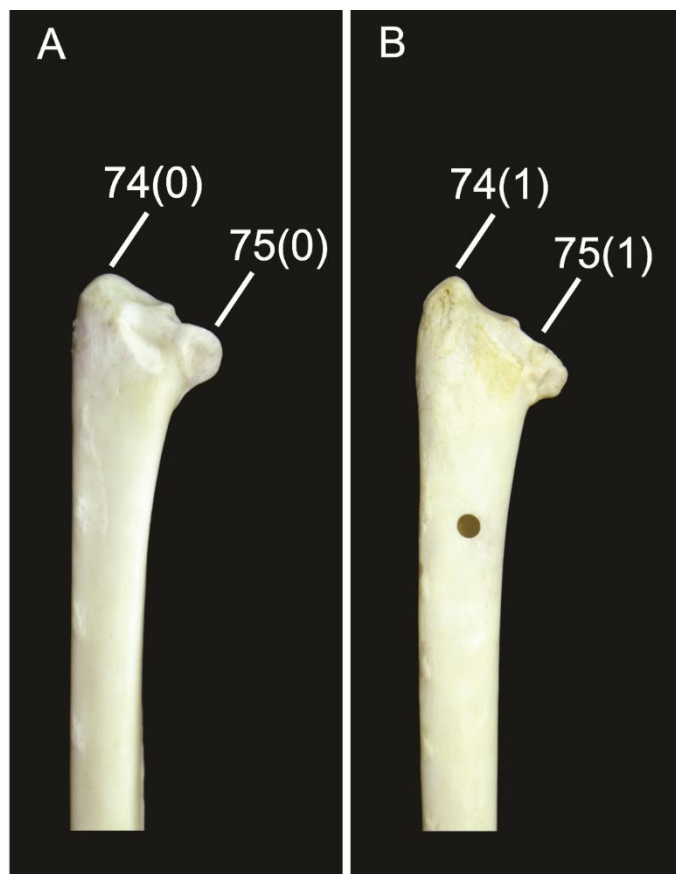


Figure 15. Dorsolateral view of the right *ulna* of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna grisea* (B; USNM 556462) illustrating characters 74 and 75. Not to scale.

78. *Radius, corpus radii* (dorsal perspective), shape: curved (0); straight (1). (1 step, CI = 1, RI = 1). Figure 16.

Note: All *Calonectris* and *Ardenna* species (excluding *A. grisea* and *A. tenuirostris*) show a curved *radius*, with *pars medialis corporis radii* rather arched, whereas *radius* is straight in *Puffinus*, with no angle between *extremities proximalis et distalis radii*.

79. *Radius, corpus radii* (dorsal perspective), thickness: thin, very slender (0); thick, *corpus radii* almost same breadth of both *extremities proximalis et distalis radii*. (1 step, CI = 1, RI = 1).

See Kuroda (1954: 86).

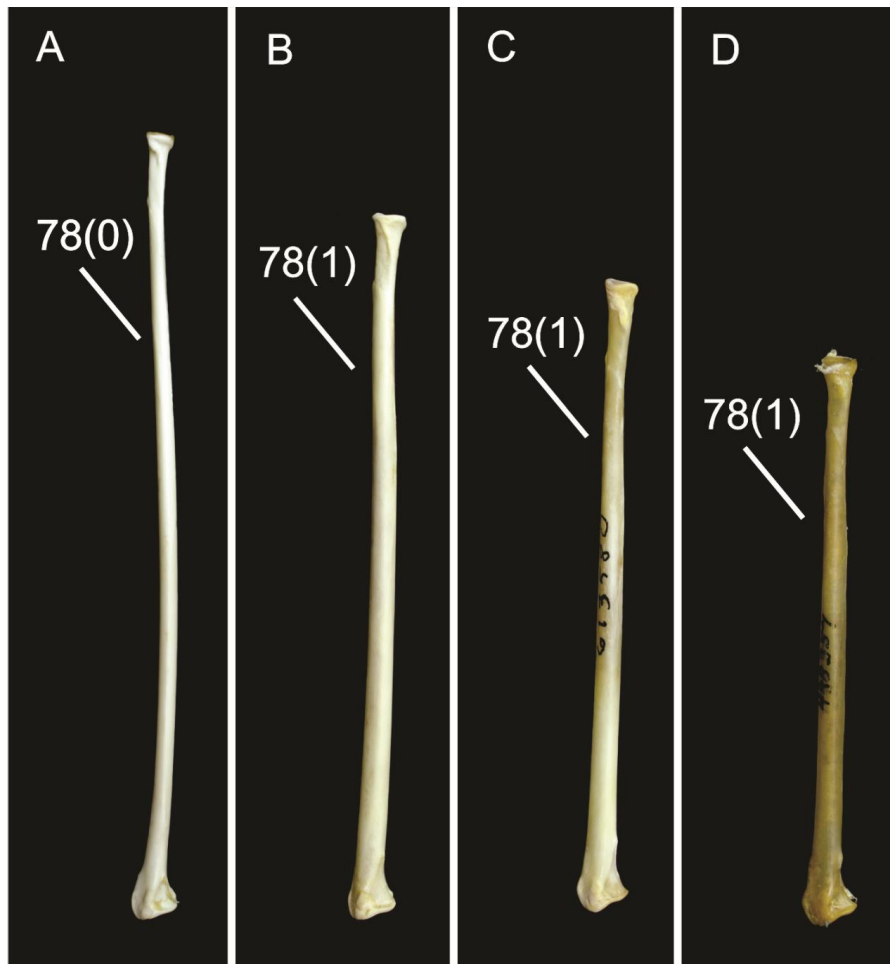


Figure 16. Dorsal view of the left *radius* of *Calonectris leucomelas* (A; USNM 559033), *Ardenna grisea* (B; USNM 556462), *Puffinus mauretanicus* (C; USNM 613580) and *Puffinus assimilis* (D; USNM 488357) illustrating character 78. Not to scale.

80. *Carpometacarpus, extremitas proximalis carpometacarpi, os metacarpale minus, facies ventralis, eminentia retinaculum flexorium of aponeurosis ventralis (sensu Livezey & Zusi, 2006): near-absent (0); present (1). (4 steps, CI = 0.250, RI = 0.400). Figure 17.*

Note: The *eminentia retinaculum flexorium* is the “small tuberculum on *os metacarpale minus, facies ventralis*, immediately distal to *synostosis metacarpalis proximalis*” (Livezey, 1998). See Livezey & Zusi (2006: 263, char. 1652).

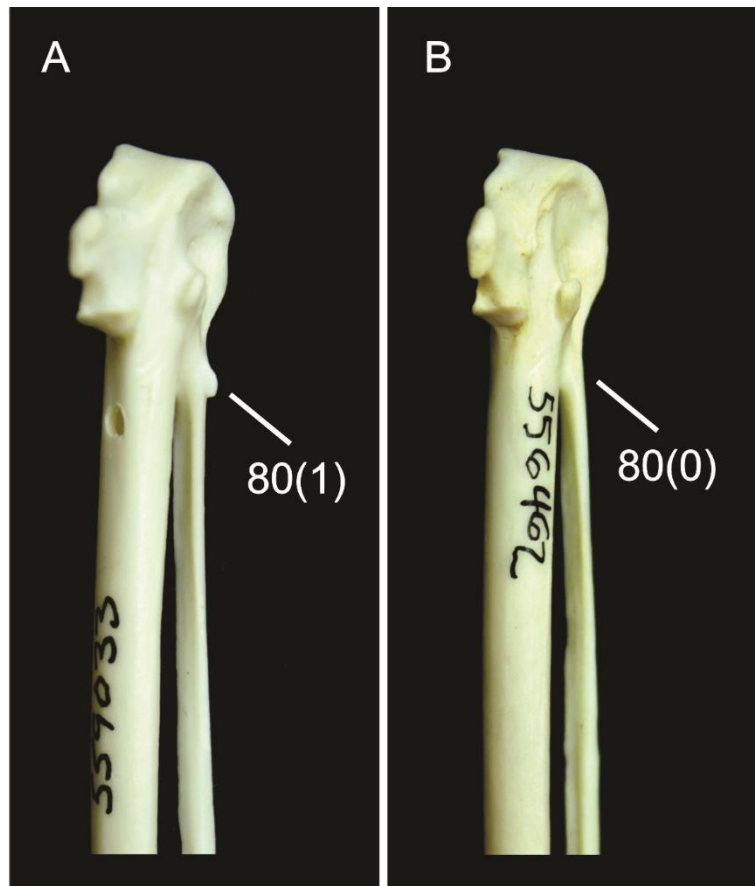


Figure 17. Ventrolateral view of the right *carpometacarpus* of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna grisea* (B; USNM 556462) illustrating character 80. Not to scale.

81. *Os coxae, ilium, ala preacetabularis illi* (lateral perspective), width: wide, *crista iliaca dorsalis* approaches *crista spinosa synsacri* (0); narrow, *crista iliaca dorsalis* curved and low, away from *crista spinosa synsacri* (1). (3 steps, CI = 0.333, RI = 0.714).

See Kuroda (1954: 88) and Livezey & Zusi (2006: 287, char. 1819).

82. *Os coxae, ilium, ala preacetabularis illi, facies dorsalis, crista iliaca lateralis*, lateral expansion: near-absent (0); present (1). (2 steps, CI = 0.500, RI = 0.500).

Figure 18.

Note: most species present a pronounced ledge from the lateral free edge of the *preacetabular ilium* (Baumel & Witmer, 1993: 107, annot. 247). See Kuroda

(1954: 88) and Smith (2010: appendix S2, char. 314).

83. *Os coxae, ilium, ala postacetabularis illi, facies dorsalis*, width: wide, laterally expanded (0); narrow (1). (3 steps, CI = 0.333, RI = 0.714). Figure 18.

Note: In dorsal view, state “0” has *ala postacetabularis illi* outspread laterally, whereas state “1” *ala* is slimmer and longer caudally. See Kuroda (1954: 88).

84. *Pelvis et os coxae, incisura marginis caudalis*, depth: shallow (0); deep (1). (1 step, CI = 1, RI = 1). Figure 19.

Note: as described by Baumel & Witmer (1993: 104, annot. 231), *incisura* is the indentation at the caudal border of the hip bone, in the region of *synostosis ilioschiadica*. It varies in depth and, here, state “1” refers to those very marked, rounded *incisura*, whereas state “0” represents *incisurae* which are only a mere separation of *spina dorsolateralis illi* and *processus terminalis ischii*. See Kuroda (1954: 88) and Livezey & Zusi (2006: 286, char. 1807).

85. *Os coxae, ilium, ala postacetabularis illi* (lateral perspective), *spina dorsolateralis illi*, shape: blunt (0); sharply pointed (1). (2 steps, CI = 0.500, RI = 0.857). Figure 18 and 19.

Note: both shape and size of *spina dorsolateralis illi* vary among species, but it is distinguishable on whether it is short and fairly rounded (state “0”) or more prominent, acuminate (state “1”). See Kuroda (1954: 88) and Livezey & Zusi (2006: 294, char. 1870), referring to its prominence in dorsal perspective.

86. *Os coxae, ilium, ala postacetabularis illi* (lateral perspective), *spina dorsolateralis illi*, orientation: caudodorsally (0); straight caudally, or nearly so (1); caudoventrally (2). (5 steps, CI = 0.400, RI = 0.667). Figure 19.

See Kuroda (1954: 88), referring to the “upper process of the ischium” and Smith (2010: appendix S2, char. 321).

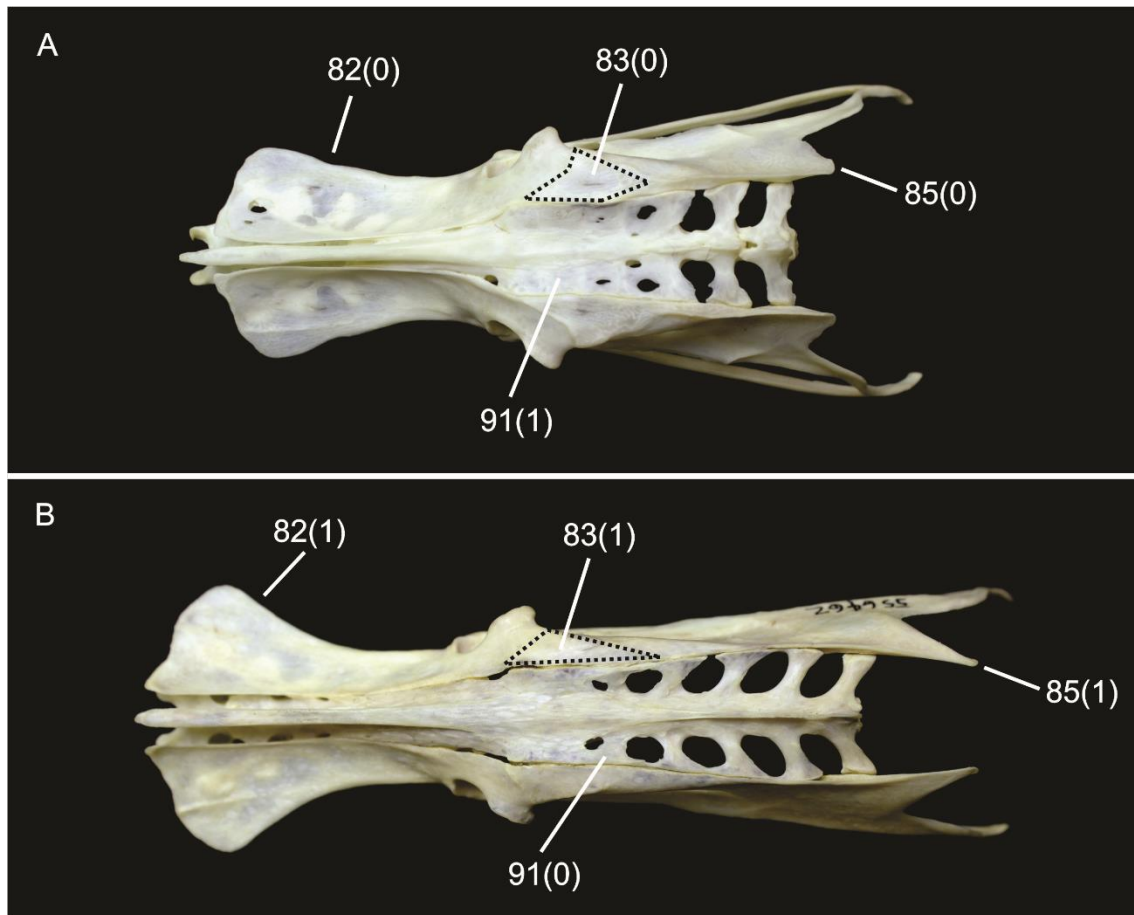


Figure 18. Dorsal view of the *pelvis* (*os coxae* + *synsacrum*) of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna grisea* (B; USNM 556462) illustrating characters 82, 83, 85 and 91. Not to scale.

87. *Ischium*, *ala ischii*, *processus terminalis ischii*, orientation: expands gradually downward (0); pronounced ventral curvature (1). (1 step, CI = 1, RI = 1).

Note: in Procellariiformes, *corpus ischii* exhibits a distinctly narrowing past midpoint, but the ventral orientation of *processus terminalis ischii* varies among species. All species assessed here have a high degree of curvature, but when examined together with *scapus pubis*, members of *Puffinus* show a strong, much greater ventral curvature, resulting in a dorsoventrally deeper *pelvis* at *margo caudalis* (state “1”). See Kuroda (1954: 88; plate 32) and Livezey & Zusi (2006: 299, char. 1907; 300, char. 1918).

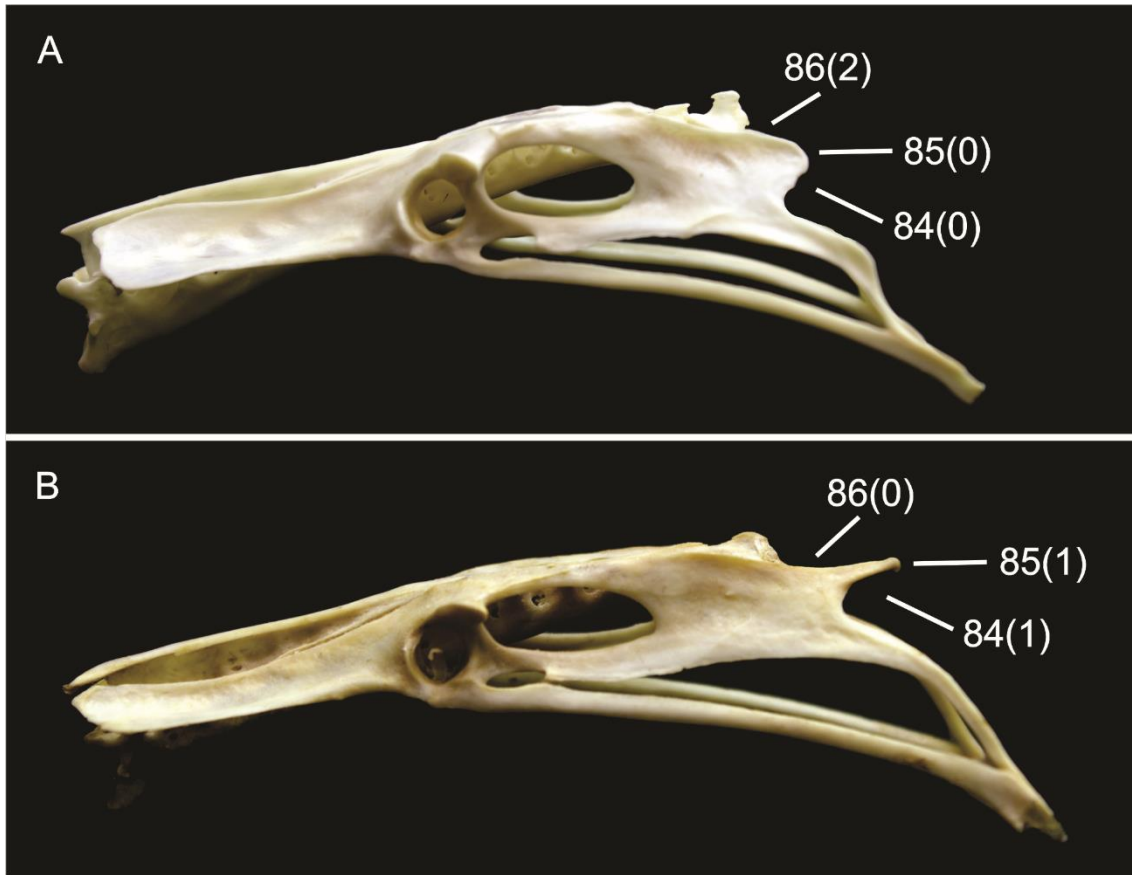


Figure 19. Lateral view of the left side of the *pelvis* (*os coxae* + *synsacrum*) of *Calonectris leucomelas* (A; USNM 559033) and *Puffinus lherminieri* (B; USNM 488402) illustrating characters 84, 85 and 86. Not to scale.

88. *Ischium et pubis, processus terminalis ischii et scapus pubis*, length: shorter (0), or longer (1), than *longitude pelvis* (4 steps, CI = 0.250, RI = 0.625).

Note: Kuroda (1954) observed, comparing the *pelvis* of *Calonectris leucomelas* and *Ardenna tenuirostris*, two contrasted extremes, as “the preacetabula ilium of *leucomelas* being about the same in length as that of much smaller bodied *tenuirostris* and the ischium and pubis of the former are even shorter than those of the latter.” See Kuroda (1954: 88; plate 32).

89. *Pelvis et os coxae, concavitas infracristalis*, concavity: shallow to planar, *concavitas* near obsolete (0); moderately concave (1). (4 steps, CI = 0.250, RI = 0.625).

Note: *concavitas infracristalis* is the wide depression, on the lateral surface of *pelvis*, caudal to the *ilioschiadicum foramen* (Baumel & Witmer, 1993: 105, annot. 235). See Livezey & Zusi (2006: 282, char. 1782).

90. *Pelvis et os coxae, facies ventralis, fossa renalis*, status: absent (0); present (1). (1 step, CI = 1, RI = 1). Figure 20.

Note: *fossa renalis* is the paired depression on each side of the *corpus synsacri* which accommodates the kidney. It is present only in *Calonectris* and in the outgroup, those species with more expanded *ala postacetabularis illi*. See Livezey & Zusi (2006: 284, char. 1793).

91. *Synsacrum, facies dorsalis, lamina transversa synsacri*, ossification of anterior portion: non-ossified, *foramina* existent (0); ossified (1). (1 step, CI = 1, RI = 1). Figure 18.

Note: as stated by Baumel & Witmer (1993: 91, annot. 141c), where the fusion of *synsacrum* is incomplete, there are windows known as *fenestrae [foramina] intertransversariae*. Kuroda (1954) observed a peculiarity in *Calonectris*, describing that “between lateral spines of each sacral vertebra there are holes. These consist of 3 to 4 pairs, but in *C. leucomelas* and in *C. in diomedea* only 1 to 2 pairs are holes and the anterior ones are more or less, or completely ossified.” See Kuroda (1954: 91; plate 30).

92. *Pelvis et os coxae, foramen ilioischiadicum*, size: small (0); large (1). (1 step, CI = 1, RI = 1).

Note: *Calonectris* present a small-sized *foramen ilioischiadicum*, relative to the total size of *pelvis*, when compared, for example, to species with much smaller *pelvis*, as some *Puffinus*. See Kuroda (1954: 88).

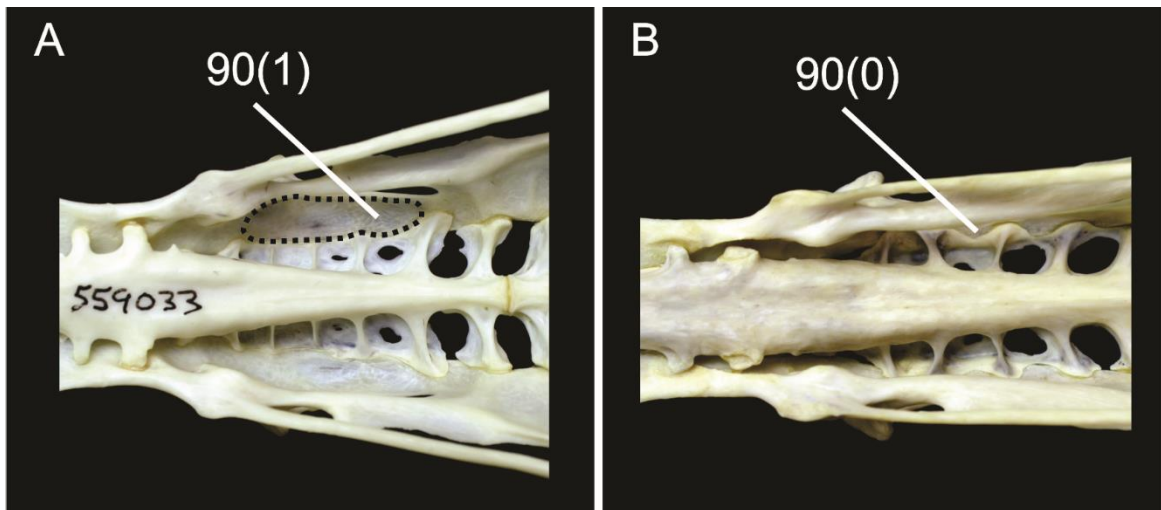


Figure 20. Ventral view of the medial part of the *pelvis* (*os coxae* + *synsacrum*) of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna grisea* (B; USNM 556462) illustrating character 90. Not to scale.

93. *Pelvis et os coxae*, general shape: broad, short and deep (0); long, narrow (1). (2 steps, CI = 0.500, RI = 0.875).

Note: Kuroda (1954), when discussing each part of the skeletal structure, observes that a long, narrow *pelvis* is a structural adaptation for aquatic habit, as “what is needed [on the water] are voluminous feet muscles for which the length [...] of *pelvis* is needed for attachment.” This characteristic is found in those highly aquatic species – herein, it was found in *Puffinus* and some *Ardenna*. The broad *pelvis* of *Calonectris*, the least aquatic group, resembles that of *Fulmarus*. See Kuroda (1954: 19; 32; 88).

94. *Femur, corpus femoris* (lateral perspective), craniocaudal shape: straight, or very weakly convex (0); significantly bowed and convex cranially (1). (3 steps, CI = 0.333, RI = 0.714). Figure 21.

See Kuroda (1954: 91; plate 35) and Livezey & Zusi (2006: 315, char. 2000).

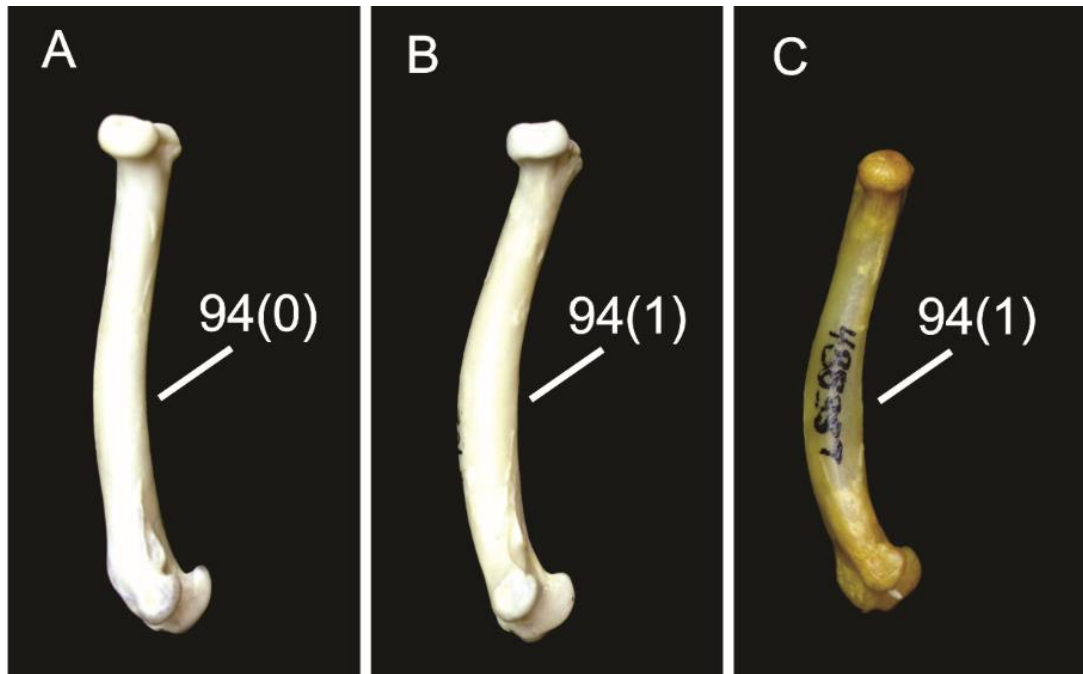


Figure 21. Lateral view of the right *femur* of *Calonectris leucomelas* (A; USNM 559033), *Ardenna grisea* (B; USNM 556462) and *Puffinus assimilis* (C; USNM 488357) illustrating character 94. Not to scale.

95. *Femur, corpus femoris*, width: considerably thinner (0), or as thick as (1) *extremitas proximalis et distalis femoris* (2 steps, CI = 0.500, RI = 0.750).

Note: Kuroda (1954) noticed the relative thicker *femur* of some *Ardenna* species, especially at the joints - once more, one of its adaptations for aquatic life. See Kuroda (1954: 91).

96. *Femur, extremitas distalis femoris* (distal perspective), *incisura intercondylaris caudalis* (*sensu* Livezey & Zusi, 2006), depth: deep (0); shallow (1). (1 step, CI = 1, RI = 1). Figure 22.

Note: state “1” includes all *Puffinus* (*sensu lato*) species, which have a wide, flat *incisura et margines* gradually sloped. This *margines* are subperpendicular to *facies caudalis corporis* in state “0”, producing a deeper and narrower *incisura*. See Livezey & Zusi (2006: 318, char. 2026).

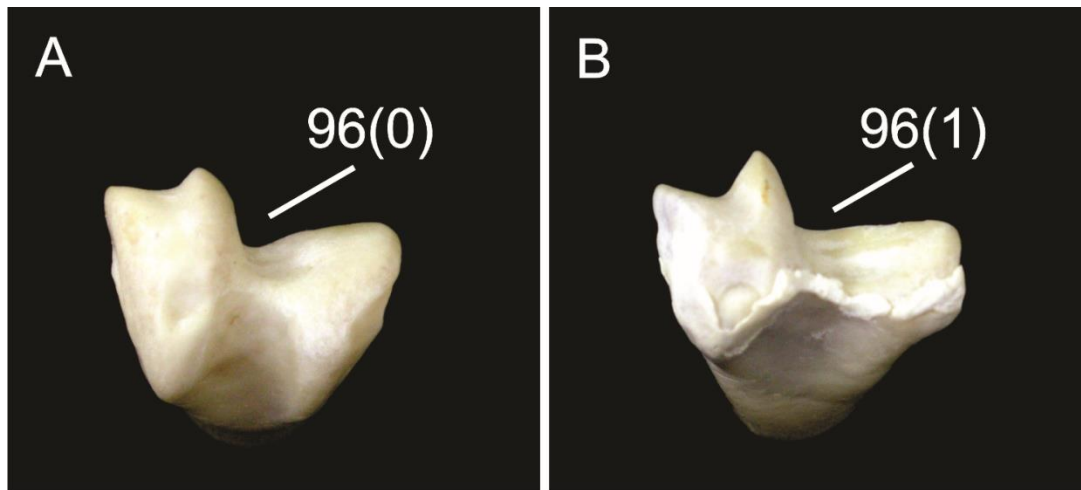


Figure 22. Distal view of the left *femur* of *Calonectris edwardsii* (A; MUCIN 994) and *Ardenna grisea* (B; MUCIN 627) illustrating character 96. Not to scale.

97. *Tibiotarsus, crista cnemialis*, size: short, slightly extended proximally (0); intermediate (1); long, greatly enlarged and extending far proximally (2). (4 steps, CI = 0.500, RI = 0.800). Figure 23.

Note: as Kuroda (1954) observed (referring to *processus rotularis*), “in the shearwater this process varies in length according to the grade of aquatic life”. The best developed *cristae cnemialis* are present in those species with the most aquatic habit, being very short for total *tibiotarsus* size in the highly aerial *Calonectris*. See Kuroda (1954: 92; plate 36) and Smith (2010: appendix S2, char. 360).

98. *Tibiotarsus, crista cnemialis cranialis* (lateral perspective), width/shape: broad, rather round or squared (0); slender, mostly pointed (1). (1 step, CI = 1, RI = 1). Figure 24.

See Kuroda (1954: 92) describing *crista* for *Calonectris*: “[...] and the shape of the process is also different from those of the others.”

99. *Tibiotarsus, extremitas proximalis tibiotarsi* (caudal perspective), *sulcus tendinis musculi ambientis*, status: absent (0); present (1). (2 steps, CI = 0.500, RI =

0.750). Figure 25.

Note: Shufeldt (1907: 120) observed, when describing the *crista cnemialis* of *Ardenna creatopus*, that “[on] the posterior aspect of the common prominence, a well-marked, transverse groove exists, apparently for the accommodation of the lower margin of the patella.”



Figure 23. Cranial view of the right *tibiotarsus* of *Calonectris leucomelas* (A; USNM 559033); *Ardenna pacifica* (B; USNM 498256), *Ardenna grisea* (C; USNM 556462) and *Puffinus gavia* (D; USNM 614345) illustrating character 97. Not to scale.

100. *Tibiotarsus*, *extremitas distalis tibiotarsi*, *sulcus musculi fibularis*, relative development: *sulcus* distinct and moderately developed (0); shallow *sulcus*, lateral rim enlarged (1). (1 step, CI = 1, RI = 1).

Note: state “1” *sulcus* is laterally bordered by an enlarged rim that separates it from *depression epicondylaris lateralis*. See Livezey & Zusi (2006: 336, char. 2169).

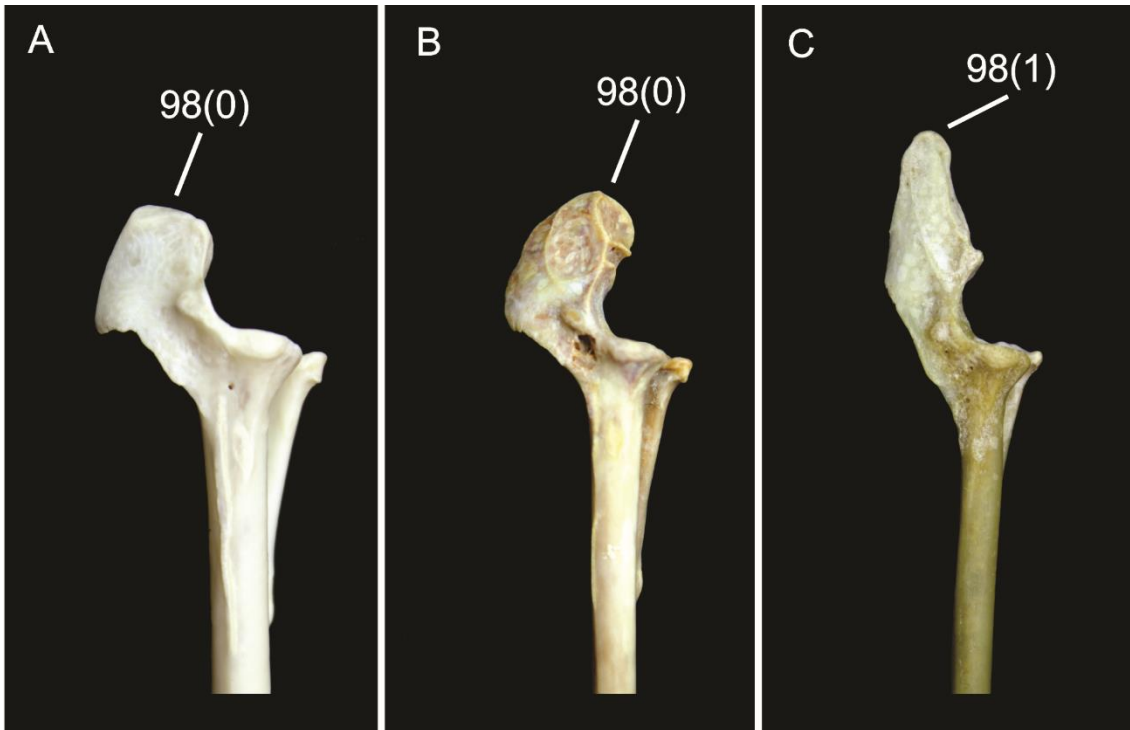


Figure 24. Lateral view of the right *tibiotarsus* of *Calonectris leucomelas* (A; USNM 559033); *Ardenna pacifica* (B; USNM 498256) and *Puffinus gavia* (C; USNM 614345) illustrating character 98. Not to scale.

101. *Tibiotarsus, extremitas distalis tibiotarsi, condylus medialis* (medial perspective), *ryma condylaris*, proximodistal position of *pars caudalis*: nearly coplanar (0); proximal (1). (1 step, CI = 1, RI = 1).

Note: the distal rim of *condylus medialis* is distinctly notched and, for some species, the two *alae* observed (caudal and cranial portions) have different sizes (state “1”). See Livezey & Zusi (2006: 334, char. 2151).

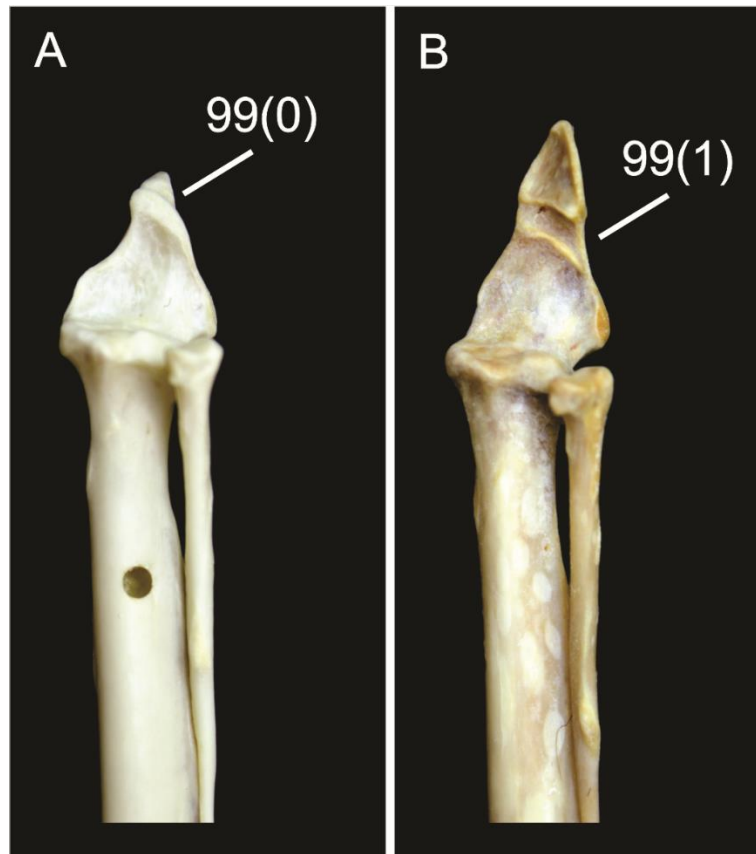


Figure 25. Caudal view of the right *tibiotarsus* (proximal extremity) of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna pacifica* (B; USNM 498256) illustrating character 99. Not to scale.

102. *Tibiotarsus*, *hypotarsus*, *canales et/aut sulci hypotarsi*, *canalis tendinis insertii musculi flexor hallucis longus* (Vanden Berge & Storer 1995: fig. 8), dorsoplantar position in relation to *canalis tendinis insertii m. flexor digitorum longus* (Vanden Berge & Storer, 1995: fig. 8): lateral (0); plantar, *canalis* protruded (1). New character. (2 steps, CI = 0.500, RI = 0.500). Figure 26.

Note: in *Calonectris*, the “*canalis tendinis insertii musculi flexor hallucis longus*” is projected, presenting a wider *sulcus ligamentosus*, *i.e.* the “transverse groove at the junction of the proximal hypotarsus and area intercotylaris” (Baumel & Witmer, 1993: 111, annot. 286). *Canalis tendinis insertii musculi flexor hallucis longus* (Vanden Berge & Storer 1995: fig. 8) corresponds to both “tendinal

passage 3” of Strauch (1978) and “anterolateral canal” of Stallcup (1954: fig. 6), whereas *canalis tendinis insertii m. flexor digitorum longus* (Vanden Berge & Storer, 1995: fig. 8) corresponds to both “tendinal passage 1” of Strauch (1978) and “anteromedial canal” of Stallcup (1954: fig. 6).

103. *Tarsometatarsus, corpus tarsometatarsi*, mediolateral compression: absent (0); present (1). (3 steps, CI = 0.333, RI = 0.600).

Note: the presence of mediolateral compression is marked, such that dorsoplantar depth exceeds mediolateral width. See Livezey & Zusi (2006: 355, char. 2287).

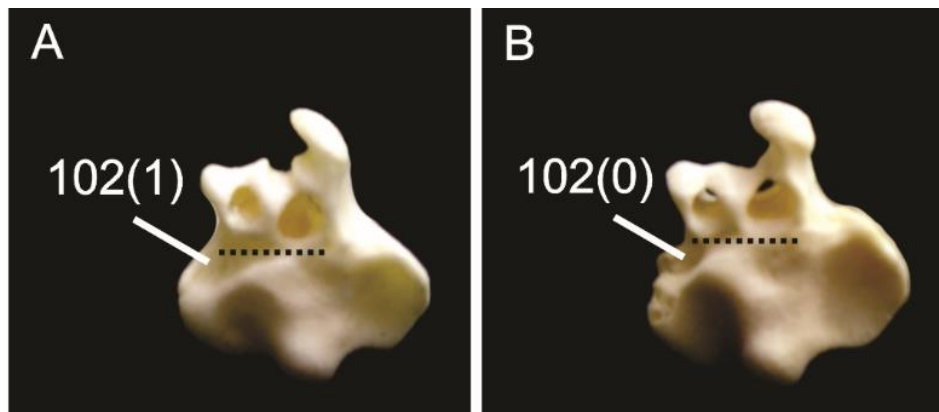


Figure 26. Proximal view of the right *tarsometatarsus* of *Calonectris leucomelas* (A; USNM 559033) and *Ardenna grisea* (B; USNM 556462) illustrating character 102. Not to scale.

PHYLOGENETIC ANALYSIS

The equal weighting analysis resulted in two most parsimonious trees (tree length = 228.583 steps, CI = 0.788, RI = 0.242), the strict consensus of which is well resolved, with collapsed nodes restricted to a few interspecific clades (Figure 27). In sum, a monophyletic *Calonectris* was recovered as sister group to a large ‘*Puffinus (sensu lato)*’. This latter clade consisted of a clade of *Ardenna pacifica* and *A. bulleri* as sister taxa to a clade containing the remaining species, and (*Ardenna grisea* + *A. tenuirostris*)

as sister group to *Puffinus (sensu stricto)*. Although all species of *Puffinus* formed a clade, species of *Ardenna* formed a grade of successive sisters to *Puffinus*.

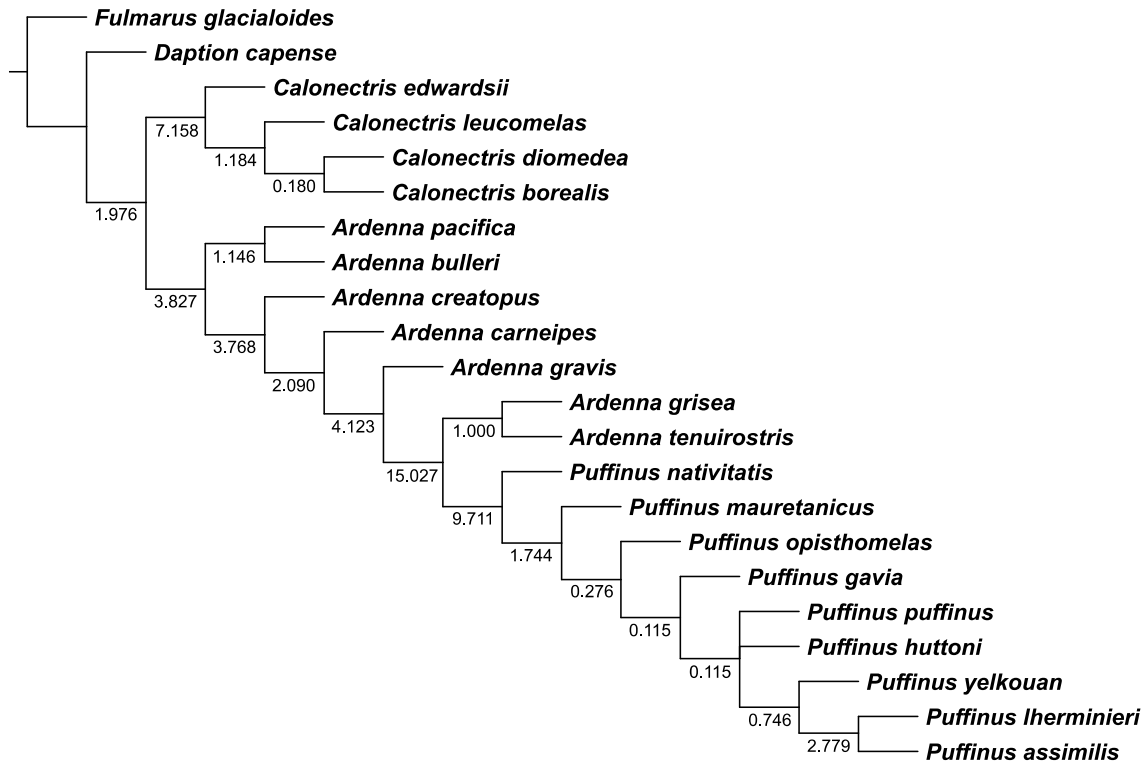


Figure 27. Strict consensus of the two most parsimonious trees under equal weight (tree length = 228.583 steps, CI = 0.788, RI = 0.242). Data matrices used in the cladistic analysis, separated here in continuous and discrete characters, are provided in Appendix 2 and 3, respectively. Numbers below nodes are respective Goodman-Bremer Supports.

The analysis under implied weighting recovered a single fittest tree for each of the 21 values of *K* (Appendix 4). The three most stable trees were those obtained from *K*9, *K*10, and *K*11 (Appendix 5). The strict consensus (tree length = 229.005 steps, CI = 0.461, RI = 0.804) from these cladograms is the final hypothesis proposed in this work (Figure 28). Synapomorphies for each node, as well as autapomorphies for each of the 20 ingroup species, are provided in Appendix 6. The numbering of nodes used here corresponds to that from TNT software.

In the implied weighting hypothesis, all nodes were resolved, as no polytomies were found (Figure 28). *Calonectris* was, again, recovered as monophyletic, with *C. leucomelas* being the sister taxa to (*C. diomedea* + *C. borealis*), and *C. edwardsii* the sister to (*C. leucomelas* (*C. diomedea* + *C. borealis*)). A monophyletic *Ardenna* was not recovered, and the grouping (*A. grisea* + *A. tenuirostris*) was, once again, found to be the sister group of a fully resolved *Puffinus* (*sensu stricto*).

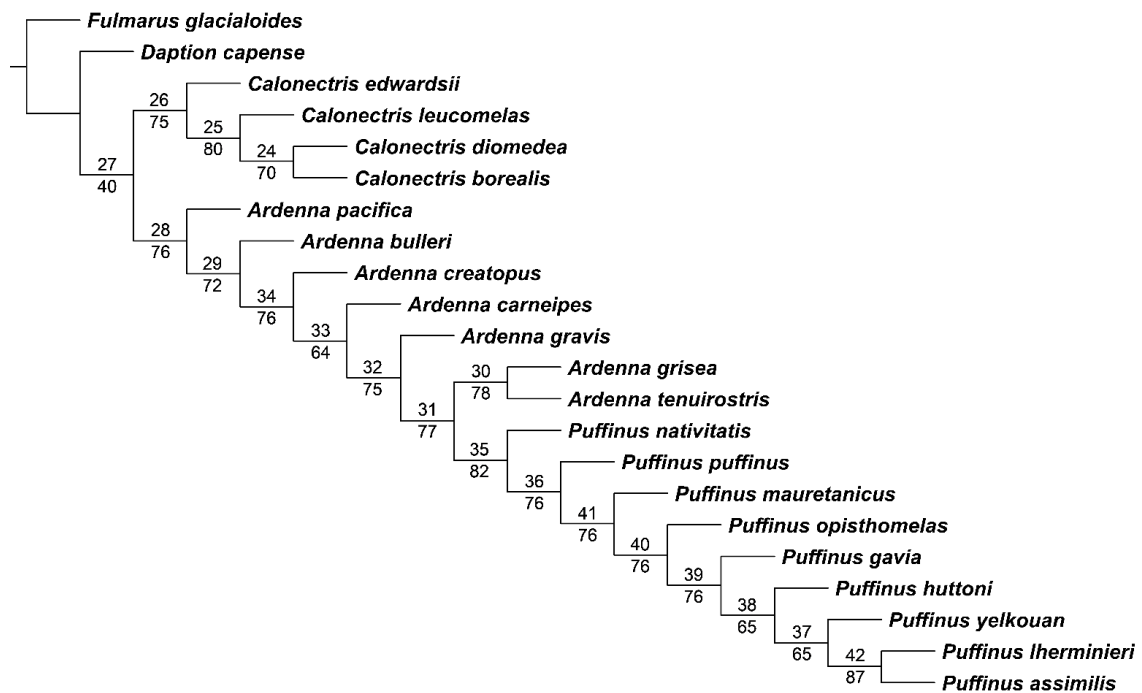


Figure 28. Strict consensus between the most stable trees under implied weight (obtained from K9, K10 and K11; tree length = 229.005 steps, CI = 0.461, RI = 0.804). Data matrices used in the cladistic analysis, separated here in continuous and discrete characters, are provided in Appendix 2 and 3, respectively. Number of nodes are shown above each node, and correspond to those from TNT. Numbers below nodes are respective Relative Bremer Supports.

DISCUSSION

THE SHEARWATER ASSEMBLAGE: PUFFININI (*SENSU* PENHALLURICK & WINK, 2004)

Phylogenetic analyses, under both equal and implied weighting, recovered a monophyletic *Calonectris* sister to a large *Puffinus (sensu lato)* clade. In the final hypothesis proposed herein, seven unambiguous synapomorphies (plus four according to either ACCTRAN or DELTRAN) were found supporting this group. A close phylogenetic relationship between *Calonectris* and *Puffinus (sensu lato)* seems well-corroborated and has been recovered in several molecular-based studies (*e.g.* Heidrich *et al.*, 1998; Nunn & Stanley, 1998; Penhallurick & Wink, 2004; Welch *et al.*, 2014). Nevertheless, conflicts exist regarding relationships within and between these two taxa.

RELATIONSHIP AMONG PUFFININI (*SENSU* PENHALLURICK & WINK, 2004)

Even with Kuroda's (1954) gradistic view of the classification of shearwaters, his proposal already assumed a close phylogenetic relationship between *Calonectris* and *Puffinus (sensu lato)*. The result of the present phylogenetic analyses reinforces the hypothesis of a sister relationship between these clades. Welch *et al.* (2014), when assessing the phylogenetic position of an extinct *Pterodroma* species through analysis of the cytochrome *b* gene, also found *Calonectris* to be sister group to *Puffinus (sensu lato)*, despite the splitting of the latter into *Ardenna* and *Puffinus (sensu stricto)*. Although all recent hypotheses based on molecular data agree on the separation of *Ardenna* and *Puffinus*, they present conflicting results regarding the relationship between *Calonectris* and these two genera.

Some works could not resolve the relationship, leaving it as a polytomy (*e.g.* Austin *et al.*, 2004; Tennyson & Shepherd, 2017). Most phylogenetic reconstructions, however, showed that *Puffinus (sensu stricto)* is sister to *Calonectris*, and that *Ardenna* is sister

to the larger clade formed by *Calonectris* and *Puffinus (sensu stricto)* (e.g. Heidrich *et al.*, 1998; Nunn & Stanley, 1998; Ramirez *et al.*, 2010; Pyle *et al.*, 2011).

The outcome of these hypotheses is a paraphyletic *Puffinus (sensu lato)*, contrary to the result of the present analysis, wherein *Calonectris* is the sister clade to a monophyletic grouping of all other shearwaters including a monophyletic *Puffinus (sensu stricto)*. Penhallurick & Wink (2004) stated that “the situation within traditional *Puffinus* is more complex, since all trees indicate that it represents a paraphyletic group.” In fact, the trees Penhallurick & Wink (2004) present have different interpretations, depending on the analysis method. While the Neighbor Joining tree indicates that *Puffinus (sensu lato)* is, indeed, paraphyletic, with *Calonectris* sister to *Puffinus (sensu stricto)*, the Maximum Parsimony tree have a polytomy that can only suggest the split of *Puffinus (sensu lato)* into two subgroups. Furthermore, their Maximum Likelihood tree shows *Calonectris* as the sister clade to *Puffinus (sensu lato)*, which is then subdivided into the two less inclusive groups, *Ardenna* and *Puffinus (sensu stricto)*; this topology does not make *Puffinus (sensu lato)* a paraphyletic group, it only shows that a monophyletic clade is, then, subdivided in two smaller ones, also monophyletic. Therefore, the topology of the Maximum Likelihood tree from Penhallurick & Wink (2004) is the same we find in Welch *et al.* (2014), and both are consistent with the hypothesis we provide herein.

CALONECTRIS

Traditionally, the species of *Calonectris* were usually placed in the same genus as the other *Puffinus* shearwaters; the genus came to be widely recognized only about 50 years after its description, based mostly on the work of Kuroda (1954) (e.g. Alexander *et al.*, 1965). In the final hypothesis of this study, *Calonectris* is supported by eight

unambiguous synapomorphies, such as the laterally nonvisible *condylus occipitalis*; the presence of a thin osseous *lamina* in *apertura nasalis ossea*, which is shared with *Puffinus nativitatis* and *P. huttoni*; and the elliptical shaft of *humerus*, not flattened as in other species of *Puffinus* (*sensu lato*). The monophyly of the group, corroborated herein, has also been recovered by previous molecular-based studies, despite the different taxonomic treatments given to the terminal taxa (*e.g.* Nunn & Stanley, 1998; Austin *et al.* 2004; Penhallurick & Wink, 2004; Welch *et al.*, 2014).

In our phylogenetic analysis, relationships among species of *Calonectris* were almost entirely established by synapomorphies from continuous characters, such as the lengths of wing bones (*e.g.* characters 9, 10, 11, and 12), and received high support (RBS \geq 70 for all nodes). *Calonectris diomedea* and *C. borealis* are sister taxa to each other, sharing seven synapomorphies from continuous characters. Most molecular phylogenies have included only one or two species of *Calonectris* as terminal taxa. Ramirez *et al.* (2010) and Tennyson & Shepherd (2017) included only *C. diomedea*, whereas some other studies also sequenced *C. leucomelas* (*e.g.* Nunn & Stanley, 1998; Austin *et al.* 2004; Pyle *et al.*, 2011; Welch *et al.*, 2014). Heidrich *et al.* (1998), when assessing relationships of Mediterranean and North Atlantic shearwaters through mtDNA, used both *C. diomedea* and *C. borealis*, although *borealis* was considered a subspecies of *C. diomedea*. In the present study, *C. leucomelas* appeared as sister to (*C. diomedea* + *C. borealis*), forming a clade supported by eleven synapomorphies (*i.e.*, nine from continuous characters, plus one unambiguous and one ambiguous). Penhallurick & Wink (2004), who included three of four species of *Calonectris*, found *C. leucomelas* to be sister to (*C. diomedea* + *C. borealis*), the same relationship we present herein. However, these authors suggested that these two taxa should continue to be treated as

subspecies, whereas most current sources consider *C. diomedea* and *C. borealis* to be valid species (*i.e.* Sangster *et al.*, 2012; Gill & Donsker, 2019).

Together with *C. leucomelas*, *C. diomedea*, and *C. borealis*, the present study has also included *C. edwardsii*, which was found to be sister to (*C. leucomelas* (*C. diomedea* + *C. borealis*)). This result contrasts with the relationship proposed by Gómez-Díaz *et al.* (2006, 2009), who also included all four species in their phylogeographic analyses based on the cytochrome *b* gene. According to these authors, *C. diomedea* and *C. edwardsii* are more closely related to each other than either is to *C. borealis*, and *C. leucomelas* is sister to all other *Calonectris* species. Nonetheless, when discussing only the biometric structure of *Calonectris* species, Gómez-Díaz *et al.* (2006) acknowledged the similarity of *C. diomedea* and *C. borealis*, the largest species that they included. According to them, *C. leucomelas* and *C. edwardsii* are, respectively, the medium-sized and smallest species of the genus. As mentioned before, the relationship proposed herein was mostly based on synapomorphies from continuous characters, which can explain the apparent clustering by body size measurements.

PUFFINUS (SENSU LATO)

The final hypothesis found all other members of shearwaters to form a single, monophyletic grouping: *Puffinus (sensu lato)*. We did not recover the split of this clade into two subgroups (*i.e.* genera *Ardenna* and *Puffinus*) as suggested by molecular-based hypotheses (*e.g.* Austin, 1996; Heidrich *et al.*, 1998; Austin *et al.*, 2004; Penhallurick & Wink, 2004; Pyle *et al.*, 2011). The *Puffinus (sensu lato)* clade, as recovered herein, is relatively well-supported (RBS = 76) and established by eight unambiguous synapomorphies, plus six optimized by either ACCTRAN or DELTRAN. Despite minor conflicts, the present hypothesis recalls early morphological studies (Kuroda, 1954;

Wragg, 1985), although the results cannot be directly compared as they did not use the same phylogenetic approach as we have; however, that is not to say we cannot discuss the congruence of these different studies.

The need for recognition of two genera among *Puffinus* (*sensu lato*) was suggested in many hypotheses based on molecular data, all using the same marker (*e.g.* Austin, 1996; Heidrich *et al.*, 1998; Austin *et al.*, 2004; Penhallurick & Wink, 2004). However, monophyly of the currently accepted *Ardenna* is not supported in the present analysis. Instead, its members form a grade of successive sisters to *Puffinus* (*sensu stricto*). The topology of the final hypothesis differs significantly from the molecular hypotheses, wherein *Ardenna* and *Puffinus* (*sensu stricto*) are shown to be two different clades, sometimes not even sister genera (*e.g.* Heidrich *et al.*, 1998; Nunn & Stanley, 1998; Ramirez *et al.*, 2010; Pyle *et al.*, 2011). Alternatively, the morphological, pre-cladistic hypotheses of Kuroda (1954) and Wragg (1985) suggested that a single “ancestral” taxon has sequentially given rise to each phylogenetic subgroup within the *Puffinus* (*sensu lato*) clade. The final hypothesis, (*Ardenna pacifica* (*A. bulleri* (*A. creatopus* (*A. carneipes* (*A. gravis* ((*A. grisea* + *A. tenuirostris*) (*Puffinus nativitatis* (*P. puffinus* (*P. mauretanicus* (*P. opisthomelas* (*P. gavia* (*P. huttoni* (*P. yelkouan* (*P. lherminieri* + *P. assimilis*))))))))))))) appears to match this perception.

Kuroda (1954), who studied shearwaters based on different types of data, including external morphology, osteology, and behaviour, proposed a classification with five monophyletic subgroups within *Puffinus* (*sensu lato*). According to him, *A. pacifica* and *A. bulleri* are closely related, classified as the ‘*Thyellodroma* subgroup’, the most “ancestral” group among all *Puffinus* (*sensu lato*). Wragg (1985), using only morphological characters, found the same result. Although *A. pacifica* and *A. bulleri* formed a clade in the equally weighted tree, they did not group together in the implied

weighting tree, as *A. pacifica* appears to be the sister taxon to all other species, followed by *A. bulleri*. A similar topology, regarding both species, was presented on the molecular-based hypothesis by Heidrich *et al.* (1998). All molecular studies support the grouping of (*A. pacifica* + *A. bulleri*), and it is typically regarded as sister to a clade comprising all other species of *Ardenna* (e.g. Penhallurick & Wink, 2004; Pyle *et al.*, 2011; Welch *et al.* 2014).

The next species, sister taxon to the remaining species of *Puffinus (sensu lato)*, is *A. creatopus*, followed by *A. carneipes*. Kuroda (1954) proposed that these species be combined in the ‘*Hemipuffinus* subgroup’, although, in the present hypothesis, they are sequentially arranged. Wragg (1985) did not discuss this subgroup, as his proposal showed a polytomy regarding the position of *A. creatopus*, *A. carneipes*, and the clade formed by the remaining species of *Puffinus (sensu lato)*. Molecular-based hypotheses typically consider (*A. creatopus* + *A. carneipes*) to be sister taxa; however, the subgroup relationship among the other *Ardenna* species is, sometimes, conflicting. Most studies indicate *A. gravis* as sister taxon to the ‘*Hemipuffinus* subgroup’ (e.g. Austin *et al.*, 2004; Penhallurick & Wink, 2004; Kawakami *et al.*, 2018), but the grouping (*A. grisea* (*A. creatopus* + *A. carneipes*)) was suggested by Tennyson & Shepherd (2017), and Ramirez *et al.* (2010) was unable to define the position of ‘*Hemipuffinus*’ within the genus due to a polytomy. Although Heidrich *et al.* (1998) did not include *A. carneipes* in their molecular analyses, which could have changed their resulting trees, the topology they presented for the relationship (*A. pacifica* (*A. bulleri* + *A. creatopus*))) is similar to the present hypothesis.

The last three *Ardenna* species, following Kuroda (1954), were divided into two other subgroups: ‘*Ardenna*’ for *A. gravis*; and ‘*Neonectris*’ for *A. grisea* and *A. tenuirostris* (*Puffinus nativitatis*, for the author, was also placed in the latter). According

to Kuroda (1954), ‘*Ardenna*’ is closely related to the group formed by ‘*Neonectris*’ and all other *Puffinus* (*sensu stricto*).

As recovered herein, *A. gravis* is sister to ((*A. grisea* + *A. tenuirostris*) + (*Puffinus* (*sensu stricto*))). Kuroda (1954) placed *P. nativitatis* in his ‘*Neonectris*’ subgroup based on external morphology and behaviour. Afterwards, osteological analysis by Wragg (1985) hypothesized that *P. nativitatis* was sister to all other *Puffinus* (*sensu stricto*) species, making ‘*Neonectris*’ a polyphyletic group. Wragg’s (1985) hypothesis is now supported by molecular-based studies (e.g. Austin, 1996; Heidrich *et al.*, 1998; Tennyson & Shepherd, 2017), considering that *Puffinus* (*sensu lato*) is currently split into two genera, and *P. nativitatis* is part of *Puffinus* (*sensu stricto*). Nevertheless, the present analysis found (*A. grisea* + *A. tenuirostris*) to be monophyletic, supported by two unambiguous synapomorphies, plus four according to either ACCTRAN or DELTRAN. Furthermore, this group appears to be the sister clade to *Puffinus* (*sensu stricto*). This relationship was previously suggested by Wragg (1985); however, it is not present in most molecular hypotheses. Austin (1996) and Heidrich *et al.* (1998) placed *A. tenuirostris* as sister taxon to (*A. gravis* + *A. grisea*), whereas other hypotheses propose (*A. tenuirostris* (*A. grisea* + *A. gravis*)) (e.g. Penhallurick & Wink, 2004; Pyle *et al.*, 2011; Welch *et al.*, 2014). The conflicting placement of these species has also produced some unresolved relationships within the genus (*i.e.* Austin *et al.*, 2004; Ramirez *et al.*, 2010; Tennyson & Shepherd, 2017; Kawakami *et al.*, 2018).

Molecular-based studies have consistently presented a monophyletic *Puffinus* (*sensu stricto*), regardless of its position in relation to *Ardenna* and *Calonectris* (e.g. Nunn & Stanley, 1998; Austin *et al.*, 2004; Pyle *et al.*, 2011; Tennyson & Shepherd, 2017). The monophyly of *Puffinus* (*sensu stricto*) in the present analysis is congruent with these hypotheses (RBS = 82), although its members are placed in the same larger *Puffinus*

(*sensu lato*) clade as *Ardenna* species in both the equal and implied weight analyses. In the present hypothesis, the monophyly of *Puffinus (sensu stricto)* was supported by 12 synapomorphies from discrete characters (*i.e.*, nine unambiguous, plus three according to either ACCTRAN or DELTRAN), such as the cranially positioned *apex carinae* of the *sternum*, and another 20 from continuous characters. *Puffinus nativitatis*, according to the present analysis, is sister to all other *Puffinus (sensu stricto)* species, congruent with both morphological (*e.g.* Wragg, 1985) and molecular-based hypotheses (*e.g.* Austin, 1996; Nunn & Stanley, 1998; Penhallurick & Wink, 2004). It should be noted, however, that *P. subalaris*, which has been found to group with *P. nativitatis* as sister to the remaining *Puffinus (sensu stricto)* (Austin *et al.*, 2004; Pyle *et al.*, 2011), was not included in these analyses.

In the present analyses, six of nine included species of *Puffinus (sensu stricto)* are from the group identified as “Manx-type shearwaters”, and two others are part of the “Little/Audubon’s complex” (Onley & Scofield, 2007). The hypothesis for the relationship of these eight species presented herein, (*Puffinus puffinus (P. mauretanicus (P. opisthomelas (P. gavia (P. huttoni (P. yelkouan (P. lherminieri + P. assimilis))))))*), is highly congruent with earlier morphological studies (Kuroda, 1954; Wragg, 1985).

Hypotheses based on molecular data have consistently shown some phylogenetic associations among these species; however, their placement within the genus is unclear. In most studies, (*P. gavia + P. huttoni*) is the sister group to the remaining species (*e.g.* Austin *et al.*, 2004; Pyle *et al.*, 2011; Tennyson & Shepherd, 2017), yet some conflicts can be found (*e.g.* Heidrich *et al.*, 1998). In the implied-weight hypothesis herein, *P. puffinus* occupies this position, sequentially followed by *P. mauretanicus*. In the molecular-based analyses, *P. mauretanicus* is sister to *P. yelkouan* (*e.g.* Austin, 1996; Pyle *et al.*, 2011; Kawakami *et al.*, 2018), but in the present hypothesis, *P. yelkouan* is

sister to (*P. lherminieri* + *P. assimilis*), whereas *P. mauretanicus* is closely related to *P. puffinus* and *P. opisthomelas*. Heidrich *et al.* (1998) and Austin *et al.* (2004) have, alternatively, suggested a monophyletic (*P. puffinus* (*P. mauretanicus* + *P. yelkouan*)). Regarding *P. opisthomelas*, the species is, herein, placed between *P. mauretanicus* and *P. gavia*, but in some molecular hypotheses it is found among species from the ‘Little-Audubon’s complex’ (e.g. Austin *et al.*, 2004; Pyle *et al.*, 2011; Tennyson & Shepherd, 2017). The only two members of this group included in the present analyses, *P. lherminieri* and *P. assimilis*, are sister taxa, grouped in the least inclusive clade of the final hypothesis.

CONCLUSION

The hypothesis that *Calonectris* is the sister taxon to a large *Puffinus* (*sensu lato*) clade, presented herein, is congruent with molecular-based hypotheses of Penhallurick & Wink (2004) (*i.e.*, their Maximum Likelihood analysis) and Welch *et al.* (2014). Despite the split of *Puffinus* (*sensu lato*) into two clades in these topologies, *Calonectris* is sister to all other shearwaters.

Although similar in ways, all hypotheses based either on morphology or on cytochrome *b* sequences present conflicting results. The morphological analysis under equal weights could not resolve all tree branches and the implied weight hypothesis have branches with low support values. In both molecular and morphological analyses, most relationships among terminal taxa, especially regarding the placement of subclades of *Puffinus* (*sensu stricto*) within the tree, are still uncertain and are usually presented as poorly resolved polytomies (e.g. Wragg, 1985; Austin *et al.*, 2004; Tennyson & Shepherd, 2017; Kawakami *et al.*, 2018). As Austin (1996) stated, in one of the first molecular-based studies to assess the phylogeny of shearwaters, “the observed

polytomies can be interpreted as a failure of the data set to resolve a truly bifurcating topology or they may be the best estimate of the true evolutionary history of the group.” The final hypothesis, presented herein, is consistent with earlier proposals (*e.g.* Kuroda, 1954) of two sister genera for the shearwaters.

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APPENDIX 1. List of studied specimens.

Institutional abbreviations: USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC; MUCIN, Museu de Ciências Naturais, Universidade Federal do Rio Grande do Sul, Imbé.

Fulmarus glacialis MUCIN 800, 830, 866; *Daption capense* MUCIN 367, 691, 755; *Calonectris diomedea* USNM 620718, 620716, 488776, 620715; *Calonectris leucomelas* USNM 559033, 559034, 558350, 559035; *Calonectris borealis* USNM 17788, 17789, 17791, 17744, MUCIN 023, 210, 327, 343, 393, 396, 397, 398; *Calonectris edwardsii* USNM 560766, 560764, 560762, 560765, MUCIN 334, 927, 994; *Ardenna pacifica* USNM 498256, 631381, 622419, 613235; *Ardenna bulleri* USNM 432186, 621656, 620814, 613921; *Ardenna grisea* USNM 556462, 498305, 614816, 556949, MUCIN 361, 627, 651, 673; *Ardenna tenuirostris* USNM 556482, 500227, 612625, 612626; *Ardenna creatopus* USNM 559556, 559555, 558424, 559558; *Ardenna carneipes* USNM 621658, 621657, 498487, 620812; *Ardenna gravis* USNM 561133, 561124, 559131, 500359, MUCIN 269, 277, 497, 799; *Puffinus nativitatis* USNM 613922, 498068, 615081, 498000; *Puffinus puffinus* USNM 610341, 488785, 611759, 491470, MUCIN 246, 273, 745, 792; *Puffinus yelkouan* USNM 289433, 555938, 487850, 487849; *Puffinus mauretanicus* USNM 613580, 620503, 613581, 620502; *Puffinus opisthomelas* USNM 559676, 19385, 559675; *Puffinus gavia* USNM 614345; *Puffinus huttoni* USNM 430212, 554704, 500860; *Puffinus lherminieri* USNM 488402, 488422, 498006, 498005; *Puffinus assimilis* USNM 488357, 488648.

APPENDIX 2. Matrix of continuous characters (0–5) used in the phylogenetic analyses. For each taxon, min–max values are shown. First row indicates the observed values (in mm) and second row indicates TNT transformed values, from 0 (lowest value measured) to 1 (highest value measured) for each character.

Taxon/character	0	1	2	3	4	5
<i>Fulmarus glacialisoides</i>	97.95–104.25 0.763–0.888	49.44–52.44 0.351–0.448	38.24–41.68 0.794–0.964	46.88–50.36 0.131–0.245	27.55–32.31 0.520–0.747	43.49–46.27 0.706–0.837
<i>Daption capense</i>	76.68–81.58 0.342–0.439	46–46.85 0.240–0.267	29.7–30.29 0.373–0.402	42.83–43.53 0.000–0.022	20.18–22.94 0.168–0.300	35.43–36.28 0.325–0.365
<i>Calonectris leucomelas</i>	92.82–104.97 0.662–0.902	50.87–54.92 0.397–0.528	35.09–38.33 0.639–0.799	50.93–56.24 0.263–0.436	29.96–37 0.635–0.971	39.41–42.2 0.513–0.645
<i>Calonectris diomedea</i>	100.63–104.85 0.816–0.900	54.49–58.19 0.514–0.634	35.13–38 0.641–0.782	53.92–60.19 0.360–0.564	31.64–37.6 0.715–1.000	42.6–45.95 0.664–0.822
<i>Calonectris borealis</i>	103.36–109.9 0.870–1.000	53.19–59.28 0.472–0.669	38.81–40.89 0.822–0.925	53.5–60.82 0.347–0.585	28.48–34.03 0.564–0.829	44.73–49.7 0.765–1.000
<i>Calonectris edwardsii</i>	87.85–91.48 0.563–0.635	46.46–51.6 0.254–0.421	30.85–34.05 0.429–0.587	47.63–52.15 0.156–0.303	25.26–27.52 0.411–0.519	35.77–40.46 0.341–0.563
<i>Ardenna pacifica</i>	80.34–88.13 0.415–0.569	46.69–50.24 0.262–0.377	31.66–34.01 0.469–0.585	44.63–50.68 0.058–0.255	23–29.92 0.303–0.633	37.86–40.34 0.440–0.557
<i>Ardenna bulleri</i>	87.58–92 0.558–0.645	45.72–47.44 0.230–0.286	30.74–36.55 0.424–0.711	45.89–48.93 0.099–0.198	25.35–28.15 0.415–0.549	37.54–40.26 0.425–0.553
<i>Ardenna grisea</i>	93.4–96.57 0.673–0.736	65.87–69.49 0.882–1.000	37.75–41.26 0.770–0.943	70.45–73.56 0.898–0.999	31.03–33.32 0.686–0.795	47.77–48.72 0.908–0.953
<i>Ardenna tenuirostris</i>	77.37–79.98 0.356–0.408	55.74–61.94 0.555–0.755	35.9–39.18 0.679–0.841	58.77–63.98 0.518–0.688	27.35–30.87 0.510–0.678	40.72–44.83 0.575–0.769
<i>Ardenna creatopus</i>	94.25–97.94 0.690–0.763	57.41–59.54 0.609–0.678	38.81–40.48 0.822–0.905	56.85–61.1 0.456–0.594	32.57–35.73 0.760–0.910	44.18–45.87 0.739–0.818
<i>Ardenna carneipes</i>	93.34–97.21 0.672–0.748	57.94–60.92 0.626–0.722	38.3–39.09 0.797–0.836	60.4–63.84 0.571–0.683	29.64–34.47 0.620–0.850	45.33–47.26 0.793–0.884
<i>Ardenna gravis</i>	97.52–98.97 0.755–0.783	56.11–59.24 0.567–0.668	38.75–42.4 0.819–1.000	55.79–59.45 0.421–0.540	29.45–36.73 0.611–0.958	44.26–47.77 0.742–0.908
<i>Puffinus nativitatis</i>	68.83–72.83 0.187–0.266	50.86–54.02 0.397–0.499	27.32–30.05 0.255–0.390	58.88–62.78 0.522–0.649	21.42–23.66 0.228–0.334	36.56–38.47 0.379–0.469
<i>Puffinus puffinus</i>	75.35–81.25 0.316–0.433	53.11–56.65 0.470–0.584	28.81–30.98 0.329–0.436	61.06–65.25 0.593–0.729	25.64–27.12 0.429–0.500	37.31–38.15 0.414–0.454
<i>Puffinus yelkouan</i>	78.76–81.61 0.383–0.440	50.67–57.46 0.391–0.610	28.21–33.17 0.299–0.544	58.09–65.91 0.496–0.751	24.04–27.32 0.353–0.509	38.68–41.97 0.479–0.634
<i>Puffinus mauretanicus</i>	83.3–90.52 0.473–0.616	60.6–63.83 0.712–0.816	31.96–34.9 0.484–0.629	63.92–72.39 0.686–0.961	23.76–30.22 0.339–0.647	40.63–43.28 0.570–0.696
<i>Puffinus opisthomelas</i>	78.62–85.72 0.381–0.521	54.35–56.2 0.510–0.570	30.69–31.64 0.422–0.468	60.71–63.04 0.581–0.657	25.54–27.52 0.424–0.519	37.09–40.4 0.404–0.560
<i>Puffinus gavia</i>	80.38 0.416	55.89 0.560	28.77 0.327	64.47 0.704	24.06 0.354	39.3 0.508
<i>Puffinus huttoni</i>	79.99–81.63 0.408–0.440	52.49–56.36 0.450–0.575	28.54–29.23 0.315–0.349	59.05–61.86 0.527–0.619	23.12–27.37 0.309–0.511	38.03–38.6 0.448–0.475
<i>Puffinus lherminieri</i>	59.35–68.39 0.000–0.178	38.58–45.03 0.000–0.208	22.14–24.71 0.000–0.126	45.14–53.17 0.075–0.336	16.64–19.03 0.000–0.114	28.54–33.46 0.000–0.232
<i>Puffinus assimilis</i>	67.05 0.152	41–42.62 0.078–0.130	24.11–26.26 0.097–0.203	44.25–45.29 0.046–0.080	17.84–19.42 0.057–0.132	32.02–34.92 0.164–0.301

APPENDIX 2 (*cont.*). Matrix of continuous characters (6–11) used in the phylogenetic analyses. For each taxon, min–max values are shown. First row indicates the observed values (in mm) and second row indicates TNT transformed values, from 0 (lowest value measured) to 1 (highest value measured) for each character.

Taxon/character	6	7	8	9	10	11
<i>Fulmarus glacialisoides</i>	47.25–50.03 0.765–0.879	30.63–32.83 0.697–0.885	23.99–26.82 0.663–0.873	107.97–113.25 0.649–0.725	105.54–112.17 0.628–0.713	103.16–109.67 0.639–0.725
<i>Daption capense</i>	38.61–40.15 0.409–0.472	25.19–26.3 0.234–0.328	20.42–20.81 0.397–0.427	82.82–87.9 0.286–0.359	79.49–84.54 0.296–0.360	77.06–81.61 0.298–0.358
<i>Calonectris leucomelas</i>	48.6–50 0.820–0.878	29.47–31.88 0.598–0.804	24.55–26.01 0.704–0.813	119.11–124.39 0.810–0.887	122.71–127.29 0.848–0.906	119.93–123.66 0.859–0.907
<i>Calonectris diomedea</i>	43.08–45.18 0.593–0.679	27.48–30.52 0.429–0.688	22.73–25.5 0.569–0.775	113.61–117.74 0.731–0.790	112.65–119.1 0.719–0.802	110.42–117.22 0.734–0.823
<i>Calonectris borealis</i>	45.44–51.44 0.690–0.937	29.97–34.18 0.641–1.000	25.5–27.74 0.775–0.941	122.22–132.2 0.855–1.000	125.99–134.6 0.890–0.999	122.55–130.71 0.893–1.000
<i>Calonectris edwardsii</i>	35.53–43.45 0.282–0.608	24.66–27.48 0.189–0.429	21.04–23.2 0.444–0.604	104.21–106.65 0.595–0.630	107.25–109.7 0.650–0.681	104.58–107.84 0.658–0.701
<i>Ardenna pacifica</i>	36.72–38.98 0.331–0.424	24.82–26.97 0.202–0.385	21.88–22.86 0.506–0.579	99.4–106.11 0.525–0.622	102.45–110.03 0.589–0.686	100.2–105.57 0.601–0.671
<i>Ardenna bulleri</i>	39.83–41.65 0.459–0.534	26.78–27.28 0.369–0.412	21.37–22.89 0.468–0.581	97.24–99.11 0.494–0.521	98.21–100.31 0.535–0.562	95.39–97.79 0.538–0.569
<i>Ardenna grisea</i>	46.55–52.96 0.736–0.999	32.44–33.31 0.851–0.925	26.45–27.88 0.845–0.951	103.77–106.97 0.588–0.635	98.45–99.6 0.538–0.553	94.89–95.98 0.531–0.546
<i>Ardenna tenuirostris</i>	42.26–47 0.559–0.754	29.33–30.71 0.586–0.704	24.04–26.02 0.666–0.813	97.3–102.93 0.495–0.576	91.71–95.95 0.452–0.506	88.63–92 0.450–0.494
<i>Ardenna creatopus</i>	45.53–50.35 0.694–0.892	32.16–32.96 0.827–0.896	25.98–27.58 0.810–0.929	112.05–114.63 0.708–0.745	110.75–113.13 0.695–0.725	107.09–109.71 0.691–0.725
<i>Ardenna carneipes</i>	46.54–47.78 0.735–0.786	31.74–33.78 0.792–0.965	24.74–26.92 0.718–0.880	111.64–113.28 0.702–0.726	111.07–115.01 0.699–0.749	107.59–111.02 0.697–0.742
<i>Ardenna gravis</i>	46.45–49.91 0.732–0.874	31.09–32.04 0.736–0.817	25.75–28.53 0.793–1.000	116.32–120.2 0.770–0.826	114.5–117.4 0.743–0.780	110.97–112.95 0.741–0.767
<i>Puffinus nativitatis</i>	38.02–39.79 0.385–0.458	25.83–27.96 0.288–0.470	18.92–20.24 0.287–0.385	78.66–83.21 0.225–0.291	79.62–82.31 0.297–0.332	77.18–79.32 0.300–0.328
<i>Puffinus puffinus</i>	39.85–43.85 0.460–0.625	27.6–29.72 0.439–0.620	19.37–20.3 0.320–0.388	76.97–79.73 0.201–0.241	69.32–73.5 0.166–0.219	66.76–70.78 0.164–0.216
<i>Puffinus yelkouan</i>	39.82–44.26 0.459–0.641	29.07–29.81 0.564–0.627	20.13–20.57 0.376–0.409	78.08 0.217	70.76 0.184	68.56 0.187
<i>Puffinus mauretanicus</i>	42.9–46.58 0.586–0.737	30.73–32.88 0.706–0.889	21.11–22.38 0.449–0.543	83.92–85.93 0.301–0.330	76.34–77.75 0.255–0.273	73.22–74.81 0.248–0.269
<i>Puffinus opisthomelas</i>	41.51–44.67 0.528–0.658	29.72–30.5 0.620–0.686	20.96–21.37 0.438–0.468	85.78–86.01 0.328–0.332	78.81–78.87 0.287–0.288	75.46–75.69 0.277–0.280
<i>Puffinus gavia</i>	43.98 0.630	29.22 0.577	19.86 0.356	74.25 0.162	65.18 0.113	62.31 0.105
<i>Puffinus huttoni</i>	40.62–43.09 0.492–0.593	27.92–28.28 0.466–0.497	18.62–19.84 0.264–0.355	75.21–75.6 0.175–0.181	67.41–68.24 0.141–0.152	65.48–65.63 0.147–0.149
<i>Puffinus lherminieri</i>	28.66–34.29 0.000–0.231	22.44–24.53 0.000–0.178	15.05–17.03 0.000–0.146	63.04–66.42 0.000–0.048	61.49–63.64 0.066–0.093	59.58–61.6 0.070–0.096
<i>Puffinus assimilis</i>	32.97–37.08 0.177–0.346	22.98–23.27 0.045–0.070	16.6–17.78 0.114–0.202	64.66 0.023	56.3 0.000	54.2 0.000

APPENDIX 2 (*cont.*). Matrix of continuous characters (12–17) used in the phylogenetic analyses. For each taxon, min–max values are shown. First row indicates the observed values (in mm) and second row indicates TNT transformed values, from 0 (lowest value measured) to 1 (highest value measured) for each character.

Taxon/character	12	13	14	15	16	17
<i>Fulmarus glacialisoides</i>	50.04–55.94 0.502–0.688	53.75–58.8 0.322–0.458	25.85–26.05 0.985–1.000	46.75–49.71 0.613–0.726	12–13.57 0.758–0.964	46.02–49.19 0.877–1.000
<i>Daption capense</i>	40.68–42.06 0.208–0.252	45.24–48.9 0.092–0.191	20.4–21.08 0.586–0.636	38.5–40.95 0.299–0.392	11–11.46 0.627–0.687	36.68–37.81 0.518–0.561
<i>Calonectris leucomelas</i>	60.13–62.12 0.820–0.882	58.04–63.7 0.437–0.590	20.91–22.05 0.623–0.707	43.9–47.63 0.504–0.647	12.14–12.69 0.776–0.849	39.04–41.46 0.609–0.702
<i>Calonectris diomedea</i>	53.75–58.82 0.619–0.779	53.69–60.1 0.320–0.493	21.33–22.29 0.654–0.724	42.65–45.32 0.457–0.559	11.41–12.4 0.681–0.811	39.19–41.07 0.615–0.687
<i>Calonectris borealis</i>	60.24–65.85 0.823–1.000	62.87–66.48 0.568–0.665	21.7–23.9 0.681–0.842	47.83–53.68 0.654–0.877	11.12–13.84 0.643–1.000	42.45–45.78 0.740–0.868
<i>Calonectris edwardsii</i>	50.45–52.05 0.515–0.566	51.7–57.55 0.266–0.424	16.73–20.68 0.317–0.606	38.05–43.79 0.281–0.500	9.42–11.73 0.419–0.723	33.44–38.11 0.393–0.573
<i>Ardenna pacifica</i>	50.62–53.65 0.521–0.616	54.9–59.77 0.353–0.484	18.1–19.61 0.418–0.528	41.11–44.43 0.398–0.525	9.93–10.62 0.486–0.577	33.73–36.72 0.404–0.520
<i>Ardenna bulleri</i>	49.51–51.21 0.486–0.539	57.78–60.23 0.430–0.496	17.74–20.08 0.391–0.562	41.25–45.84 0.403–0.578	9.81–11.7 0.471–0.719	35.43–37.96 0.470–0.567
<i>Ardenna grisea</i>	54.16–55.86 0.632–0.685	75.49–78.34 0.908–0.985	20.24–20.91 0.574–0.623	54.73–56.88 0.918–0.999	11.39–12.64 0.678–0.842	37.06–38.81 0.533–0.600
<i>Ardenna tenuirostris</i>	49.09–51.57 0.473–0.551	62.6–66.8 0.560–0.674	17.56–19.3 0.378–0.505	48.56–53.15 0.682–0.857	10.15–11.6 0.514–0.706	36.53–38.1 0.512–0.573
<i>Ardenna creatopus</i>	58.38–60.03 0.765–0.817	64.9–68.24 0.622–0.712	20.67–23.83 0.606–0.837	47.12–51.56 0.627–0.797	11.72–13.34 0.721–0.934	39.49–41.56 0.626–0.706
<i>Ardenna carneipes</i>	57.09–59.43 0.724–0.798	64.06–67.26 0.600–0.686	21.44–22.7 0.662–0.754	48.21–51.02 0.669–0.776	11.55–13 0.699–0.889	39.01–40.47 0.608–0.663
<i>Ardenna gravis</i>	59.56–61.89 0.802–0.875	71.18–78.89 0.792–1.000	21.18–23.29 0.643–0.797	54.59–55.9 0.912–0.962	11.1–12.67 0.640–0.846	40.72–42.65 0.673–0.748
<i>Puffinus nativitatis</i>	43.36–47.03 0.292–0.408	49.97–54.12 0.220–0.332	14.78–15.87 0.174–0.254	39.11–40.83 0.322–0.387	8.4–8.8 0.286–0.338	27.91–29.41 0.180–0.238
<i>Puffinus puffinus</i>	42.03–44.34 0.251–0.323	51.28–56.23 0.255–0.389	14.4–16.29 0.147–0.285	39.69–42.79 0.344–0.462	7.49–8.65 0.166–0.318	29.06–31.29 0.225–0.311
<i>Puffinus yelkouan</i>	42.97 0.280	52.54–56.87 0.289–0.406	13.71–17.06 0.096–0.341	42.08–44.97 0.435–0.545	7.91–9.1 0.221–0.377	30.01–30.81 0.261–0.292
<i>Puffinus mauretanicus</i>	45.07–47.62 0.346–0.426	58.8–60.63 0.458–0.507	16.86–18.07 0.327–0.415	44.5–46.56 0.527–0.606	8.84–9.65 0.343–0.450	31.91–34.49 0.334–0.434
<i>Puffinus opisthomelas</i>	45.98–46.01 0.375–0.376	55.42–57.51 0.367–0.423	16.42–17.99 0.295–0.409	41.83–43.66 0.426–0.495	8.85–9.34 0.345–0.409	33.05–33.43 0.378–0.393
<i>Puffinus gavia</i>	39.5 0.171	56.44 0.394	15.6 0.234	39.5 0.337	8.57 0.308	30.81 0.292
<i>Puffinus huttoni</i>	40.38–40.87 0.199–0.214	52.48–53.25 0.287–0.308	15.49 0.226	37.81–39.46 0.272–0.335	7.91–8.32 0.221–0.275	29.86–30.66 0.255–0.286
<i>Puffinus lherminieri</i>	34.41–36.54 0.011–0.078	41.8–47.65 0.000–0.157	12.39–14.03 0.000–0.120	30.66–32.56 0.000–0.072	6.22–7.17 0.000–0.124	23.21–26.08 0.000–0.110
<i>Puffinus assimilis</i>	34.04 0.000	47.99–48.47 0.166–0.179	13.91–15.25 0.111–0.209	35.93–37 0.200–0.241	6.71–7.88 0.064–0.217	25.8–26.94 0.099–0.143

APPENDIX 2 (*cont.*). Matrix of continuous characters (18–22) used in the phylogenetic analyses. For each taxon, min–max values are shown. First row indicates the observed values (in mm) and second row indicates TNT transformed values, from 0 (lowest value measured) to 1 (highest value measured) for each character.

Taxon/character	18	19	20	21	22
<i>Fulmarus glacialisoides</i>	3.8–4.09 0.619–0.739	91.1–95.3 0.694–0.789	82.11–86.79 0.840–0.964	8.12–8.99 0.095–0.162	47.91–52.35 0.470–0.663
<i>Daption capense</i>	3.32–3.73 0.421–0.590	79.15–83.1 0.424–0.513	70.69–74.64 0.538–0.643	8.46–9.09 0.121–0.170	43.8–45.76 0.291–0.376
<i>Calonectris leucomelas</i>	3.69–3.86 0.574–0.644	83.68–86.88 0.526–0.598	74.86–78.55 0.648–0.746	8.33–8.82 0.111–0.149	52.07–53.82 0.651–0.727
<i>Calonectris diomedea</i>	3.79–4.02 0.615–0.710	78.83–84.29 0.416–0.540	71.11–75.48 0.549–0.665	7.63–8.81 0.057–0.148	48.2–51.91 0.482–0.644
<i>Calonectris borealis</i>	4.2–4.54 0.785–0.925	88.94–96.04 0.645–0.805	79.77–86.74 0.778–0.963	9.17–10.03 0.176–0.241	54.71–58.88 0.766–0.948
<i>Calonectris edwardsii</i>	3.32–3.68 0.421–0.570	72.9–77.76 0.282–0.392	66.02–69.83 0.415–0.515	6.88–7.93 0.000–0.080	44.43–47.09 0.318–0.434
<i>Ardenna pacifica</i>	3.4–3.6 0.454–0.537	76.7–82.33 0.368–0.495	66.45–71.53 0.426–0.560	10.06–10.8 0.244–0.302	46.89–49.74 0.425–0.549
<i>Ardenna bulleri</i>	3.44–3.77 0.471–0.607	82.55–86.21 0.500–0.583	71.55–74.97 0.561–0.651	11–11.45 0.317–0.352	50.81–51.43 0.596–0.623
<i>Ardenna grisea</i>	4.21–4.72 0.789–1.000	100.2–103.2 0.900–0.967	82.9–83.53 0.861–0.878	17.3–19.86 0.802–0.999	55.1–56.12 0.783–0.827
<i>Ardenna tenuirostris</i>	03.77–4.17 0.607–0.772	92.47–97.72 0.725–0.843	76.91–81.37 0.703–0.821	15.4–16.35 0.656–0.729	50.98–53.93 0.603–0.732
<i>Ardenna creatopus</i>	4.04–4.38 0.719–0.859	91.88–95.35 0.711–0.790	77.87–81.75 0.728–0.831	13.1–14.01 0.479–0.549	53.17–55.22 0.699–0.788
<i>Ardenna carneipes</i>	3.78–4.22 0.611–0.793	90.52–91.8 0.681–0.710	76.88–78.84 0.702–0.754	12.96–13.64 0.468–0.520	53.63–55.68 0.719–0.808
<i>Ardenna gravis</i>	4.51–4.67 0.913–0.979	100.85–104.62 0.914–1.000	85.3–88.13 0.925–0.999	15.55–17.08 0.667–0.785	57.74–60.07 0.898–1.000
<i>Puffinus nativitatis</i>	2.84–3.11 0.223–0.334	70.93–75.96 0.238–0.351	59.16–62.22 0.233–0.314	11.77–13.74 0.376–0.528	42.77–45.57 0.246–0.368
<i>Puffinus puffinus</i>	3.2–3.4 0.371–0.454	76.36–78.9 0.360–0.418	62.36–63.98 0.318–0.361	14–15.03 0.548–0.627	44.01–45.71 0.300–0.374
<i>Puffinus yelkouan</i>	3.18–3.39 0.363–0.450	79.51 0.432	65.18 0.392	14.33 0.573	48.18 0.481
<i>Puffinus mauretanicus</i>	3.35–3.75 0.433–0.599	84.48–86.28 0.544–0.585	69.09–70.01 0.496–0.520	15.33–16.66 0.651–0.753	48.31–49.98 0.487–0.560
<i>Puffinus opisthomelas</i>	3.32–3.6 0.421–0.537	79.73–82.03 0.437–0.489	66.3–68.92 0.422–0.491	13.11–13.43 0.479–0.504	46.3–49 0.400–0.517
<i>Puffinus gavia</i>	2.94 0.264	77.26 0.381	63.65 0.352	13.61 0.518	44.47 0.320
<i>Puffinus huttoni</i>	3.22–3.23 0.380–0.384	75.27 0.336	61.89 0.305	13.38 0.500	42.47 0.233
<i>Puffinus lherminieri</i>	2.3–2.6 0.000–0.123	60.4–66.29 0.000–0.133	50.33–54.05 0.000–0.098	10.07–12.24 0.244–0.412	37.12–40.03 0.000–0.126
<i>Puffinus assimilis</i>	2.95–3.09 0.268–0.326	71.3 0.246	58.21 0.208	13.09 0.478	40.21 0.134

APPENDIX 3. Matrix of discrete characters (23–103) used in the phylogenetic analyses.

Characters	23–32	33–42	43–52	53–62	63–72	73–82	83–92	93–103
<i>Fulmarus glacialoides</i>	1100010110	1010110000	1100000110	0100001000	0000101000	1000000000	0000000100	00000001000
<i>Daption capense</i>	1100010100	0010111000	1110001110	0100002000	1000101000	0000000000	0001000100	00001011001
<i>Calonectris leucomelas</i>	0000000110	1110000000	0001000101	1000000000	0000100000	0000000100	0002000110	00000000010
<i>Calonectris diomedea</i>	0000000110	1110000000	0001000101	1100000000	0000100000	0000000101	0001000110	00000000000
<i>Calonectris borealis</i>	0000000110	1110000000	0001010101	1100000000	0000100000	0000000101	0002000110	00000000010
<i>Calonectris edwardsii</i>	1000000110	1110000000	0001010101	1100000000	0000100000	0000000001	0002000110	00000000010
<i>Ardenna pacifica</i>	1101000110	1010010010	0101000001	1001001000	0010101000	0000000111	1012000001	11011010001
<i>Ardenna bulleri</i>	0110110110	1020110010	0001000001	0001001000	1101101000	0000000111	1002001001	01011010001
<i>Ardenna grisea</i>	1110111100	0001121111	1111110011	0101110010	1101102101	1111211011	1110010001	11112011101
<i>Ardenna tenuirostris</i>	1111111100	0001021111	1111110010	0001110010	1101102101	1001211011	1110010001	11112011101
<i>Ardenna creatopus</i>	1110011110	1010110010	0101000111	0101000000	0111101101	0100000001	0002000001	00111011000
<i>Ardenna carneipes</i>	1110101110	1011110110	0101000001	0001000010	0101101101	0100000001	0112010001	00111011001
<i>Ardenna gravis</i>	0110111110	1011110010	0111110101	0001000000	0101101101	0000100011	1112011001	11111011001
<i>Puffinus nativitatis</i>	1100011111	1111121000	1111100011	0110112111	1111112111	1111111011	1111000001	11012111101
<i>Puffinus puffinus</i>	1110111001	0011021110	1111111010	0111112111	1101112111	1111111011	1110001001	11012111101
<i>Puffinus yelkouan</i>	1111111001	0010121110	1111111010	0111111111	1101012111	1111111011	1110111001	11012111101
<i>Puffinus mauretanicus</i>	1110111001	0011021110	1111111111	0111112111	1111112111	1111111011	1110110001	11012111101
<i>Puffinus opisthomelas</i>	0110011001	0010021111	1111111011	0111111111	1101112111	1111111111	1110111001	11011111101
<i>Puffinus gavia</i>	0110111001	0001021110	1011111011	0111112111	1101112111	1111111011	1110111001	11012111101
<i>Puffinus huttoni</i>	0110111001	0110021110	1111111010	0111112111	1101112111	1111111011	1110111001	11012111101
<i>Puffinus lherminieri</i>	0101111001	0010121110	1101111011	0011112111	1101112111	0111111011	1110101001	11012111101
<i>Puffinus assimilis</i>	1111111001	0011121110	1001111010	0111112111	0101112111	1111111011	1110101001	11012111101

APPENDIX 4. Results of implied weight analysis with different constants of concavity, *K*. Cladograms used to construct the final hypothesis are those shaded in grey (see Appendix 5). Ci = consistency index; Ri = retention index.

<i>K</i>	N° of trees	Steps	Tree Fit	Adjusted homoplasy	CI	RI
K0 = 1.164	1	231.075	63.87	39.13	0.457	0.801
K1 = 1.261	1	231.075	65.16	37.84	0.457	0.801
K2 = 1.366	1	231.075	66.47	36.53	0.457	0.801
K3 = 1.481	1	231.075	67.78	35.22	0.457	0.801
K4 = 1.607	1	231.075	69.11	33.89	0.457	0.801
K5 = 1.746	1	231.075	70.46	32.54	0.457	0.801
K6 = 1.899	1	231.075	71.82	31.18	0.457	0.801
K7 = 2.069	1	230.342	73.19	29.81	0.459	0.802
K8 = 2.259	1	230.342	74.58	28.42	0.459	0.802
K9 = 2.473	1	229.005	76.00	27.00	0.461	0.804
K10 = 2.715	1	229.005	77.43	25.66	0.461	0.804
K11 = 2.992	1	229.005	78.89	24.11	0.461	0.804
K12 = 3.312	1	227.859	80.37	22.63	0.464	0.806
K13 = 3.685	1	227.859	81.90	21.10	0.464	0.806
K14 = 4.126	1	227.859	83.44	19.56	0.464	0.806
K15 = 4.655	1	227.859	85.02	17.98	0.464	0.806
K16 = 5.301	1	227.859	86.62	16.38	0.464	0.806
K17 = 6.109	1	227.859	88.25	14.75	0.464	0.806
K18 = 7.149	1	227.583	89.93	13.07	0.464	0.806
K19 = 8.534	1	227.583	91.64	11.36	0.464	0.806
K20 = 10.473	1	227.583	93.40	9.60	0.464	0.806

APPENDIX 5. Pairwise SPR distances for the 21 fittest cladograms resulting from the analysis under implied weights with different constants of concavity, K (see Appendix 4). Cladograms used to construct the final hypothesis are those shaded in grey.

Trees	K0	K1	K2	K3	K4	K5	K6	K7	K8	K9	K10	K11	K12	K13	K14	K15	K16	K17	K18	K19	K20
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
0	–	0	0	0	0	0	0	2	2	4	4	4	5	5	5	5	5	5	6	6	6
1	0	–	0	0	0	0	0	2	2	4	4	4	5	5	5	5	5	5	6	6	6
2	0	0	–	0	0	0	0	2	2	4	4	4	5	5	5	5	5	5	6	6	6
3	0	0	0	–	0	0	0	2	2	4	4	4	5	5	5	5	5	5	6	6	6
4	0	0	0	0	–	0	0	2	2	4	4	4	5	5	5	5	5	5	6	6	6
5	0	0	0	0	0	–	0	2	2	4	4	4	5	5	5	5	5	5	6	6	6
6	0	0	0	0	0	0	–	2	2	4	4	4	5	5	5	5	5	5	6	6	6
7	2	2	2	2	2	2	2	–	0	2	2	2	3	3	3	3	3	3	4	4	4
8	2	2	2	2	2	2	2	0	–	2	2	2	3	3	3	3	3	3	4	4	4
9	4	4	4	4	4	4	4	2	2	–	0	0	1	1	1	1	1	1	2	2	2
10	4	4	4	4	4	4	4	2	2	0	–	0	1	1	1	1	1	1	2	2	2
11	4	4	4	4	4	4	4	2	2	0	0	–	1	1	1	1	1	1	2	2	2
12	5	5	5	5	5	5	5	3	3	1	1	1	–	0	0	0	0	0	1	1	1
13	5	5	5	5	5	5	5	3	3	1	1	1	0	–	0	0	0	0	1	1	1
14	5	5	5	5	5	5	5	3	3	1	1	1	0	0	–	0	0	0	1	1	1
15	5	5	5	5	5	5	5	3	3	1	1	1	0	0	0	–	0	0	1	1	1
16	5	5	5	5	5	5	5	3	3	1	1	1	0	0	0	0	–	0	1	1	1
17	5	5	5	5	5	5	5	3	3	1	1	1	0	0	0	0	0	–	1	1	1
18	6	6	6	6	6	6	6	4	4	2	2	2	1	1	1	1	1	1	–	0	0
19	6	6	6	6	6	6	6	4	4	2	2	2	1	1	1	1	1	1	0	–	0
20	6	6	6	6	6	6	6	4	4	2	2	2	1	1	1	1	1	1	0	0	–
Total	64	64	64	64	64	64	64	50	50	44	44	44	47	47	47	47	47	47	62	62	62

APPENDIX 6. List of character transformations obtained from the final hypothesis analysis, for both continuous and discrete characters. Those marked with an asterisk (*) represent ambiguous character-states transformations resolved using either ACCTTRAN or DELTRAN. Node numbers are those assigned by TNT, as used in Figure 28.

SYNAPOMORPHIES	Char. 59: (1) > (0)
Node 27:	Char. 69: (1) > (0)
Char. 28: (1) > (0)*	Char. 91: (0) > (1)
Char. 37: (1) > (0)*	Char. 97: (1) > (0)*
Char. 43: (1) > (0)	Char. 99: (1) > (0)*
Char. 46: (0) > (1)	Char. 102: (0) > (1)
Char. 51: (1) > (0)	Char. 103: (1) > (0)*
Char. 52: (0) > (1)	Node 25:
Char. 53: (0) > (1)*	Char. 0: (90.57-92) > (92.82-121.98)
Char. 80: (0) > (1)*	Char. 4: (27.55-28.15) > (29.96-31.64)
Char. 82: (0) > (1)	Char. 9: (106.11-106.65) > (113.61-117.74)
Char. 86: (1) > (2)	Char. 10: (107.25-109.7) > (112.65-119.1)
Char. 100: (1) > (0)	Char. 11: (104.58-107.84) > (110.42-117.22)
Node 26:	Char. 12: (51.21-52.05) > (53.75-58.82)
Char. 24: (1) > (0)	Char. 14: (20.67-21.08) > (21.33-21.7)
Char. 28: (1) > (0)*	Char. 17: (37.96-38.1) > (39.19-41.07)
Char. 34: (0) > (1)	Char. 18: (3.73-3.77) > (3.79-3.86)
Char. 37: (1) > (0)*	Char. 23: (1) > (0)
Char. 38: (1) > (0)	Char. 80: (0) > (1)*
Char. 44: (1) > (0)	Node 24:
Char. 53: (0) > (1)*	Char. 5: (40.34-42.2) > (42.6-44.73)

Char. 6: (43.09-45.18) > (45.44-48.6)

Char. 9: (113.61-117.74) > (119.11-122.22)

Char. 10: (112.65-119.1) > (122.71-125.99)

Char. 11: (110.42-117.22) > (119.93-122.55)

Char. 12: (53.75-58.82) > (60.13-60.24)

Char. 22: (48.2-51.91) > (52.07-53.82)

Node 28

Char. 21: (8.81-8.99) > (10.06-10.8)

Char. 41: (0) > (1)

Char. 50: (1) > (0)

Char. 54: (1) > (0)

Char. 56: (0) > (1)

Char. 81: (0) > (1)*

Char. 83: (0) > (1)*

Char. 90: (1) > (0)

Char. 92: (0) > (1)

Char. 94: (0) > (1)*

Char. 96: (0) > (1)

Char. 97: (0) > (1)*

Char. 99: (0) > (1)*

Char. 103: (0) > (1)*

Node 29:

Char. 21: (10.06-10.8) > (11-11.45)

Char. 22: (47.91-49.74) > (50.81-51.43)

Char. 25: (0) > (1)

Char. 27: (0) > (1)*

Char. 28: (0) > (1)*

Char. 37: (0) > (1)*

Char. 53: (1) > (0)*

Char. 64: (0) > (1)

Char. 66: (0) > (1)

Node 34:

Char. 0: (90.57-92) > (93.34-94.25)

Char. 1: (46.77-50.24) > (57.41-57.94)

Char. 2: (34.05-36.55) > (38.3-39.36)

Char. 3: (48.93-50.68) > (56.85-60.4)

Char. 4: (27.55-28.15) > (29.64-30.87)

Char. 5: (40.34-40.46) > (44.18-44.83)

Char. 6: = (41.65-43.45) > (45.53-46.54)

Char. 7: (27.28-27.48) > (31.09-31.74)

Char. 8: (22.89-23.2) > (25.75-25.98)

Char. 9: (106.11-106.65) > (111.64-112.05)

Char. 10: (105.54-109.7) > (110.75-111.07)

Char. 11: (103.16-105.57) > (107.09-107.59)

Char. 12: (51.21-52.05) > (57.09-58.38)

Char. 13: (57.78-60.23) > (64.9-66.8)

Char. 15: (44.43-45.84) > (47.12-51.02)

Char. 17: (37.96-38.1) > (39.01-39.49)

Char. 18: (3.73-3.77) > (4.04-4.17)

Char. 19: (83.1-86.21) > (91.8-91.88)

Char. 20: (74.64-74.97) > (77.87-78.84)

Char. 21: (11-11.45) > (13.1-13.64)

Char. 22: (50.81-51.43) > (53.17-53.93)

Char. 29: (0) > (1)

Char. 59: (1) > (0)

Char. 70: (0) > (1)

Char. 72: (0) > (1)

Char. 74: (0) > (1)

Char. 80: (1) > (0)*

Char. 81: (1) > (0)*

Char. 83: (1) > (0)*

Char. 94: (1) > (0)*

Char. 95: (0) > (1)

Char. 100: (0) > (1)

Node 33:

Char. 27: (0) > (1)*

Char. 36: (0) > (1)

Char. 40: (0) > (1)*

Char. 61: (0) > (1)*

Char. 84: (0) > (1)

Char. 85: (0) > (1)

Char. 88: (0) > (1)

Node 32:

Char. 21: (13.1-13.64) > (14-15.55)

Char. 45: (0) > (1)

Char. 47: (0) > (1)

Char. 48: (0) > (1)

Char. 77: (0) > (1)

Char. 81: (0) > (1)

Char. 83: (0) > (1)

Char. 93: (0) > (1)

Char. 94: (0) > (1)

Node 31:

Char. 3: (59.45-60.4) > (62.78-63.04)

Char. 9: (111.64-112.05) > (102.93-103.77)

Char. 10: (110.75-111.07) > (95.95-98.45)

Char. 11: (107.09-107.59) > (92-94.89)

Char. 12: (57.09-58.38) > (51.57-54.16)

Char. 14: (20.68-21.18) > (19.3-20.24)

Char. 17: (39.01-39.49) > (37.06-38.1)

Char. 31: (1) > (0)*

Char. 33: (1) > (0)*

Char. 38: (1) > (2)

Char. 39: (0) > (1)

Char. 43: (0) > (1)

Char. 51: (0) > (1)

Char. 54: (0) > (1)*

Char. 57: (0) > (1)

Char. 58: (0) > (1)

Char. 61: (0) > (1)*

Char. 63: (0) > (1)	Char. 9: (102.93-103.77) > (83.21-83.92)
Char. 69: (1) > (2)	Char. 10: (95.95-98.45) > (79.62-82.31)
Char. 73: (0) > (1)	Char. 11: (92-94.89) > (77.18-79.32)
Char. 75: (0) > (1)*	Char. 12: (51.57-54.16) > (45.07-47.03)
Char. 76: (0) > (1)	Char. 13: (64.9-66.8) > (56.23-56.44)
Char. 78: (0) > (1)	Char. 14: (19.3-20.24) > (16.29-16.42)
Char. 79: (0) > (1)	Char. 15: (48.21-53.15) > (41.83-42.79)
Char. 86: (2) > (0)	Char. 16: (11.39-11.6) > (8.8-8.84)
Char. 97: (1) > (2)	Char. 17: (37.06-38.11) > (31.29-31.91)
Char. 101: (0) > (1)	Char. 18: (4.04-4.17) > (3.32-3.35)
Node 30:	Char. 19: (91.8-97.72) > (78.9-79.73)
Char. 31: (1) > (0)*	Char. 20: (77.87-81.37) > (63.98-66.3)
Char. 33: (1) > (0)*	Char. 22: (53.63-53.93) > (45.71-46.3)
Char. 35: (1) > (0)*	Char. 32: (0) > (1)
Char. 40: (0) > (1)*	Char. 54: (0) > (1)*
Char. 42: (0) > (1)	Char. 55: (0) < (1)
Char. 77: (1) > (2)	Char. 59: (0) > (2)
Node 35:	Char. 60: (0) > (1)
Char. 1: (57.41-57.94) > (55.89-56.65)	Char. 62: (0) > (1)
Char. 2: (37.75-39.36) > (30.69-30.98)	Char. 68: (0) > (1)
Char. 4: (29.64-30.87) > (25.54-25.64)	Char. 71: (0) > (1)
Char. 5: (44.26-44.83) > (38.47-39.3)	Char. 75: (0) > (1)*
Char. 6: (46.45-46.54) > (42.9-43.85)	Char. 88: (1) > (0)*
Char. 7: (30.71-31.74) > (29.72)	Char. 95: (1) > (0)
Char. 8: (25.75-25.98) > (20.3-20.96)	Char. 98: (0) > (1)

Node 36:

Char. 10: (79.62-82.31) > (76.34-77.75)

Char. 11: (77.18-79.32) > (73.22-74.81)

Char. 30: (1) > (0)

Char. 31: (1) > (0)*

Char. 33: (1) > (0)*

Char. 37: (1) > (0)

Char. 40: (0) > (1)*

Char. 49: (0) > (1)

Char. 89: (0) > (1)*

Node 41:

Char. 87: (0) > (1)

Char. 88: (0) > (1)*

Node 40:

Char. 21: (14-15.03) > (13.43-13.61)

Char. 23: (1) > (0)

Char. 36: (1) > (0)*

Char. 89: (0) > (1)*

Node 39:

Char. 2: (30.69-30.98) > (28.77)

Char. 4: (25.54-25.64) > (24.06)

Char. 7: (29.72) > (29.22)

Char. 8: (20.3-20.96) > (19.86)

Char. 9: (83.21-83.92) > (75.21-75.6)

Char. 10: (76.34-77.75) > (67.41-68.24)

Char. 11: (73.22-74.81) > (65.48-65.63)

Char. 12: (45.07-45.98) > (40.38-40.87)

Char. 14: (16.29-16.42) > (15.6)

Char. 15: (41.83-42.79) > (39.5)

Char. 16: (8.8-8.84) > (8.57)

Char. 17: (31.29-31.91) > (30.81)

Char. 18: (3.32-3.35) > (3.18-3.22)

Char. 19: (78.9-79.73) > (77.26)

Char. 20: (63.98-66.3) > (63.65)

Char. 22: (45.71-46.3) > (44.47)

Node 38:

Char. 3: (62.78-63.04) > (59.05-61.86)

Char. 7: (29.22) > (28.28-29.07)

Char. 13: (56.23-56.44) > (52.54-53.25)

Char. 14: (15.6) > (15.49)

Char. 16: (8.57) > (7.91-8.32)

Char. 17: (30.81) > (30.01-30.66)

Char. 36: (1) > (0)*

Char. 52: (1) > (0)

Node 37:

Char. 23: (0) > (1)*

Char. 26: (0) > (1)

Char. 37: (0) > (1)

Node 42:

Char 0: (78.76-80.38) > (67.05-68.39)

Char. 1: (50.67-55.89) > (42.62-45.03)

Char. 2: (28.21-30.85) > (24.71-26.26)

Char. 3: (58.09-61.86) > (45.29-53.17)

Char. 4: (24.04-24.06) > (19.03-19.42)

Char. 5: (38.6-38.68) > (33.46-34.92)

Char. 6: (39.83-43.09) > (34.29-37.08)

Char. 7: (28.28-29.07) > (23.27-24.53)

Char. 8: (19.84-19.86) > (17.03-17.78)

Char. 9: (75.21-75.6) > (64.66-66.42)

Char. 10: (67.41-68.24) > (61.49-63.64)

Char. 11: (65.48-65.63) > (59.58-61.6)

Char. 12: (40.38-40.87) > (34.41-36.54)

Char. 13: (52.54-53.25) > (47.99-48.47)

Char. 15: (39.46-39.5) > (35.93-37)

Char. 16: (7.91-8.32) > (7.17-7.88)

Char. 17: (30.01-30.66) > (26.08-26.94)

Char. 18: (3.18-3.22) > (2.95-3.09)

Char. 19: (75.27-77.26) > (71.3)

Char. 20: (61.89-63.65) > (58.21)

Char. 21: (13.38-13.61) > (13.09)

Char. 22: (42.47-44.47) > (40.21)

Char. 45: (1) > (0)

Char. 88: (1) > (0)

AUTAPOMORPHIES

Calonectris edwardsii

Char. 4: (27.55-28.15) > (25.56-27.52)

Char. 15: (44.43-45.32) > (38.05-43.79)

Char. 18: (3.73-3.77) > (3.32-3.68)

Char. 19: (83.1-84.29) > (72.9-77.76)

Char. 20: (74.64-74.97) > (66.02-69.83)

Char. 21: (8.81-8.82) > (6.88-7.93)

Char. 22: (47.91-49.74) > (44.43-47.09)

Char. 48: (0) > (1)

Char. 80: (1) > (0)

Calonectris leucomelas

Char. 54: (1) > (0)

Char. 82: (1) > (0)

Calonectris diomedea

Char. 86: (2) > (1)

Char. 102: (1) > (0)

Calonectris borealis

Char. 2: (35.13-38) > (38.81-40.89)

Char. 15: (44.43-47.63) > (47.83-53.68)

Char. 17: (39.19-41.46) > (42.45-45.78)

Char. 18: (3.79-3.86) > (4.2-4.54)

Char. 19: (83.68-86.88) > (88.94-96.04)

Char. 20: (74.86-78.55) > (79.77-86.74)

Char. 21: (8.81-8.82) > (9.17-10.03)

Char. 22: (52.07-53.82) > (54.71-58.88)

Char. 48: (0) > (1)

Ardenna pacifica

Char. 0: (90.57-92) > (80.34-88.13)

Char. 2: (34.05-36.55) > (31.66-34.01)

Char. 6: (41.65-43.45) > (36.72-38.98)

Char. 7: (27.28-27.48) > (24.82-26.97)

Char. 8: (22.89-23.2) > (21.88-22.86)

Char. 14: (20.08-21.08) > (18.1-19.61)

Char. 16: (11.55-11.7) > (9.93-10.62)

Char. 17: (37.96-38.1) > (33.73-36.72)

Char. 18: (3.73-3.77) > (3.4-3.6)

Char. 19: (83.1-84.29) > (76.7-82.33)

Char. 20: (74.64-74.97) > (66.45-71.53)

Char. 26: (0) > (1)

Char. 28: (1) > (0)*

Char. 37: (1) > (0)*

Char. 52: (0) > (1)*

Char. 65: (0) > (1)

Char. 80: (0) > (1)*

Char. 81: (0) > (1)*

Char. 83: (0) > (1)*

Char. 85: (0) > (1)

Char. 93: (0) > (1)

Char. 94: (0) > (1)*

Ardenna bulleri

Char. 1: (46.77-50.24) > (45.72-47.44)

Char. 5: (40.34-40.46) > (37.54-40.26)

Char. 9: (106.11-106.65) > (97.24-99.11)

Char. 10: (105.54-109.7) > (98.21-100.31)

Char. 11: (103.16-105.57) > (95.39-97.79)

Char. 23: (1) > (0)

Char. 27: (0) > (1)*

Char. 35: (1) > (2)

Char. 54: (1) > (0)

Char. 63: (0) > (1)

Char. 80: (0) > (1)*

Char. 81: (0) > (1)*

Char. 83: (0) > (1)*

Char. 89: (0) > (1)

Char. 94: (0) > (1)*

Ardenna creatopus

Char. 2: (38.3-39.36) > (38.81-40.48)

Char. 4: (29.64-30.87) > (32.57-35.73)

Char. 7: (31.09-31.74) > (32.16-32.96)

Char. 16: (11.55-11.7) > (11.72-13.34)

Char. 27: (1) > (0)*

Char. 50: (0) > (1)

Char. 51: (0) > (1)

Char. 54: (0) > (1)

Char. 65: (0) > (1)

Char. 103: (1) > (0)

Ardenna carneipes

Char. 5: (44.26-44.83) > (45.33-47.26)

Char. 14: (20.67-21.18) > (21.44-22.7)

Char. 28: (1) > (0)

Char. 40: (0) > (1)*

Char. 61: (0) > (1)*

Ardenna gravis

Char. 0: (93.34-95.84) > (97.52-98.97)

Char. 9: (111.64-112.05) > (116.32-120.2)

Char. 10: (110.75-111.07) > (114.5-117.4)

Char. 11: (107.09-107.59) > (110.97-112.95)

Char. 12: (57.09-58.38) > (59.56-61.89)

Char. 13: (64.9-66.8) > (71.18-78.89)

Char. 15: (48.21-53.15) > (54.59-55.9)

Char. 17: (39.01-39.49) > (40.72-42.65)

Char. 18: (4.04-4.17) > (4.51-4.67)

Char. 19: (91.8-97.72) > (100.85-104.62)

Char. 20: (77.87-81.37) > (85.3-88.13)

Char. 22: (53.63-53.93) > (57.74-60.07)

Char. 23: (1) > (0)

Char. 40: (1) > (0)*

Char. 50: (0) > (1)

Char. 61: (1) > (0)*

Char. 74: (1) > (0)

Char. 89: (0) > (1)

Ardenna grisea

Char. 1: (57.41-61.94) > (65.87-69.49)

Char. 3: (62.78-63.98) > (70.45-73.56)

Char. 4: (29.64-30.87) > (31.03-33.32)

Char. 5: (44.26-44.83) > (47.77-48.72)

Char. 7: (30.71-31.74) > (32.44-33.31)

Char. 8: (25.75-26.01) > (26.45-27.88)

Char. 13: (64.9-66.8) > (75.49-78.34)

Char. 15: (48.56-53.15) > (54.73-56.88)

Char. 18: (4.04-4.17) > (4.21-4.72)

Char. 19: (92.47-97.72) > (100.2-103.2)

Char. 20: (77.87-81.37) > (82.9-83.53)

Char. 21: (15.4-16.35) > (17.3-19.86)

Char. 22: (53.63-53.93) > (55.1-56.12)

Char. 54: (0) > (1)*

Char. 75: (0) > (1)*

Ardenna tenuirostris

Char. 0: (80.38-130.04) > (77.37-79.98)

Char. 26: (0) > (1)

Char. 37: (1) > (0)

Char. 52: (1) > (0)

Char. 54: (1) > (0)*

Char. 74: (1) > (0)

Char. 75: (1) > (0)*

Puffinus nativitatis

Char. 0: (78.06-81.25) > (68.83-72.83)

Char. 1: (54.32-56.65) > (50.86-54.02)

Char. 2: (30.69-30.98) > (27.32-30.05)

Char. 4: (25.54-25.64) > (21.42-23.66)

Char. 6: (42.9-43.85) > (38.02-39.79)

Char. 7: (29.72) > (25.83-27.96)

Char. 8: (20.3-20.96) > (18.92-20.24)

Char. 13: (56.23-56.44) > (49.97-54.12)

Char. 14: (16.29-16.42) > (14.78-15.87)

Char. 15: (41.83-42.79) > (39.11-40.83)

Char. 17: (31.29-31.91) > (27.91-29.41)

Char. 18: (3.32-3.35) > (2.84-3.11)

Char. 19: (78.9-79.73) > (70.93-75.96)

Char. 20: (63.98-66.3) > (59.16-62.22)

Char. 21: (14-15.03) > (11.77-13.74)

Char. 22: (45.71-46.3) > (42.77-45.57)

Char. 25: (1) > (0)

Char. 27: (1) > (0)

Char. 31: (0) > (1)*

Char. 33: (0) > (1)*

Char. 34: (0) > (1)

Char. 40: (1) > (0)*

Char. 41: (1) > (0)

Char. 48: (1) > (0)

Char. 56: (1) > (0)

Char. 65: (0) > (1)

Char. 86: (0) > (1)

Char. 88: (1) > (0)*

Puffinus puffinus

Char. 5: 38.47-39.3) > (37.31-38.15)

Char. 9: (83.21-83.92) > (76.97-79.73)

Char. 10: (76.34-77.75) > (69.32-73.5)

Char. 11: (73.22-74.81) > (66.76-70.78)

Char. 12: (45.07-45.98) > (42.03-44.34)

Char. 16: (8.8-8.84) > (7.49-8.65)

Char. 52: (1) > (0)

Char. 88: (1) > (0)*

Char. 89: (0) > (1)*

Puffinus mauretanicus

Char. 0: (78.06-81.25) > (83.3-90.52)

Char. 1: (54.32-56.65) > (60.6-63.83)

Char. 2: (30.69-30.98) > (31.96-34.9)

Char. 3: (62.78-63.04) > (63.92-72.39)

Char. 5: (38.6-39.3) > (40.63-43.28)

Char. 7: (29.72) > (30.73-32.88)

Char. 8: (20.3-20.96) > (21.11-22.38)

Char. 13: (56.23-56.44) > (58.8-60.63)

Char. 14: (16.29-16.42) > (16.86-18.07)

Char. 15: (41.83-42.79) > (44.5-46.56)

Char. 19: (78.9-79.73) > (84.48-86.28)

Char. 20: (63.98-66.3) > (69.09-70.01)

Char. 21: (14-15.03) > (15.33-16.66)

Char. 22: (45.71-46.3) > (48.31-49.98)

Char. 50: (0) > (1)

Char. 65: (0) > (1)

Char. 89: (1) > (0)*

Puffinus opisthomelas

Char. 9: (83.21-83.92) > (85.78-86.01)

Char. 10: (76.34-77.75) > (78.81-78.87)

Char. 11: (73.22-74.81) > (75.46-75.69)

Char. 16: (8.8-8.84) > (8.85-9.34)

Char. 17: (31.29-31.91) > (33.05-33.43)

Char. 26: (1) > (0)*

Char. 27: (1) > (0)

Char. 42: (0) > (1)

Char. 59: (2) > (1)

Char. 80: (0) > (1)

Char. 97: (2) > (1)

Puffinus gavia

Char. 3: (62.78-63.04) > (64.47)

Char. 6: (42.9-43.85) > (43.98)

Char. 9: (75.21-75.6) > (74.25)

Char. 10: (67.41-68.24) > (65.18)

Char. 11: (65.48-65.63) > (62.31)

Char. 12: (40.38-40.87) > (39.5)

Char. 18: (3.18-3.22) > (2.94)

Char. 35: (1) > (0)

Char. 36: (0) > (1)*

Char. 54: (1) > (0)

Puffinus huttoni

Char. 34: (0) > (1)

Puffinus yelkouan

Char. 8: (19.84-19.86) > (20.13-20.57)

Char. 9: (75.21-75.6) > (78.08)

Char. 10: (67.41-68.24) > (70.76)

Char. 11: (65.48-65.63) > (68.56)

Char. 12: (40.38-40.87) > (42.97)

Char. 15: (39.46-39.5) > (42.08-44.97)

Char. 19: (75.27-77.26) > (79.51)

Char. 20: (61.89-63.65) > (65.18)

Char. 21: (13.38-13.61) > (14.33)

Char. 22: (42.47-44.47) > (48.18)

Char. 23: (0) > (1)*

Char. 59: (2) > (1)

Char. 67: (1) > (0)

Puffinus lherminieri

Char. 13: (47.99-48.47) > (41.8-47.65)

Char. 15: (35.93-37) > (30.66-32.56)

Char. 18: (2.95-3.09) > (2.3-2.6)

Char. 19: (71.3) > (60.4-66.29)

Char. 20: (58.21) > (50.33-54.05)

Char. 21: (13.09) > (10.07-12.24)

Char. 22: (40.21) > (37.12-40.03)

Char. 23: (1) > (0)*

Char. 25: (1) > (0)

Char. 52: (0) > (1)

Char. 54: (1) > (0)

Char. 73: (1) > (0)

Puffinus assimilis

Char. 10: (61.49-63.64) > (56.3)

Char. 11: (59.58-61.6) > (54.2)

Char. 12: (34.41-36.54) > (34.04)

Char. 23: (0) > (1)*

Char. 36: (0) > (1)

Char. 44: (1) > (0)

Char. 63: (1) > (0)

CONCLUSÕES GERAIS

A partir de uma análise morfológica comparada, 104 caracteres osteológicos foram codificados para 20 espécies viventes de petréis dos gêneros atualmente reconhecidos *Calonectris*, *Ardenna* e *Puffinus* (*sensu stricto*). A hipótese de que *Calonectris* é táxon-irmão de um único grande clado, *i.e.*, *Puffinus* (*sensu lato*), apresentada aqui, é congruente com as hipóteses de Penhallurick & Wink (2004) (pelo menos em relação à análise de Máxima Verossimilhança) e Welch *et al.* (2014), ambas baseadas na evidência molecular. Apesar da divisão de *Puffinus* (*sensu lato*) em dois clados, indicada por esses autores, *Calonectris* parece ser, ainda sim, grupo-irmão de todos os outros *shearwaters*. A hipótese final aqui apresentada, de apenas dois gêneros para os *shearwaters*, é consistente também com as classificações pré-cladistas baseadas na evidência morfológica (*e.g.* Kuroda, 1954).

O princípio mais importante de uma classificação baseada no método cladista é a de que todos os táxons devem ser, necessariamente, monofiléticos; além disso, as relações entre táxons-irmãos devem ser sempre facilmente reconhecidas (Carlos, 2017). A transposição das informações contidas em um cladograma para a classificação hierárquica (Linneana) pode ser feita por dois métodos, *i.e.*, subordinação, proposto por Hennig (1968), e sequenciamento, proposto por Nelson (1973). Independentemente de qual seja o método de transposição escolhido, é importante discutir que, se no cladograma de Máxima Verossimilhança de Penhallurick & Wink (2004) *Calonectris* é um gênero, irmão de um clado que contém todas as outras espécies, então *Puffinus* (*sensu lato*) teria de seguir a mesma lógica e deveria ser considerado como gênero, subdividido em dois clados menos inclusivos (*Lugensa*, o outro membro do clado Puffinini seria, então, um táxon redundante, *i.e.*, monotípico em vários níveis).

A classificação filogenética das aves, tradicionalmente baseada em descrições morfológicas, tem sido, mais recentemente, caracterizada por uma inundação de análises baseadas em sequências de DNA; os resultados, muitas vezes, são conflitantes com as classificações tradicionais pré-cladistas (Livezey & Zusi, 2007). O método de comparação de hipóteses construídas com diferentes tipos de evidências para testar uma relação em particular é, como discutido por Santos & Capellari (2009), semelhante ao princípio de iluminação recíproca de Hennig (1968). Neste, dois tipos de dados são complementares entre si e tem o potencial de esclarecer um ao outro. A morfologia, diferente do que muitos autores afirmam, apresenta um importante papel na discussão das relações filogenéticas dos diversos grupos animais, e, juntamente com as hipóteses moleculares, pode nos ajudar a elucidar relações ainda bastante controversas.

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