UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL

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RELAÇÕES FILOGENÉTICAS DO "CLADO DAS AVES AQUÁTICAS", COM ÊNFASE NAS "AVES TOTIPALMADAS" (AVES: NATATORES *AUT* AEQUORNITHES)

Tese 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 Doutor em Biologia Animal.

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RELAÇÕES FILOGENÉTICAS DO "CLADO DAS AVES AQUÁTICAS", COM ÊNFASE NAS "AVES TOTIPALMADAS" (AVES: NATATORES AUT AEQUORNITHES)

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“Ao verme que primeiro roeu as frias carnes do meu cadáver dedico como [nem tão] saudosa lembrança [este trabalho].”

Agradecimentos

Esta é, provavelmente, a seção mais lida de qualquer trabalho acadêmico. Seja por pura curiosidade ou, carências emocionais ou desejo de reconhecimento, a maioria das pessoas gasta (não investe) algum tempo lendo as frequentes pieguices, idiossincrasias e, pior, metafísicas de cunho religioso que frequentemente povoam esta seção do trabalho. O presente autor, porém, prefere um modo mais discreto, nem por isso menos sincero, de expressar sua gratidão: logo abaixo são listadas, por ordem alfabética do sobrenome (*de facto* ou praticado), aquelas pessoas que, de alguma forma, prestaram auxílio na, ou fizeram algum favor de boa vontade para, realização deste estudo.

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"Só existe um problema filosófico realmente sério: é o suicídio. Julgar se a vida vale ou não vale a pena ser vivida é responder à questão fundamental da filosofia. O resto, se o mundo tem três dimensões, se o espírito tem nove ou doze categorias [se as aves Pelecaniformes são ou não monofiléticas], aparece em seguida. São jogos."

Albert Camus, in "O mito de Sísifo"

Sumário

Resumo

A sistemática do 'clado das aves aquáticas'; *i.e.*, aquele formado por aves pelágicas, pernaltas e afins é interessante, porque se constitui num misto de congruências e conflitos entre as abordagens fenotípica e molecular das relações filogenética entre seus membros. Dentro desse clado, mais interessante e controversa são as relações das famílias incluídas na tradional ordem Pelecaniformes: Pelecanidae, Sulidae, Anhingidae, Fregatidae e Phaethontidae. A monofilia dessa ordem vem sendo discutida há bastante tempo, mesmo antes do advento da cladística molecular. As análises baseadas em caracteres fenotípicos apoiam, ou não, a monofilia da ordem, enquanto as análises moleculares, independentemente do tipo de marcador utilizado, foram quase unânimes em rejeitar a monofilia da mesma. A maior dúvida sobre a constituição de Pelecaniformes refere-se a Phaetonthidae, a qual provavelmente não está proximamente relacionada com as demais famílias, e a proximidade filogenética entre Pelecanidae, Scopidae e Balaeniciptidae, estas duas últimas frequentemente alocadas junto com as cegonhas, ibises e colhereiros na ordem Ciconiiformes. O presente estudo teve como objetivo reavaliar as relações filogenéticas entre os táxons mais inclusivos (acima do nível de família) do "clado de aves aquáticas", com ênfase nas "Pelecaniformes", a partir de de caracteres craniais, a maioria reformulado de trabalhos anteriores. Esta análise inclui 29 táxons terminais, sendo o grupo de estudo composto por, pelo menos, um representante de cada uma das famílias que compõem "clado de aves aquáticas". Os grupos externos foram Anatidae e Tinamidae, este último servido como raiz dos cladogramas. Neste

trabalho, empregou-se a análise de parcimônia com pesos implícitos, segundo a qual, no processo de busca pelos cladogramas, os caracteres são ajustados conforme seu grau de homoplasia, de modo que, em havendo conflito entre caracteres, prevalece aqueles menos homoplásticos. A análise recuperou um único cladograma por cada valor de constante de concavidade, *K*, sendo os obtidos com o nono e décimo primeiro valores considerados os mais estáveis; o consenso estrito desses dois cladogramas é hipótese final deste trabalho. As relações filogenéticas recuperadas neste trabalho, assim como em outros que também empregaram a evidência fenotípica, são um misto de congruências e conflitos com as hipóteses baseadas em dados moleculares. No entanto, há pontos de convergência que merecem destaque. O primeiro diz respeito ao clado que inclui a maior parte das "Pelecaniformes" e os táxons mais proximamente relacionados: Ardeidae, Scopidae e Balaeneciptidae. A presente análise recuperou um clado com as seguintes relações: (Scopidae + (Balaeneciptidae + ((Ardeidae + Phaenthontidae) + (Pelecanidae + (Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae))))). Esse é, pelo menos no que se refere aos seus membros, muito semelhante aquele recuperado nas análises moleculares, sendo as diferenças percebidas nas relações dentro do clado. O segundo e mais importante ponto refere-se à monofilia de ((Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae)))), este recuperado quase que exclusivamente pelas análises moleculares.

Apresentação

Este trabalho acadêmico é apresentado conforme Resolução Nº23/2009 deste Programa de Pós-graduação em Biologia Animal 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 tese está estruturado sob a forma de um artigo científico redigido em língua inglesa, de acordo com as "instruções aos autores" de "Anais da Academia Brasileira de Ciências" (Anexo 1; também disponível em: http://www.scielo.br/revistas/aabc/iinstruc.htm). Por esse motivo, e cumprindo as recomendações da referida resolução, são apresentados dois capítulos extras. O primeiro contém, além de uma introdução ao problema abordado pelo presente estudo, o principal resultado obtido, qual seja, o cladograma das relações filogenéticas entre os táxons estudados. O segundo, posicionado após o texto principal, traz as principais conclusões. Cumpre mencionar que, para auxiliar neófito no campo da pesquisa ornitológica e também aqueles que não têm familiaridade com esse ramo da zoologia e que, por quaisquer motivos, sejam eles de simples curiosidade ou de obrigação, venham a ler este trabalho, optou-se por incluir um pequeno glossário dos nomes aplicados aos clados e categorias taxonômicas mencionadas (Anexo 2).

Capítulo 1

introdução e principais resultados

Após um período de relativa inércia, desencadeado pela exaustão do modelo gradista de sistemática e pela resistência, por parte dos ornitólogos, à adoção do método cladista, o conhecimento sobre as relações filogenéticas dos grandes táxons de aves modernas, Neornithes Gadow, 1893 avançou bastante, impulsionado, principalmente, pelas investigações baseadas em dados da genética molecular (*e.g.*, CRACRAFT et al., 2004; FAIN; HOUDE, 2004; ERICSON et al., 2006; HACKETT et al., 2008; JARVIS et al., 2014). No geral, a despeito de certas incongruências nos resultados obtidos, as hipóteses geradas através da inferência molecular concordam quanto a vários clados, alguns dos quais bastante diferentes daqueles grupos propostos pela sistemática pré-cladistica (*e.g.*, FÜRBRINGER, 1888; GADOW, 1891, 1893).

Por certo, também existem, embora em menor número, hipóteses sobre as relações filogenéticas dentro de Neornithes baseadas em caracteres fenotípicos, mormente os osteológicos. Desses, o mais abrangente é, sem dúvida, o de Livezey e Zusi (2006b, 2007), cuja matriz inclui 150 táxons e 2,954 caracteres. Com efeito, alguns clados recuperados nas análises moleculares também o foram na de Livezey e Zusi (2007). Não obstante, tais clados são admitidos como incontroversos e, por consequência, amplamente aceitos (MAYR, 2010). Evidentemente, há diversos pontos de discordâncias entre a proposta moleculares e fenotípicas.

Nesse contexto, o dito “agrupamento o clado das aves aquáticas” (“Natatores” *sensu* LIVEZEY; ZUSI, 2007; “Aequornithes” *sensu* MAYR, 2011) caracteriza-se como um objeto de estudo particularmente interessante, pois se constitui em um misto de concordâncias e discordâncias entre as abordagens molecular e fenotípica (Figure 1). A principal concordância entre as hipóteses baseadas em diferentes tipos de evidências diz respeito aos membros do agrupamento, o qual inclui aves pelágicas (pinguins, albatrozes fragatas, atobás; e, em algumas propostas, os rabos-de-palha), aves pernaltas (cegonhas, “cegonha”-bico-de-sapato, ave-martelo; e, em algumas propostas, os flamingos) e outras aves aquáticas (mergulhões-do-hemisfério-norte, biguatingas, anhingas; e, em algumas hipóteses, os mergulhões) (LIVEZEY; ZUSI, 2007; HACKETT et al., 2008; SMITH, 2010). Por outro lado, os maiores pontos de controvérsia então presentes nas interelações entre os membros do agrupamento, particularmente no que se refere às hipóteses de monofiletismo das ordens Ciconiiformes Bonaparte, 1854 e Pelecaniformes Sharpe, 1891. Esta última é, inclusive, o principal foco deste estudo.

Tradicionalmente; *i.e.*, à luz da sistemática gradista (e antes desta), Pelecaniformes incluía entre 50–60 espécies de aves aquáticas de médio a grande porte, divididas em seis famílias, a saber: Phaethontidae Brandt, 1840 (rabos-de-palha), Pelecanidae Rafinesque, 1815 (pelicanos), Fregatidae Degland and Gerbe, 1867 (fragats), Sulidae Reichenbach, 1849 (atobás), Anhingidae Reichenbach, 1849 (biguás-tinga) e Phalacrocoracidae Reichenbach, 1850 (biguás) (WETMORE, 1960; DEL HOYO et. al., 1992; NELSON, 2006). Contudo, a monofilia (“naturalidade” ou holofilia) vem sendo discutida há bastante tempo, inclusive muito antes do advento da cladística molecular. As análises cladisticas baseadas em caracteres fenotípicos apoiam (CRACRAFT, 1985; LIVEZEY; ZUSI, 2007) ou não (BOURDON et al., 2005; MAYR, 2003; SMITH, 2010) a monofilia da ordem. Em contrapartida, as análises moleculares, independentemente do tipo de marcador genético utilizado, foram quase unânimes em rejeitar a hipótese de monofilia de Pelecaniformes (*e.g.*, CRACRAFT et al., 2004; FAIN; HOUDE, 2004; ERICSON et al., 2006; HACKETT et al., 2008; Fig. 1). A maior dúvida sobre a constituição de Pelecaniformes refere-se a Phaetonthidae, a qual provavelmente não está proximamente relacionada com as demais famílias da ordem, e a proximidade filogenética entre Pelecanidae e *Scopus umbretta* Gmelin, 1789 (Scopidae Bonaparte, 1849) and *Balaeniceps rex* Gould, 1850 (Balaeniciptidae Bonaparte, 1853), táxons estes que têm sido frequentemente alocados, juntamente com as cegonhas, ibises e colhereiros, na ordem Ciconiiformes (WETMORE, 1960; DEL HOYO et. al., 1992).

Em ambos os tipos de inferências cladística, a hipótese de monofilia do clado constituído por Sulidae, Phalacrocoracidae e Anhingidae — superfamília Suloidea Reichenbach, 1849 — foi apoiada. No entanto, dúvidas permanecem quanto ao grupo irmão de Suloidea, porque, invariavelmente, as análises molecular recuperaram Fregatidae nessa posição (*e.g.*, ERICSON et al., 2006; HACKETT et al., 2008), enquanto que em quase todas as análises fenotípicas, Pelecanidae apareceu como grupo irmão de Suloidea, com Fregatidae como grupo irmão subsequente num clado chamado de Steganopodes Chandler, 1916 (CRACRAFT, 1985; BOURDON et al., 2005; SMITH, 2010). Assim sendo, a ideia de Fregatidae como grupo irmão de Suloidea é tomada aqui como hipótese de trabalho. Atualmente, esse clado é reconhecido como ordem Suliformes Sharpe, 1891 (*e.g.*, CHESSER et al., 2010, GILL; DONSKER, 2015).

Se por um lado, os últimos anos testemunharam uma crescente preferência, entre os ornitólogos, pelos métodos moleculares de inferência filogenética, por outro, também presenciaram uma renovação, ainda que moderada, dos estudos de anatomia com vistas às análises cladísticas. Nesse contexto, o crânio das aves é considerado como uma das partes fenotipicamente mais diversificada; e, por esse motivo, mais propensa a oferecer dados para as análises cladísticas (ZUSI, 1993; LIVEZEY; ZUSI, 2006). Com tudo isso exposto, o presente estudo tem como objetivo reavaliar as relações filogenéticas entre os táxons mais inclusivos (*i.e.*, acima daqueles mais frequentemente colocados no nível de família) do “agrupamento de aves aquáticas”, mas com ênfase nas “Pelecaniformes”, a partir de um conjunto de caracteres craniais, a maioria dos quais reformulados de trabalhos anteriores.

Esta análise inclui 29 táxons terminais, sendo o grupo de estudo composto por, pelo menos, um representante das famílias que compõem o clado Natatores (*sensu* LIVEZEY; ZUSI, 2007), exceto as Gaviiformes e da ordem fóssil Odontopterygiformes. Os grupos externos foram Anatidae Vigors, 1825 e Tinamidae Huxley, 1872, este último servido par enraizamento dos cladogramas.

Neste trabalho, empregou-se a análise de parcimônia com pesos (ou ajuste) implícitos, segundo Goloboff (1993, 1995). Nessa abordagem, durante o processo de busca pelos cladogramas, os caracteres são ajustados segundo seu grau de homoplasia, de modo que, em havendo conflito entre caracteres, este é resolvido em favor daqueles menos homoplásticos. Assim, o método procura por cladogramas que maximizem uma função de ajuste dos caracteres. Essa função de ajuste atinge seu valor máximo quando o caráter não apresenta passos extras (*i.e.*, não é homoplástico); o ajuste (ou peso) diminui à medida em que o grau de homoplasia aumenta. A severidade do ajuste 'contra' a homoplasia é dada por uma constante, *K*, donde se conclui que a utilização de diferentes valores de *K* pode produzir diferentes cladogramas (GOLOBOFF, 1993; 1995).

Talvez, o aspecto mais subjetivo, por assim dizer, da análise com ajuste implícito seja a seleção dos valores de *K*. Mirande (2009), porém, propôs um método em que a seleção dos valores da constante levem em consideração a média de passos extras dos caracteres de um conjunto de dados. Dessa forma, os valores de *K* selecionados neste trabalho são aqueles que atribuem a um, vamos dizer, 'caráter homoplástico mediano' 50, 52, 54, 56, 58, 60, 62, 64, 66, 68, 70, 72, 74, 76, 78, 80, 82, 84, 86, 88, e 90% do 'peso' de um caráter não homoplástico. O principal critério para a seleção dos cladogramas que compõem a hipótese final deste trabalho foi a estabilidade; *i.e.*, são considerados mais estáveis aqueles cladograms que compartilham o maior número de clados com os demais.

A análise recuperou um único cladograma por cada valor de *K*, sendo os cladogramas obtidos com o nono e décimo primeiro valores considerados os mais estáveis. Portanto, o cladograma de consenso estrito entre esses dois cladogramas é a hipótese final deste trabalho (Figura 2).

As relações filogenéticas recuperadas neste trabalho, assim como em outros que também empregaram a evidência fenotípica (*e.g.*, LIVEZEY; ZUSI, 2007; SMITH, 2010), é um misto de congruências e conflitos com as hipóteses baseadas em dados moleculares (*e.g.*, ERICSON et al., 2006; HACKETT et al., 2008). No entanto, há pontos de convergência que merecem destaque. O primeiro diz respeito ao clado que inclui a maior parte das "Pelecaniformes" e os táxons mais proximamente relacionados: Ardeidae, Scopidae e Balaeneciptidae. A presente análise recuperou um clado com as seguintes relações: (Scopidae + (Balaeneciptidae + ((Ardeidae + Phaenthontidae) + (Pelecanidae + (Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae))))). Esse clado é, pelo menos no que se refere aos seus membros, muito semelhante ao clado recuperado, por exemplo, na análise de Hackett et al. (2008), sendo as diferenças percebidas nas relações dentro do clado. O segundo e mais importante ponto diz respeito à monofilia de "Suliformes", clado este recuperado em todas as análises moleculares (*cf*. Figura 1).

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Figura 1 – Relações filogenéticas dentro do clado das aves aquáticas a partir de dados genéticos (azul: HACKETT et al., 2008) e fenotípicos (verde: LIVEZEY; ZUSI, 2007).

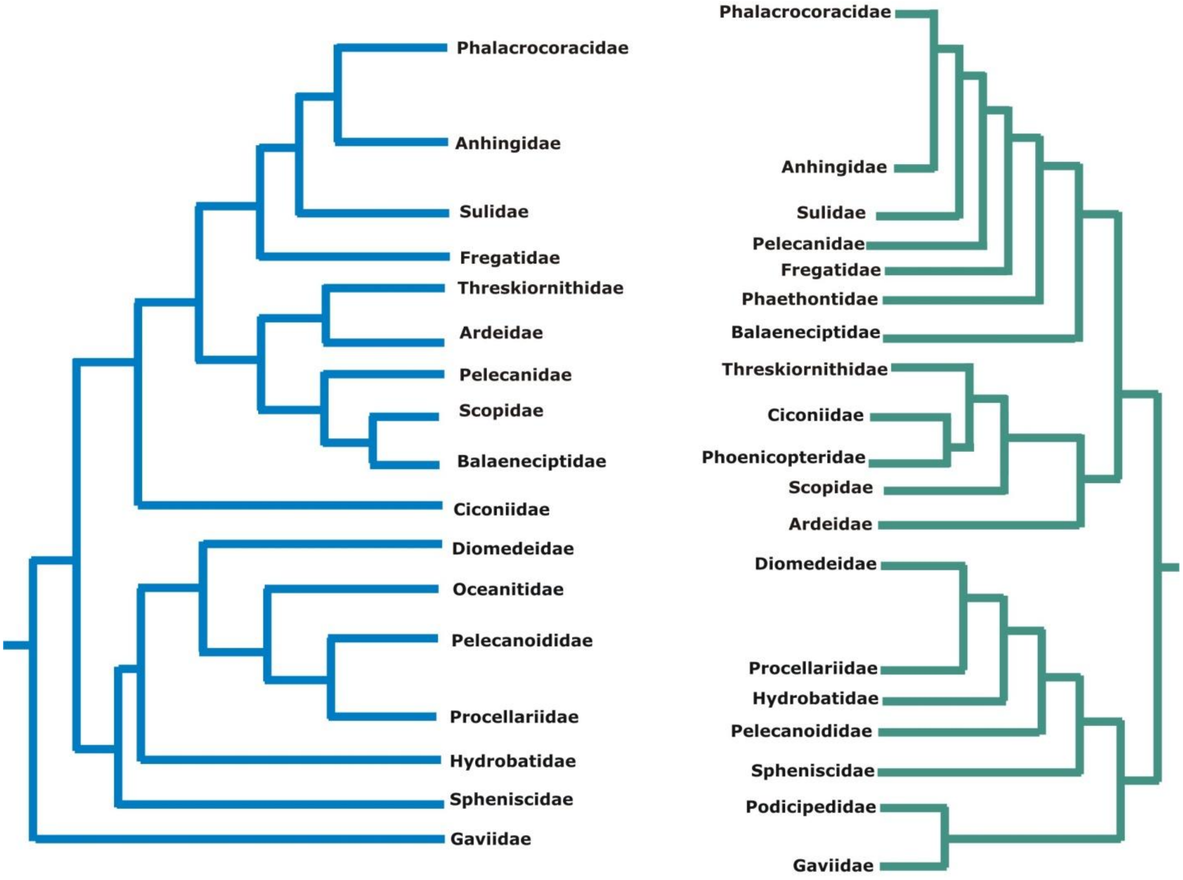
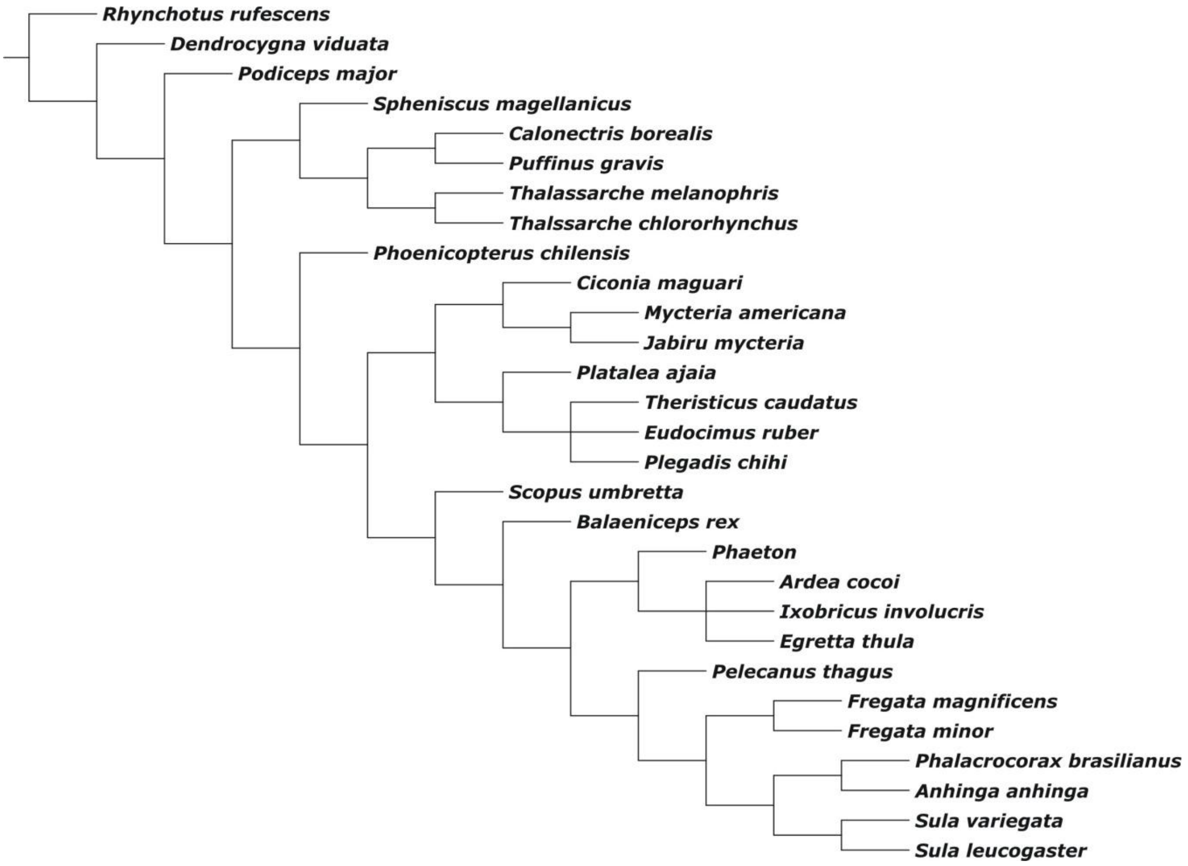


Figura 2 – Hipótese final de relacionamento filogenético entre os táxons dos grupos interno e externo.



A further turn of the spiral path: the phylogenetic relationships of the ‘waterbird assemblage’, with emphasis on the so-called ‘totipalamte birds’ (Aves: Natatores aut Aequornithes)

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ABSTRACT

The systematic of the ‘waterbird assemblage’, especially that concerning the so-called ‘totipalmate birds’ (Pelecaniformes) represents a mix of dispute and concordance between molecular and phenotypic approaches to the phylogeny of the group. In this work, the phylogenetic relationships of ‘waterbird assemblage’ were assessed by analyzing 78 ostelogical characters and 27 species-level ingroup taxa under implied weights for characters. Overall, the present hypothesis is more similar to the molecular-based hypotheses than to phenotypic ones, at least with regard to the within-group relationships. The main differences refer to the arrangement of Pelecanidae, Threskiornithidae, and Phaethontidae, the last-named being the most controversial taxon among, or near to, the ‘waterbird assemblage’. Regarding the ‘totipalmate birds’, the present analysis recovered Fregatidae as sister to (Sulidae + (Phalacrocoracidae + (Anhigidae), and Pelecanidae as sister to them in a monophyletic ‘Steganopodes’. The alleged polyphyly of ‘Steganopodes’; *i.e.*, that

Pelecanidae belongs to a different clade that includes Balaenicipitidae and Scopidae, as recovered in the molecular-based hypotheses, is at best contentious. Therefore, this conflict should be reconciled through reanalysis of existing data and/or the analysis of new characters/DNA sequences.

INTRODUCTION

In 1959, German ornithologist Erwin Stresemann expressed his view that the gradistic systematics of the higher taxa of birds (above family level) had exhausted its possibilities of further development. His well-known statement (p. 277) that ‘as far as the problem of the relationship of the orders of birds is concerned, so many distinguished investigators have labored in this field in vain, that little hope is left for spectacular beak-throughs [*sic*]’ best summarizes the state-of-art in the field of avian beta taxonomy in the early 20th century. In fact, at the time of Stresemann's writing, not much had changed in the classification of birds since the 19th century classical and comprehensive works of Fürbringer (1888) and Gadow (1891, 1893).

In the second half of the 20th century the ‘phylogenetic systematics’ (also referred to as ‘cladistics’) was introduced by Willi Hennig (1966, 1968 [1955]), and became popular among zoologists, particularly entomologists and ichthyologists (Hull 1988). However, ornithologists, more than other zoologists, put a strong resistance against this method (*e.g.*, E. Mayr 1974). Thus, it is not surprising that, despite some cladistic-based efforts (*e.g.*, Cracraft 1981, 1988), it was the publication, in 1990, of the Sibley's and Ahlquist's essentially 'phenetics' classification based on DNA–DNA hybridization that gave new breath to the debate over the phylogeny of higher taxa of birds. The proposal of Sibley and Ahlquist (1990) greatly differed from that of the gradistic approach (*e.g.*, Wetmore 1960); however, it was never widely adopted. Stresemann's unexpected 'breakthroughs' had to wait until the development of molecular cladistics in the 2000s.

In the past decade, several studies have addressed the phylogenetic relationships among the higher taxa of modern birds, Neornithes Gadow, 1893, based on DNA sequencing data (*e.g.*, Cracraft et al. 2004, Fain and Houde 2004, Ericson et al. 2006, Hackett et al. 2008). These studies yielded strikingly different results, depending on which dataset and analytical methods are used; nevertheless, they all agree in a number of 'statistically well-supported' clades, some of which depart from traditional, non-cladistic classifications of 19th and 20th centuries (*e.g.*, Fürbringer 1888; Gadow 1891, 1893; Beddard 1898; Wetmore 1960). Although comparatively fewer, attempts have also been made to investigate the phylogeny of Neornithes by means of analysis of phenotypic characters, the most comprehensive of which being that of Livezey and Zusi (2006b, 2007), whose matrix comprised 150 ingroup taxa and 2,954 characters.

Some clades recovered by molecular investigations also appeared in the Livezey's and Zusi's (2007) cladogram, but most of these are, in the words of G. Mayr (2008: 63), 'uncontroversial and meanwhile generally accepted.’ Naturally, there are not a few examples of conflicts between molecular- and phenotype-based phylogenies (for a review, see G. Mayr 2008, 2010). In this scenario, the systematics of the so-called ‘waterbird assemblage’ becomes interesting to study, as it consist of a mix of congruent and incongruent results between genetic and phenotypic approaches. The ‘waterbird assemblage’ (‘Natatores’ *sensu* Livezey and Zusi 2007; ‘Aequornithes’ *sensu* G. Mayr 2011) includes pelagic (penguins, albatrosses, petrels and allies, frigatebirds, boobies, gannets; and, in some proposals, tropicbirds), wading (storks, herons, shoebill, hamerkops; and, in some proposals, flamingos), and other aquatic (loons, cormorants, anhingas and, in some proposals, grebes) birds (*e.g.*, Livezey and Zusi 2007, Hackett et al. 2008, Smith 2010). The phylogenetic relationships within this clade have been controversial, with phenotype- (*e.g.*, Livezey and Zusi 2007, Smith 2010) and molecular-based (*e.g.*, Ericson et al. 2006, Hackett et al. 2008) analyses differing in both constituent taxa and topologies, particularly with regard to the monophyly and within-group relationships of the orders Ciconiiformes Bonaparte, 1854 and Pelecaniformes Sharpe, 1891, the last-named being the main focus of the present study.

In the traditional or gradistic approach, extant Pelecaniformes includes some 50–60 species of medium- to large-sized waterbirds divided into six families, *viz*. Phaethontidae Brandt, 1840 (tropicbirds), Pelecanidae Rafinesque, 1815 (pelicans), Fregatidae Degland & Gerbe, 1867 (frigatebirds), Sulidae Reichenbach, 1849 (boobies and gannets), Anhingidae Reichenbach, 1849 (anhingas or darters), and

Phalacrocoracidae Reichenbach, 1850 (cormorants) (Wetmore 1960, del Hoyo et. al. 1992, Nelson 2006). The monophyly (or holophyly) of this group has been the subject of much debate, even much before the advent of DNA sequencing-based cladistics. The phenotype-based, cladistic analyses either supported (Cracraft 1985, Livezey and Zusi 2007) or denied (Bourdon et al. 2005, Mayr 2003, Smith 2010) ordinal monophyly. Most sequencing-based analyses of both mitochondrial and nuclear DNAs congruently indicated the non-monophyly of Pelecaniformes (*e.g.*, Cracraft et al. 2004, Fain and Houde 2004, Ericson et al. 2006, Hackett et al. 2008); however, at least one study, that by Kennedy and Spencer (2004), confirmed the monophyly of the traditionally constituted order. The controversy whether Pelecaniformes is monophyletic or not is almost entirely due to Phaethontidae, which has been hypothesized to be not directly related to the other members of the group, and to a proposed closer relationship of Pelacanidae with *Scopus umbretta* Gmelin, 1789 (Scopidae Bonaparte, 1849) and *Balaeniceps rex* Gould,1850 (Balaeniciptidae Bonaparte, 1853); the last two-named taxa frequently placed together with storks, herons, ibises, and spoonbills in the order Ciconiiformes Bonaparte, 1854 (Wetmore 1960, del Hoyo et. al. 1992).

Nevertheless, despite those discordances, the monophyly of a clade that includes Sulidae, Phalacrocoracidae, and Anhingidae—superfamilly Suloidea Reichenbach, 1849 (also referred to as parvorder Sulida Reichenbach, 1849 by Livezey and Zusi 2007)—has been consistently supported by both phenotypic and molecular cladistic inferences. Doubts remain as to the sister-taxon to Suloidea, because molecular analyses recovered Fregatidae in this position (*e.g.*, Ericson et al. 2006, Hackett et al. 2008), whereas almost phenotypic ones recovered Pelecanidae as the sister-taxon to Suloidea, with Fregatidae as the sister-taxon to them in a clade often referred to as suborder Steganopodes Chandler, 1916 (Cracraft 1985, Mayr 2003, Bourdon et al. 2005, Smith 2010). For the sake of convenience, a sister-taxon relationship between Fregatidae and Suloidea is thus accepted herein as a 'provisional working hypothesis' mainly supported by molecular evidence; this clade is now recognized as the order Suliformes Sharpe, 1891 (*e.g.*, Chesser et al. 2010, Gill and Donsker 2015).

Between late 19th century and early 1900s, before the emergence and establishment of cladistic methodology, descriptive anatomy has been extensively used in avian systematic (for a brief review, see Livezey and Zusi 2006b, 2007). As to the 'traditional Pelecaniformes', the most comprehensive works were those by Brandt (1839), Shufeldt (1888, 1902), and Pycraft (1898). All these authors relied primarily on skeletal evidence to formulate hypotheses about inter-familiar relationships within Pelecaniformes, and although (often) employing idiosyncratic concepts of systematic, they brought important information that is still useful, irrespective of their conclusions.

A renewed, though modest, emphasis (from the end of 1990s onwards) was put on studying avian anatomy, as it provides a significant resource of information for cladistic inference. In this context, the skull is reputed as one of the most structurally diverse partitions of the avian skeleton, thus perhaps being the part from which the largest number of characters is to be delineated (Zusi 1993, Livezey and Zusi 2006b). In the present study, the phylogenetic relationships among taxa within the ‘waterbird assemblage’ were re-examined based on a set of skull characters, which were newly delineated or redefined from previous studies.

MATERIAL AND METHODS

Taxon sampling and survey

The caldistic analysis included 29 terminal taxa, the nomenclature of which follows Gill and Donsker (2015). The ingroup is composed of at least one species belonging to all family-level taxa within the clade ‘Natatores’ (*sensu* Livezey and Zusi 2007), except Gaviiformes and †Odontopterygiformes, *viz*. *Spheniscus magellanicus* (Forster, 1781) (Spheniscidae Bonaparte, 1831); *Thalassarche melanophris* (Temminck, 1828); *T*. *chlororhynchos* (Gmelin, 1789) (Diomedeidae Gray, 1840); *Calonectris borealis* (Cory, 1881); *Puffinus gravis* (O'Reilly, 1818) (Procellariidae Leach, 1820); *Podiceps major* (Boddaert, 1783) (Podicipedidae Bonaparte, 1831); *Phoenicopterus chilensis* Molina, 1782 (Phoenicopteridae Bonaparte, 1831); *Phaethon* spp.; *Mycteria americana* Linnaeus, 1758; *Ciconia maguari* (Gmelin, 1789); *Jabiru mycteria* (Lichtenstein, 1819) (Ciconiidae Sundevall, 1836); *Theristicus caudatus* (Boddaert, 1783); *Eudocimus ruber* (Linnaeus, 1758); *Plegadis chihi* (Vieillot, 1817); *Platalea ajaja* Linnaeus, 1758 (Threskiornithidae Poche, 1904); *Ixobrychus involucris* (Vieillot, 1823); *Ardea cocoi* (Linnaeus, 1766); *Egretta thula* (Molina, 1782) (Ardeidae Leach, 1820); *Balaeniceps rex* (Balaenicipitidae); *Scopus umbretta* (Scopidae); *Pelecanus thagus* Molina, 1782 (Pelecanidae); *Fregata magnificens* Mathews, 1914; *F. minor* (J.F. Gmelin, 1789) (Fregatidae), *Sula variegata* (Tschudi, 1843); *S. leucogaste*r (Boddaert, 1783) (Sulidae); *Phalacrocorax brasilianus* (J.F. Gmelin, 1789) (Phalacrocoracidae); and *Anhinga anhinga* (Linnaeus, 1766) (Anhingidae). Furthermore, *Rhynchotus rufescens* (Temminck, 1815) (Tinamidae Huxley, 1872) and *Dendrocygna viduata* (Linnaeus, 1766) (Anatidae Vigors, 1825) were selected as outgroups, with the former being selected to root the cladograms.

Skulls (*crania*) of full-grown specimens were observed under a 3X magnifying glass and/or a stereomicroscope with magnification of 10–160X. Most specimens were directly examined, except *Phaenton* spp. and *Balaeniceps rex*, for which characters were coded based on descriptions and illustrations in the literature (Brandt 1839; Parker 1862, Reinhardt 1862; Shufeldt 1888, 1902; Beddard 1897; Cottan 1957).

The material examined is housed in the following collections: Museum, Smithsonian Institution, Washington, DC; Field Museum of Natural History, Chicago; Museum of Vertebrate Zoology, Berkeley; Museu Paraense Emílio Goeldi, Belém; Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo, São Paulo; Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Sul; Museu de Ciências Naturais, Centro de Estudos

Costeiros, Limnológicos e Marinhos do Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Imbé; and Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (Appendix 1).

The importance of a standardized nomenclature is without question critical not only to descriptive anatomy, but also to cladistic inference (Livezey and Zussi 2006a, b). Therefore, anatomical terminology rendered in Latin and italicized, except when otherwise indicated, is according to 'Nomina Anatomica Avium'; more specifically, the chapter regarding *osteologia* (Baumel and Witmer 1993). The strict use of Latin terms for designating anatomical features is considered herein, as in Livezey and Zussi (2006b), to have an importance similar to that of the nomenclature of zoological taxa. The value of Latin for nomenclature mainly resides in its stability; *i.e.*, since it is relatively rarely spoken, it evolves very little at most, thus limiting unnecessary variation of terms and promoting precise and consistent definitions.

In this work, the logic and terminology of phenotypic characters follow Sereno (2007), according to whom, a 'character' is viewed as a feature expressed in the form of an independent variable, and 'states' as the mutually exclusive conditions of a character. When combined, both the character and its states form the 'character statement', which in turn includes up to four components (locator, variable, variable qualifier, and states), and assumes two types: 'neomorphic' and 'transformational'. Neomorphic characters are those composed of locators, and their states are simply ‘present’ or ‘absent’ (or ‘near-absent’), whereas transformational characters also include a variable and its qualifier, and their states are mutually exclusive conditions of the variable (Sereno 2007).

Livezey and Zusi (2006b) presented an annotated list of 2,954 phenotypic character statements, most of which are not in line with the logic adopted herein. Actually, there are a number of ‘chimerical’ character-statements wherein the neomorphic state ‘absent’ is mixed with transformational states. Furthermore, transformational characters are not always well-constructed, either due imprecisely defined variables or missing qualifiers. Accordingly, most character-statements used in the present analysis were either delineated from anatomical descriptions of ingroup taxa (Carlos MS) or redefined from Livezey and Zusi (2006b).

Cladistic analysis

An equal-weight maximum parsimony analyses of the taxon/character matrix resulted in six most parsimonious trees (265 steps, CI = 0.32 RI = 0.68), the strict consensus of which was not well resolved at the most inclusive nodes (Figure 1). Nevertheless, a monophyletic Suliformes was recovered sister to Ardeidae, whereas Pelecanidae grouped in a distinct clade with Balaenicipitidae and Scopidae.

In order to improve the resolution of the cladogram(s), an analysis with implied weighting (Goloboff 1993, 1995; Goloboff et al. 2008a) was carried as implemented in the software TNT v.1.1 (IW; Goloboff et al.

1998b). In this approach, during the cladogram-search process, each character is weighted relative to its fit, *F*, to a cladogram under consideration, according to the function:

$$F = K/(S + K)$$

where *S* is the number homoplastic transformations (i.e., extra steps) and *K* denotes the constant of concavity. The value of *K* determines the 'severity' of differential weighting; lower values weight stronger against homoplastic characters, whereas higher values weight less drastically against it (Goloboff 1993, 1995). Furthermore, under IW, the optimal cladograms are not necessarily the shortest ones, but those with the highest sum of implied weights or total fit.

Perhaps the only difficulty in using IW is to objectively (or less subjectively) select the values of *K*. However, Mirande (2009) proposed a method wherein the values of *K* are calculated from the formula:

$$K = (F \times S)/(1 - F)$$

where *F* is the fit attributed to an 'average' character with respect to the fit of a character without homoplasy, and *S* is a measure of the average of homoplasy per character, calculated as follows:

$$S = (S - S\,min)/(S\,min)$$

where *S* is the number of steps in the most parsimonious cladogram(s) found in the analysis with equally weighted characters (265 steps in the present study) and *S min* is the sum of the minimum number of steps for each character (77 steps). The 21 values of *K* used herein were 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.

In TNT, tree searches were heuristic, using tree-bisection-reconnection branch swapping with 1,000 replicates and 10 trees saved per replication.

In the present work, similarly to Mirande (2009), the main criterion to select among the fittest cladogram(s) obtained at each value of *K* is their stability; thus, the more stable trees would be those that share a higher number of nodes with the remaining ones. The measurement used to compare cladograms was the 'Subtree-Prune-and-Regraft-Distance' (SPR), which consists in the minimum number of 'SPR moves' necessary to convert one cladogram to another (Goloboff 2007). In TNT, SPR distances were calculated with 1,000 replications per comparison. The preferred cladograms combined into a strict consensus cladogram.

The degree of support of the non-refuted clades (*sensu* Grant and Kluge 2008) was estimated using Relative Bremer Support (or Relative Fit Difference; RBS), which takes in account the evidence supportive of, or contradictory to, a given group. The RBS varies from 0 to 100, with both these extremes indicating a completely unsupported and completely uncontradicted group, respectively (Goloboff and Farris 2001). In TNT, RBS were calculated by searching cladograms suboptimal by 0.001, 0.0025, 0.005 . . . 0.025, 0.03, 0.04 . . . 0.2 units of fit, saving up to 10,000 trees at each stage.

Furthermore, stability of clades was assessed using Symetric Resampling, which unlike Bootstrap and Jackknife, is not affected by differential characters weights (Goloboff et al. 2003). The SR is expressed in the form of both absolute frequencies and frequency difference. This latter refers to the frequency of a given group minus the frequency of the most frequent contradictory group (Groups present/Contradicted; GC). The values of GC vary from -100 to 100, with 100 indicating maximum support, 0 indifferent support, and -100 maximum contradiction (Goloboff and Farris 2001); in practice, only clades with positive values of GC are interpreted as having some stability. In TNT, the values of GC were calculated using 'traditional search' with 1,000 replicates and change probability of 33%.

RESULTS

Description of characters

The 78 character-statements used in the cladistic analysis are described below, most of which with additional explanatory notes. Several character states are illustrated in figures 2–6. Multistate characters are treated as unordered. The data matrix analyzed is provided as Appendix 2.

Calvaria cranii:

1. *Cranium*, dorsoventral depth: exceeding (0), or less than (1), bilateral width. (1 step, CI =1, RI =1). The state 1 refers to a condition wherein *dorsum cranii* is conspicuously flattened, the '*platycalvaria*' of Livezey and Zusi (2006b: 28, character 6), and is restricted to members of Suloidea. The width of *cranium* is taken between the bases of left and right *processus postorbitalis* or *homolugus situs*. See also Siegel-Causey (1988: 900, character 10), and Smith (2010: appendix S2, character 75).

Lamina externa cranii:

2. *Regio frontalis*, *facies dorsalis*, superficial shape: mediolaterally concave (0); planar (1). (4 steps, CI = 0.25, RI = 0.57). Most examined species exhibit a longitudinal median indentation on *facies dorsale regionis frontalis et pars rostralis regionis parietalis*, whereas members of Suloidea lack such an indentation and *regiones frontalis et parietalis* are planar to slightly convex (state 1). Modified from Bourdon *et al*. (2005: appendix 1, character 10) and Livezey and Zusi (2006b: 29, character 14).

Occiput (region occipitalis calvarii):

3. *Condylus occipitalis* (caudal perspective), shape: circular (0); bilobate (1). (6 steps, CI = 0.16, RI = 0.44). In most examined species, including most members of the ingroup, *condylus occipitalis* is more-or-less circular in caudal perspective (state 0), whereas in a group of species, it has a bilobate structure, the lobes being partitioned by an inconspicuous *incisura mediana condyli* (state 1). See Livezey and Zusi (2006b: 30, character 21).

4. *Prominentia cerebellaris*, shape: slight elevation with a distinguishable *linea (aut crista) medialis* (0); oblong, smooth-surfaced dome (1). (3 steps, CI = 0.33, RI = 0.33). In most examined species, *prominentia cerebellaris* is an inconspicuous convexity of *region suppraoccipitalis*, the surface of which is marked by a variably distinguishable *linea (aut crista) medialis* (state 0). In a small group of species, this structure is well-developed, oblong-shaped and smooth-surfaced (state 1). Modified Livezey and Zusi (2006b: 32, character 31), and Smith (2010: appendix S2, character 78).

5. *Regiones occipitalis et squamosalis, cristae laminae externae cranii* (*sensu* Livezey and Zusi 2006b): absent (0); present (1). (1 steps, CI = 1, RI = 1). This term refers to an elongate, concave *lamina* bordered by *cristae nuchalis transversa et lateralis*, *otica dorsalis et post-zygomatica*; present in *Phaethon*, members of Ardeidae, *Pelecanus thagus*, *Fregata*, and members of Suloidea. See Livezey and Zusi (2006b: 32, character 35) and Smith (2010: appendix S2, character 83).

6. *Regio supraoccipitalis, foramina efferens ramorum occipitalium arteriarum ophtalmicum externarum* (*sensu* Elzanowski and Galton 1991), position: within *regio occipitalis propria* (0); at or very near to *crista nuchalis transversa* (1). (2 steps, CI = 0.50, RI = 0.66). In most examined species, bilateral *foramina* for the passage of *rami occipitalis arteriarum ophtalmica externae* open within *regio occipitalis propria* (state 0), whereas in *Calonectris borealis*, *Puffinus gravis*, *Phalacrocorax brasilianus*, and *Anhinga anhinga*, these foramina are positioned at or very near to *crista nuchalis transversa* (state 1) See Beddard (1898: 314), as 'median supra-occipital foramen'. Modified from Bourdon *et al*. (2005: appendix 1, character 18) and Livezey and Zusi (2006b: 37, character 77).

7. *Regio supraoccipitalis, fonticulus occipitalis*: absent (0); present (1). (3 steps, CI = 0.33, RI = 0.60). Among the examined species, bilateral *fonticula* are present in *Dendrocygna viduata*, and in members of Threskiornithidae (state 1). See Livezey and Zusi (2006b: 37, character 78) and Smith (2010: appendix S2, character 61).

8. *Regio supraoccipitalis, foramina efferens venarum occipitalium externarum*: present (0); absent (1). (3 steps, CI = 0.33, RI = 0.60). The paired grooves containing *foramina* for the passage of *venae occiptales externae* are present in most examined species (state 0), whereas *Scopus umbretta*, *Pelecanus thagus*, and members Suloidea lack them (state 1); in these taxa, *venae occiptales interna et externa* are confluent and exit *cavum cranii* as *vena occipitalis communis* through *intervallum atlantico-occipitalis*. See Bourdon *et al*. (2005: appendix 1, character 19), Livezey and Zusi (2006b: 38, character 79), and Smith (2010: appendix S2, character 60).

9. (Principally) *Regio ossis laterosphenoidalis, processus postorbitalis*: present (0); absent (1). (1 step, CI = 1, RI = 1). A variably developed and shaped *processus postorbitalis* is present in most examined species, except in *Phalacrocorax brasilianus* and *Anhinga anhinga* wherein it is reduced to a small *tuberositas*. Modified from

Livezey and Zusi (2006b: 40, character 93); see also Siegel-Causey (1988: 900, character 5).

10. *Regiones frotalis et laterosphenoidalis*, 'second *processus postorbitalis*' (*sensu* Siegel-Causey 1988): absent (0); present (1). (2 steps, CI = 0.50, RI = 0.75). The term refers to a pointed, variably developed outgrowth rostral to *processus postorbitalis*, or *homologus situs*, present in members of members of Ardeidae, and in *Phalacrocorax brasilianus* and *Anhinga anhinga*. See Siegel-Causey (1988: 900, character 6) and Smith (2010: appendix S2, character 86).

11. *Os parasphenoidale, rostrum parasphenoidale, pars ventrocaudalis rostri*, shape: semicylindrical (0); lateromedially compressed (1). (2 steps, CI = 0.50, RI = 0.83). *Rostrum parasphenoidale* is an extension of *basis cranii externa* wherein *margo ventralis saepti interorbitales* joins and *ossa palatinum et pterygoideum* articulate. It has a shape resembling that of a cone in which the apex is turned and projects rostrad. In most examined species, *pars ventrocaudalis rostri* is semicylindrical (state 0), whereas in members of Ardeidae and Suloidea, it is lateromedially compressed, forming a medial '*carina parasphenoidalis*' (state 1). Modified from Livezey and Zusi (2006b: 42, characters 106 and 107); see also Bourdon *et al*. (2005: appendix 1, character 37) and Smith (2010: appendix S2, character 63).

12. *Os parasphenoidale, rostrum parasphenoidale, processus basypterigoideus*: present (0); near-absent (1). (2 steps, CI = 0.50, RI = 0.66). This process is a projection on each side of *rostrum* *parasphenoidale* for articulation with *os pterygoideum*; it is absent, or at best weakly developed, in most examined species. Modified from Livezey and Zusi (2006b: 42, character 108) and Smith (2010: appendix S2, character 62).

13. ***Os parasphenoidale, lamina parasphenoidalis*, conformation: completely fused with (0), or rostrally free from (1), *os basisphenoidale***. (2 steps, CI = 0.50, RI = 0.75). *Lamina parasphenoidalis* assumes different conformations in various birds; nevertheless, in all examined taxa, it is triangular- or trapezium-shaped, with apex or shorter parallel side turned rostrad. In most examined species, the lamina is completely fused with subjacent *ossa basisphenoidales* (state 0), whereas in members of Ardeidae, *Phalacrocorax brasilianus*, and *Anhinga anhinga*, it has a free apex that projects rostrad over part of *basis rostri parasphenoidalis* (state 1). Modified from Livezey and Zusi (2006b: 43, character 116).

14. ***Os parasphenoidale, laminae parasphenoidalis, tuberculum basilare (et processus medialis laminae parasphenoidales)*: near-absent (0); present (1)**. (4 steps, CI = 0.25, RI = 0.72). *Tubercula basilares* are located at *vertices rostralium ossis basioccipitalis*, just where *musculi cervicalis* insert, especially *musculi rectus capitis dorsalis*. In most examined species, these *tubercula* are variably developed, from just a distinct knob to a well-developed (high) swelling. In a group of species, *tubercula* are absent or very weakly developed (state 0). Modified from Livezey and Zusi (2006b:44, character 123).

15. ***Os parasphenoidale, (ala parasphenoidalis) processus lateralis laminae parasphenoidales*****, caudal extension: towards (0), or up to (1),** ***processus paraoccipitalis ossis exocipitales.*** (3 steps, CI = 0.33, RI = 0.80). Although appearing to be a lateral extension of *lamina parasphenoidalis*, processus *lateralis laminae parasphenoidales* is actually formed from a different centre of ossification that eventually coalesces with *lamina*. In most examined species, this process variably extends laterocaudad, but never joins *processus paraoccipitalis ossis exocipitales* (state 0); in members of Threskiornithidae, Ardeidae, and Suloidea, it projects farther caudad as a thin ridge of bone, and contact *basis processus paraoccipitalis* (state 0). Modified from Livezey and Zusi (2006b: 44, character 122); see also Chu (1998: appendix 1, character 17).

16. ***Os parasphenoidale*****,** ***tuba auditiva (pharyngotympanica)*****,** ***facies rostroventralis*****, conformation: tubes completely (or nearly so) ossified (0); tubes lacking lateral osseous wall (1).** (5 steps, CI = 0.20, RI = 0.55). In birds, bilateral osseous tubes converge, from *cavum tympani* along *margines rostrolateralis laminae parasphenoidalis* to form *tuba auditiva (pharyngotympanica) et ostium pharingeale in facies ventralis basis rostri parasphenoidales* (Baumel and Witmer 1993). These tubes are completely ossified (state 0), or they are laterally open along their lengths (state 1). Modified from Livezey and Zusi (2006b: 45, character 126).

17. *Regio exoccipitalis, processus paraoccipitalis, apex (terminus) processus*, orientation: ventrolateral (0), or caudal (1), to *occiput.* (1 step, CI = 1, RI = 1). *Processus paraoccipitalis* is a variably developed expansion of *os exoccipitale* that forms *partes caudales meatus acusticus externi et cavi tynpanica*, and serves as attachment site for *ligamentum occipitomandibularis et musculus depressor mandibulae*. In most examined species, *apex processus* is directed ventrad (state 0), whereas in members of Suloidea, it extends distinctly caudad (state 1). Modified from Livezey and Zusi (2006b: 46, character 132); see also Bourdon *et al*. (2005: 21) and Smith (2010: appendix S2 character 66).

18. *Regio squamosalis, fossa musculorum temporalium* (*sensu* Zusi and Livezey 2000), depth: *pars ventralis fossae* as shallow as (0), or distinctly deeper than (1), *pars dorsalis* (new character)*.* (5 steps, CI = 0.20, RI = 0.60). *Regio squamosalis* is synonym with *regio temporalis*, and consist of a set of concavities, the most conspicuous of which is *fossa musculorum temporalium* (= *fossa temporalis* of Baumel *et al*. 1993: 84–5, annot. 104). It is found caudal to *processus postorbitalis*, or *homologus situs*, and dorsal to *meatus acusticus externus.* In most examined species, this concavity is more or less uniformly shallow (state 0), whereas in *Spheniscus magellanicus*, members of Ardeidae, *Fregata*, and members of Suloidea, it is strongly etched into *cranium*, particularly ventrally (state 1).

19. *Regio squamosalis, processus suprameaticus*: near-absent (0); present (1). (7 steps, CI = 0.14, RI = 0.33). Most examined species have a variably developed, but always distinct, *processus suprameaticus* (state 0), whereas in a group of species, *processus* is indiscernible so that *margo rostralis meatus acusticus externi* appears continuous. See Livezey and Zusi (2006b: 47, character 143), and (Smith 2010: appendix S2, character 53).

20. *Ossa squamosalis et prooticum*, *cotylae quadratica squamosi et otici*, conformation: continuous to (0), juxtaposed to (1), or separated from (2), each other (unordered). (2 steps, CI = 1, RI = 1). Although associated with *regio squamosalis*, *cotylae quadratica squamosi et otici* embryologically originates from *ossa otica*. The state 0 refers to a condition wherein both *cotylae* are confluent and oblong-shaped, and is exclusive to *Rhynchotus rufescens*. In the state 1, two *cotylae* are readily discernible, although their margins are close together; in the state 2, *cotylae* are distinctly separated from each other. Modified from Livezey and Zusi (2006b: 48, character 150).

21. (*Principally*) *Regio parietalis, axis medialis cranii, crista (linea) nuchalis sagittalis*: absent (0); present (1) (5 steps, CI = 0.20, RI = 0.50). In a group of species, left and right *cristae temporales dorsalis* meet in *planum medianum* to form a low *crista (aut linea) nuchalis sagittalis* (state 1) See Baumel *et al*. (1993: 69, annot. 17).

22. (Principally) *Regio frontalis, facies dorsualis, fossa glandulae nasalis*: present (0); absent (1) (3 steps, CI = 0.33, RI = 0.66). In some examined species, including *Rhynchotus rufescens*, *glandula nasalis* (the so called 'salt-gland') occupies a depression on *facies dorsalis* *regionis frontalis* (state 0). For some (e.g., Mayr 2003, Bourdon *et al*. 2005, Livezey and Zusi 2006b), members of Tinamidae lack this depression; however, according to Parker (1864), Silveira and Höfling (2007), and the preset authors (pers. obs.), they do possess this feature, which nevertheless is less developed in comparison with those of *Spheniscus magellanicus*, *Thalassarche*, *Calonectris borealis*, and *Puffinus gravis*. See Livezey and Zusi (2006b: 30, character 20) and Smith (2010: appendix S2, character 40).

23. *Regio frontalis, facies orbitalis (ventralis), pars rostromedialis, impressio glandulae nasalis*: absent (0); present (1). (1 steps, CI = 1, RI = 1). In all 'totipalmate taxa' but *Phaethon*, *pars rostroventralis regionis frontalis* bears a shallow concavity for *glandula nasalis* (state 1; Technau 1936, Siegel-Causey 1990). See Bourdon *et al*. (2005: appendix 1, character 39), Livezey and Zusi (2006b: 51–2, character 172), and Smith (2010: appendix S2, character 44).

Os lacrimale:

Baumel *et al*. (1993) recognized three major *partes ossis lacrimalis*: a dorsal and ventral, enlarged extremity (*processus supraorbitalis et orbitalis*, respectively), with a constriction in between along which *ductus nasolacrimalis* passes to enter *cavum nasi* (*incisura ducti nasolacrimalis*). However, Cracraft (1969), in a review of the phenotypic variation of *os lacrimale* among several avian taxa, referred to these parts, respectively, as ‘head’, foot’, and ‘descending process’; this nomenclature is adopted herein, but with terms in Latin: *caput*, *pes et processus descendens*.

24. ***Os lacrimale, processus descendens, incisura (aut foramen) ducti nasolacrimalis*****: present (0); near-absent (1).** (7 steps, CI = 0.14, RI = 0.33). Modified from Livezey and Zusi (2006b: 54, character194).

25. ***Os lacrimale, processus descendens, foramina pneumatica*****: absent (0); present (1).** (3 steps, CI = 0.33, RI = 0.50). See Livezey and Zusi (2006b: 55, character 197) and Smith (2010: appendix S2, character 12).

26. ***Os lacrimale*****,** ***processus descendens et pes*****, length: extending up to (0), or towards (1),** ***archus jugalis.*** (5 steps, CI = 0.20, RI = 0.63)*. Processus descendens* terminates in a variably developed *pes lacrimalis* that may ventrally contact *arcus jugalis* (state 1). This character is considered not-applicable to *Dendrocygna viduata* wherein *processus descendens* is perpendicular to *axis dorsoventralis cranii*, not parallel to it, as in the remaining species.

27. ***Ossa frontale et lacrimale*****,** ***junctura (naso-) frontolacrimalis*****, type: synartroshis (0); syndesmosis (1)**. (2 steps, CI = 0.50, RI = 0.88). Synarthrosis, or immovable joint, refers to both *sutura et synostosis*. Modified from Livezey and Zusi (2006b:102, character 564).

28. ***Ossa frontale et lacrimale (et nasale), junctura (naso) frontolacrimalis*****, position: lateral (0), or ventrocaudal (1), to** ***zona flexoria craniofacialis***. (2 steps, CI = 0.50, RI = 0.75)*.* In most examined species, *caput ossis lacrimalis* joins *region frontalis* just lateral to *zona flexoria craniofacialis* (the so-called 'craniofacial hinge'; state 0), whereas in members of Suloidea, this joint is positioned ventrocaudal to *zona flexoria craniofacialis* (state 1). Modified from Bourdon *et al*. (2005: appendix 1, character 9); see also Livezey and Zusi (2006b: 102, character 564) and Smith (2010: appendix S2, character 41).

29. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, position: caudal (0), intermediate (1), or rostromedial (2), to *cotylae quadratica squamosi et otici* (unordered). (5 steps, CI = 0.40, RI = 0.70). *Partes ossea meatus acusticus externi* are dorsally and caudally formed by *os squamosum et processus paraoccipitalis ossis exoccipitales*, respectively. The meatus leads to *cavum tympani* (the so-called 'middle ear cavity'), which consists of a shallow concavity with at least three main openings, viz. *recessus tympanorum dorsalis et caudalis et fenestra vestibuli* (Baumel and Witmer 1993). In most examined species, most of *recessus tympanicus dorsalis* is positioned between *cotylae quadratica squamosi et otici* (state 1), whereas in a group of species, most of this opening is rostral/rostromedial to *cotylae* (state 2). The state 0 is exclusive to *Rhynchotus rufescens*. Modified from Livezey and Zusi (2006b: 58, character 223); Bourdon *et al*. (2005: appendix 1, character 31) and Smith (2010: appendix 1, character 67).

30. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, size: similar to (0), or distinctly larger than (1), *recessus tympanicus caudalis*. (4 steps, CI = 0.25, RI = 0.66). In a group of examined species, including some ‘totipalmate taxa’, *recessus tympanicus dorsalis* is distinctly larger than *recessus tympanicus caudalis* (see annotation under character 29). Modified from Bourdon *et al*. (2005: appendix 1, character 32) and Smith (2010: appendix S2, character 68).

Orbita:

31. *Pars rostralis orbitae, os ectethmoidale*: present (0); near-absent (1). (5 steps, CI = 0.20, RI = 0.66). In many avian taxa, *pars rostralis orbitae* is mostly formed by *os ectethmoidale* (Baumel and Witmer 1993), which, however, is at the very best, poorly-developed in a group of examined species, including most ‘totipalmate taxa’. Modified from Livezey and Zusi (2006b: 52, character 189) and Smith (2010: appendix S2, character 15).

32. *Pars rostralis orbitae, ossa ectethmoidale et lacrimale*, conformation: joined to (0), or separated from (1), each other. (2 steps, CI = 0.50, RI = 0.80). In some examined taxa, including members of the ingroup, *os ectethmoidale* laterally contacts *pes ossis lacrimalis* forming the so-called ‘lacrimal-ectethmoid complex’ (Cracraft 1968). This character is non-comparable in taxa lacking *os ectethmoidale* (see character 31).

33. *Pars medialis orbitae, saeptum interorbitale osseum, fonticulus interorbitalis*: present (0); absent (1). (3 steps, CI = 0.33, RI = 0.83). *Os mesethmoidale* forms much of *saeptum interorbitale osseum* (*i.e.*, the thin lamina separating the left and right *partes* *lateralium orbitae*), which dorsally joins *facies ventralis ossis frontalis*, caudally *regio ossis laterosphenoidalis*, and ventrally *rostrum parasphenoidale* (Baumel and Witmer 1993). In a group of examined species, the septum is perforated by one or more *fonticuli interorbitales* (state 0), whereas in other group, it is not fenestrated (state 1). Modified from Livezey and Zusi (2006b: 63, character 247).

34. *Partes medialis et caudalis orbitae, fonticulus interorbitalis et foramen opticum*, conformation: separated from (0), or confluent with (1), each other. (3 steps, CI = 0.33, RI = 0.60). In a group of examined species, *fonticulus interorbitalis* (see annotation under character 33) is separated from *foramen opticum* by a thin osseous partition (state 0), whereas in other group, both foramina are continuous with each other. This character is non-comparable in taxa lacking *fonticulus interorbitalis*. Modified from Livezey and Zusi (2006b: 63, character 247).

35. *Pars caudalis orbitae, fonticulus orbitocranialis*: present (0); absent (1). (5 steps, CI = 0.20, RI = 0.69). A group of examined species has paired *fonticuli orbitocraniales*, which may or may not be continuous with the also-paired *foramina nervorum olfactorii* (state 0). *Fonticuli orbitocraniales* is lacking in other group of species (state 1). Modified from Livezey and Zusi (2006b: 63, character 248).

36. *Pars caudalis orbitae, area muscularis aspera*, '*processus* P1': absent (0); present (1) (new character). (3 steps, CI = 0.33, RI = 0.75). The state 1 refers to a variably developed spur-like outgrowth at the centre of *area muscularis area*, present in members of Ciconiidae and

Threskiornithidae, and in *Scopus umbretta* and *Pelecanus thagus*. See Ferreira and Donatelli (2005: 534–35, figs. 7–9) regarding Threskiornithidae.

Ossa faciei:

37. *Rostrum maxillae, facies ventralis rostri, sulcus paratomialis* (*sensu* Livezey and Zusi 2006b): absent (0); present (1). (4 steps, CI = 0.25, RI = 0.72). The term refers to bilateral grooves that run the entire length, or almost the entire length, of *facies ventralis rostri maxillae*; present in most members of the ingroup. Modified from Livezey and Zusi (2006b: 64–5, character 258).

38. *Rostrum maxillae, facies ventralis rostri, sulcus paratomialis*, rostral extension: towards (0), or up to (1), *apex rostri maxillae.* (3 steps, CI = 0.33, RI = 0.60). This character is non-comparable in taxa lacking *sulcus paratomialis*. Modified from Livezey and Zusi (2006b: 64–5, character 258).

39. *Rostrum maxillae, facies dorsalis rostri, apex (terminus) rostri*, shape: decurved (0); hamulate (1); straight (2) (unordered). (9 steps, CI = 0.22, RI = 0.50). In the state 0, *apex rostri* is approximately at the same level of *crista tomialis*, whereas in state 1, it ventrally exceeds *crista tomialis*, forming a nearly right angle with *axis rostrocaudalis maxillae*. Modified from Livezey and Zusi (2006b: 66, character 265) and Smith (210: appendix S2, character 1).

40. *Rostrum maxillae, facies dorsalis rostri, sulci nasi* (*sensu* Livezey and Zusi 2006b): absent (0); present (1) (3 steps, CI = 0.33, RI = 0.50). The term refers to variably excavated, bilateral grooves that start from *margines rostrales aperturarum nasales ossearum*, and project rostrad towards, or up to, *apex maxillae*. See Livezey and Zusi (2006b: 66, character 272) and Smith (2010: appendix S2, character 6).

41. *Rostrum maxillae, margo tomialis* exclusive of *apex (terminus) rostri* (lateral view), conformation: curved (0); straight (1) (5 steps, CI = 0.20, RI = 0.50). In most examined species, the basal three-fourths of *margo tomialis rostri* have a a variably concave outline (state 0), whereas in members of Ciconiidae and Ardeidae, and in *Podiceps major* and *Anhinga anhinga*, *margo tomialis* is straight to apex (state 1). Modified from Livezey and Zusi (2006b: 66, character 268).

42. *Rostrum maxillae, facies ventralis rostri, fenestra ventromedialis* (*sensu* Livezey and Zusi 2006b): present (0); absent (1). The term refers to a variably conformed medial opening between *ossa maxillaria* on *facies ventralis rostri*. Modified from Livezey and Zusi (2006b: 289) (2 steps, CI = 0.50, RI = 0.03).

43. *Os maxillare, terminus caudalis cristae tomialis, 'processus* P2': absent (0); present (1). (3 steps, CI = 0.33, RI = 0.81). The state 1 refers to the caudal prolongation of *terminus caudalis cristae tomialis* as a pointed to rounded *processus* variably separated from *processus jugalis ossis maxillaries*. Modified from Livezey and Zusi (2006b: 84, character 408); see also Chu (1998: appendix 1, character 43).

44. ***Os maxillare, pons-maxillaro jugalis*** **(*sensu* Livezey and Zusi 2006b): absent (0); present (1)** (1 step, CI = 1, RI = 1). The term refers to a strut of bone that connects *processus palatus ossis maxillaries* to *archus jugalis*, present in *Thalassarche*, *Calonectris borealis*, and *Puffinus gravis.* See Chu (1998: appendix 1, character 47), Livezey and Zusi (2006b: 84, character 412), and Dénes and Silveira (2007: 52, fig. 24).

45. ***Ossa maxillares*****,** ***processus palati*** **(*sensu* Livezey and Zusi 2006a), conformation: separated from (0), or fused with (1), each other along *axis medialis*.** (2 steps, CI = 0.50, RI = 0.83)*. Processus palatus ossis maxillaris* (= *processus maxillopalatinus* of Baumel and Witmer [2003: 76, annotation 58]) arises from *os maxillare* near its junction with *processus rostralis ossis palatatini* (Livezey and Zusi 2006a). In most examined species, including all members of the ingroup, paired *processus* are fused with each other in *planum medianum* Modified from Livezey and Zusi (2006b: 85, character 421).

Cavum nasi:

46. ***Apertura nasalis ossea*****: present (0); near-absent (1).** (5 step, CI = 0.50, RI = 0.85). In all 'totipalmate taxa' but *Phaethon*, and in *Balaeniceps rex*, *aperturae nasales osseae* are much reduced or ever occluded by bone, as in *Sula*. See Livezey and Zusi (2006b: 75, character 331) and Smith (2010: appendix S2, character 8).

47. *Saeptum nasale (nasi) osseum*: present (0); absent (1). (5 steps, CI = 0.20, RI = 0.63). In this paper, as previously in Livezey and Zusi (2006b), *saeptum nasale osseum* is not regarded as deriving from *os mesethmoidale* (see annotation under character 33), but is considered to originate, in large part, from the ossification of a cartilaginous partition. Modified from Livezey and Zusi (2006b: 76, character 349).

48. *Conchae nasalis osseae*: present (0); near-absent (1). (1 step, CI = 1, RI = 1). See Technau (1936), Bang and Wenzel (1985), and Livezey and Zusi (2006b: 77, character 353).

49. *Fossa antorbitalis, fenestra premaxillaris* (*sensu* Livezey and Zusi 2006b): absent (0); present (1). (2 steps, CI = 0.50, RI = 0.88). The term refers to air-containing spaces within *ossa premaxillaria*. The state 1 occurs in all 'totipalmate taxa', and in *Balaeniceps rex* and *Scopus umbretta*. See Bourdon *et al*. (2005: appendix 1, character 8), Livezey and Zusi (2006b: 79, character 372), and Smith (2010: appendix 1, character 2).

Os palatinum:

The nomenclature pertaining to *os palatinun* as used herein follows Livezey and Zusi (2006a), who re-described phenotypic variation of this bone among several bird taxa, and revised and expanded the existing terminology of its parts. According to them, *os palatinun* can be divided into four main parts, viz*. partes maxillaries*, *choanalis*, *lateralis et pterygoideus*.

50. *Os palatinum*, *pars maxillaris*, *processus rostralis*, length: subequal to (0), or distinctly longer than (1), *pars choanalis* (new character)*.* (4 steps, CI = 0.25, RI = 0.62). *Pars maxillaris* consists of a long, dorsoventrally flattened *processus rostralis*, which joins *processus palatinus premaxillaris et palatus maxillaris* rostrad. Immediately caudal to its *junctura* with *os premaxillaris*, *processus rostralis* has a bending zone, *zona flexoria palatina*. In a group of examined species, including some 'totipalmate taxa', the length of *processus rostralis* exceeds that of the rest of *os palatinum* (state 1).

51. *Os palatinum*, *pars choanalis*, conformation: separated from (0), or joined to (1), each other at *planum medianum.* (2 steps, CI = 0.50, RI = 0.87). *Pars choanalis* is continuous with *margo caudalis partis maxillaris* (see annotation under character 50) and largely comprises paired *lamellae dorsales et ventrales*, which respectively, enclose *partes rostrodorsalis et caudoventralis fossae choanalis* (Baumel and Witmer 1993, Livezey and Zusi 2006a). In most 'totipalmate taxa', and in *Balaeniceps rex*, *pars choanalis* is joined to its symmetrical pair at *planum medianum*. Modified from Livezey and Zusi (2006b: 87, character 440) and Smith (2010: appendix S2, character 21).

52. *Os palatinum*, *pars choanalis*, *lamellae dorsales*: present (0); near-absent (1). (2 steps, CI = 0.50, RI = 0.75). Variably-shaped *lamellae dorsalis* are present in most taxa (state 0), whereas it is acking or at best poorly developed in *Spheniscus magellanicus*, and in members of Suloidea (state 0). Modified from Livezey and Zusi (2006b: 87, chars. 436, 439, and 440) and Smith (2010: appendix S2, character 22).

53. ***Os palatinum, pars choanalis, lamellae ventrales*****: near-absent (0); present (1).** (6 steps, CI = 0.16, RI = 0.37). *Lamellae ventrales* are also present in most examined species, whereas it is lacking in *Rhynchotus rufescens*, *Dendrocygna viduata*, *Spheniscus magellanicus*, *Phaethon*, *Fregata*, *Phalacrocorax brasilianus*, and *Anhinga anhinga*. Modified from Livezey and Zusi (2006b: 87, character 441).

54. ***Os palatinum, pars lateralis, angulus (processus) caudolateralis*** **(*****sensu*** **Livezey and Zusi 2006b): present (0); absent (1).** (5 steps, CI = 0.20, RI = 0.55). *Pars lateralis palatina*, as the name implies, is a lateral to ventrolateral expanse that provides the main surface for the attachment of *musculus pterigoydeus*; *i.e.*, a muscle that interconnects *ossa palatinum et pterygoideum* to *mandibula* (Baumel and Witmer 1993, Livezey and Zusi 2006a). *Angulus caudolateralis* is placed at the contact between *margines lateralia partium lateralis et pterygoidei,* and is present in a group of examined species (state 0). See Livezey and Zusi (2006b: 88, character 454).

55. ***Os palatinum, pars pterygoidea, processus pterygoideus*****: near-absent (0); present (1).** (4 steps, CI = 0.25, RI = 0.40). *Pars pterygoideus palatini* is found caudal and caudalmedial to *pars choanalis* and connects *ossa palatinum et pterygoideus*; however, in adult specimens it frequently cannot be accurately delimited because *sutura pterygopalatina* is usually obscured through synostosis (Livezey and Zusi

2006a). In many avian taxa, *pars pterygoideus* exhibits a caudally directed *processus pterygoideus*, which, nevertheless, is at best poorly-developed in a group of examined species (state 0). See Livezey and Zusi (2006b: 89, character 458).

56. ***Os palatinum, pars pterygoidea, facies parasphenoidalis, crista dorsalis palatina*****: absent (0); present (1).** (4 steps, CI = 0.25, RI = 0.66). The term refers to a dorsal extension of *facies parasphenoidalis partis pterygoideae* that braces *rostrum parasphenoidalis*. This character is non-comparable in species lacking *processus pterygoideus palatini*. See Livezey and Zusi (2006b: 89, character 459).

Ossa vomeres:

57. ***Vomer*****: present (0); absent (1).** (2 steps, CI = 0.50, RI = 0.75). In *Pelecanus thagus*, and in members of Suloidea, *vomer* is lacking. See Smith (2010: appendix S2, character 24).

Os pterygoideum:

58. ***Pes pterygoidei, lamella dorsalis*****: absent (0); present (1).** (5 steps, CI = 0.25, RI = 0.75). The term refers to a dorsal, laminar extension of *pes pterygoidei* that laterally clasp *rostrum parasphenoidalis*. See Livezey and Zusi (2006b: 92, character 479).

Arcus jugalis:

59. *Axis craniocaudalis arcus*, position: approximately aligned with (0), or forming an acute angle with (1), *planum palati ossei.* (2 steps, CI = 0.50, RI = 0.87). *Archus jugalis* is a slender bar (except in *Balaeniceps rex*) that connects *maxilla* to *os quadratum*. In most examined species, *axis craniocaudalis arcus* is approximately aligned with *planum palati ossei*, whereas in members of Ciconiidae, Threskiornithidae, and Ardeidae, and in *Balaeniceps rex* and *Scopus umbretta*, *axis arcus* forms a variable acute angle with *planum palati*. Modified from Livezey and Zusi (2006b: 68, character 291).

60. *Junctura maxillo-arcuatilis*, position: approximately aligned with (0), or dorsal to (1), *terminus caudalis tomium maxillae.* (4 steps, CI = 0.25, RI = 0.82). In most examined species, *junctura maxillo-arcualis* in lateral view is virtually aligned with *tomium maxillae* (state 0), whereas it is distinctly dorsal to *tomium* in members of Ardeidae and Threskiornithidae, and in *Dendrocygna viduata* and *Scopus umbretta* (state 1). Modified from Livezey and Zusi (2006b: 68, character 292).

Os quadratum:

Besides being a keystone of cranial kinesis, *os quadratum* also articulates *mandibula* with the neurocranium. This bone consists of a robust shaft, *corpus ossis quadrati*, from which a dorsal, medial and ventral process originates, *viz*. *processus oticus*, *orbitalis et mandibularis*, respectively.

61. ***Os quadratum*****,** ***corpus (et processus oticus)*****,** ***facies caudomedialis*****,** ***foramen pnematicus*****: absent (0); present (1)**. (5 steps, CI = 0.20, RI = 0.55). See Livezey and Zusi (2006b: 96, character 509) and Smith (2010: appendix S2, character 32).

62. ***Os quadratum*****,** ***basis processus orbitalis*****,** ***facies (ventro-) medialis*****,** ***foramen pnematicus*****: absent (0); present (1).** (4 steps, CI = 0.25, RI = 0.72). See Livezey and Zusi (2006b: 96, character 508) and Smith (2010: appendix S2, character 31).

63. ***Os quadratum*****,** ***processus mandibularis*****,** ***condylus medialis*****,** ***facies articularis*****, superficial shape: convex (0); concave (1).** (3 steps, CI = 0.33, RI = 0.84). Modified from Livezey and Zusi (2006b: 97, character 518).

64. ***Os quadratum*****,** ***processus mandibularis*****,** ***condylus medialis*****,** ***(sub-) condylus pterygoideus*****, position (lateral perspective): aproximately coplanar (0), or dorsal (1), to** ***cotyla quadratojugalis***. (3 steps, CI = 0.33, RI = 0.71). Modified from Livezey and Zusi (2006b: 97, character 521).

65. ***Os quadratum*****,** ***processus mandibularis*****,** ***condylus lateralis*****,** ***sulcus intercondylaris*****,** ***foramina pneumatica*****: absent (0); present (1)**. (3 steps, CI = 0.33, RI = 0.33). See Livezey and Zusi (2006b: 98, character 528) and Smith (2010: appendix S2, character 39).

66. ***Os quadratum*****,** ***processus orbitalis,*** **length: subequal to (0), shorter (1), or longer than (2),** ***processus oticus*** **(unordered).** (4 steps, CI = 0.50, RI = 0.75). There are marked differences in the length and shape of *processus orbitalis quadrati* among the examined species. In *Phoenicopterus chilensis*, *Fregata*, and members of Ardeidae, this process is well-developed and long, extending dorso-mediad parallel to *paries caudalis orbitae* (state 2) In contrast, in members of Suloidea, *processus orbitalis* is much reduced, especially in *Phalacrocorax brasilianus* and *Anhinga anhinga*. Modified from Livezey and Zusi (2006b: 99, character 535) and Smith (2010: appendix S2, character 36).

67. *Zona feloxoria craniofacialis*, conformation: indistinct *jugum* (0); distinct, transverse *lamina* (1); distinct *sulcus* bordered by *eminentia ossea* (2) (unordered). (8 steps, CI = 0.25, RI = 0.53). Modified from Livezey and Zusi (2006b: 108, character 604) and Smith (2010: appendix S2, character 11); see also Baumel *et al*. (1993: annot. 46, p. 153).

Mandibula:

In birds, each *ramus mandibulae* is generally constituted of *ossa articulare*, *prearticulare*, *supra-angulare*, *angular*, *spleniale et dentale*; the last-named being considered as the principal bone. Three *partes rami mandibulae* are also often recognized, viz. *symphisialis*, *intermedia et caudalis* (Baumel and Witmer 1993, Zusi 1993).

68. *Ramus mandibulae, facies dorsualis, sulcus paratomialis* (*sensu* Livezey and Zusi 2006b): absent (0); present (1). (3 steps, CI = 0.33, RI = 0.84). In many avian taxa, *facies medialis (lingualis) et ventralis partis intermediae rami mandibulae* are usually formed by *os* *spleniale* (Baumel and Witmer 1993); however, in some examined species, including most 'totipalmate taxa', this bone too contributes to a variable degree to *facies dorsalis*. As a result, in dorsal view, *pars intermedia mandibulae* appears variably wide and slightly concave, forming a shallow groove. Modified from Livezey and Zusi (2006b: 113, character 643).

69. *Rostrum (symphysis) mandibulae, fascies dorsalis*, surface shape: concave (0); planar (1); convex (2). (6 steps, CI = 0.33, RI = 0.42). *Pars symphisialis*, *or rostrum mandibulae*, includes that rostral, (often) pointed segment where the two opposite *rami mandibularum* fuse with each other (Baumel and Witmer 1993). See Livezey and Zusi (2006b: 114, character 645).

70. *Ramus mandibulae, pars intermedia, margo ventralis*, shape (lateral perspective): decurved (0), straight (1), or recurved (2), relative to *margo ventralis partis caudalis mandibulae.* (7 steps, CI = 0.28, RI = 0.44). Decurvature does not refer to that resulting from *angulus ventralis mandibulae*. State 2 refer to a condition wherein *margo ventralis rami mandibulae* is distinctly curved upward and is exclusive to *Balaeniceps rex*. Modified from Livezey and Zusi (2006b: 116, character 673).

71. *Ramus mandibulae, pars intermedia, facies medialis (lingualis), fossa medialis* (*sensu* Livezey and Zusi (2006b): absent (0); present (1). (5 steps, CI = 0.20, RI = 0.60). The term refers to a variably long and deep concavity on *facies medialis (lingualis)* *mandibulae*; present in a group of examined species, including most 'totipalmate taxa'. Modified from Livezey and Zusi (2006b: 115, character 668).

72. *Ramus mandibulae, pars symphisialis*, length: less (0), or more (1), than one-third of the total length of *mandibula.* (3 steps, CI = 0.33, RI = 0.66). In most examined species, *rostrum mandibulae* is short (*i.e.*, often occupies less than 10% of the total length of *ramus*; state 0), whereas in members of Ciconiidae and Ardeidae, and in *Phoenicopterus chilensis*, it corresponds to more than one-third of the total length. Modified from Livezey and Zusi (2006b: 115, character 676) and Smith (2010: appendix S2, character 90).

73. *Ramus mandibulae, pars caudalis, fossa aditus canalis neurovascularis*, shape: pronounced, (often) rostrally delimited by an expansion of *os prearticulare* (0); short, dorsoventrally narrow (1). (4 steps, CI = 0.25, RI = 0.25). This character in non comparable in *Phoenicopterus chilensis* wherein *fossa aditus canalis neurovascularis* is absent. Modified from Livezey and Zusi (2006b: 118, character 689) and Smith (2010: appendix S2, character 94).

74. *Fossa articularis quadratica, processus retroarticularis mandibulae*: present (0); near-absent (1) (4 steps, CI = 0.25, RI = 0.70).

75. *Ramus mandibulae, pars caudalis, fenestra rostralis mandibulae*: absent (0); present (1). (4 steps, CI = 0.25, RI = 0.75). Modified from Livezey and Zusi (2006b: 117, character 689).

Ossa acessoria cranii:

76. *Os nuchale*: absent (0); present (1). (1 step, CI = 1, RI = 1). See Livezey and Zusi (2006b: 714); also, Bourdon *et al*. (2005: 17)

77. *Os suprajugale*: absent (0); present (1). (1 step, CI = 1, RI = 1). See Livezey and Zusi (2006b: 121, character 720) and Smith (2010: appendix S2, character 28).

78. *Os lacrimopalatinum*: absent (0); present (1). (2 steps, CI = 0.50, RI = 0.83). See Livezey and Zusi (2006b: 122, character 722).

Parsimony analysis

The analysis recovered a single fittest cladogram for each value of *K* (Table I), the most stable of which were those obtained from the analyses with *K8* and *K9* (Table II). The strict consensus (CI = 0.31, RI = 0.68) between these cladograms is the final hypothesis proposed in this work (Figure 6). Synapomorphies for each node are listed below. Those marked with an asterisk (*) represent ambiguous character-states resolved using ACCTRAN. The numbering of nodes used here corresponds to numbering from TNT. Symmetric resampling expressed as absolute frequencies and GC values, and Relative Bremer Support are shown within parenthesis. Negative values are indicated by an ‘en-dash’ (−) sign.

Node 30 (100/100/100)

Synapomorphies:

1*. *Ossa squamosalis et prooticum*, *cotylae quadratica squamosi et otici*, conformation (character 20): (0 > 2) separated from each other.

2*. (Principally) *Regio frontalis*, *facies dorsualis*, *fossa glandulae nasalis* (character 22): (0 > 1) absent. Reversed in node 32. Paralleled in node 42.

3*. *Os lacrimale*, *processus descendens*, *incisura (aut foramen) ducti nasolacrimalis* (character 24): (0 > 1) near-absent. Reversed in node 32. Paralleled in nodes 35, 40, and 47.

4*. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, position (character 29): (0 > 1) intermediate to *cotylae quadratica squamosi et otici*. Paralleled in *Anhinga anhinga*.

5*. *Os palatinum*, *pars pterygoidea*, *processus pterygoideus* (character 55): (0 > 1) present. Reversed in node 51, and in *Phaethon*. Paralleled in node 54.

6*. *Zona feloxoria craniofacialis*, conformation (character 67): (0 > 1) distinct, transverse *lamina*. Reversed in node 37. Paralleled in nodes 48 and 50, and in *Platalea ajaia* and *Scopus umbretta*.

Node 31 (9/2/)

((*Spheniscus magellanicus* + ((*Calonectris borealis* + *Puffinus gravis*) + (*Thalassarche melanophris* + *T. chlororhynchos*))): Procellariimorphae (*sensu* Livezey and Zusi 2007) or Austrodyptornithes (*sensu* Yuri et al. 2013)

Synapomorphies:

1*. *Occiput*, *condylus occipitalis* (caudal perspective), shape (character 3): (0 > 1) bilobate. Reversed in node 36. Paralleled in nodes 48 and 50, and in *Dendrocygna viduata* and *Ciconia maguari*.

2*. *Occiput*, *prominentia cerebellaris*, shape (character 4): (0 > 1) oblong, smooth-surfaced dome. Reversed in node 35. Paralleled in *Pelecanus thagus*.

3*. *Regio squamosalis*, *fossa musculorum temporalium*, depth (character 18): (0 > 1) *pars ventralis fossae* distinctly deeper than *pars dorsalis*. Reversed in node 35. Paralleled in nodes 48 and 51.

4*. *Regio squamosalis*, *processus suprameaticus* (character 19): (1 > 0) near-absent. Reversal of synapomorphy 2 of node 33. Reversed in node 34. Paralleled in node 53, and in *Balaeniceps rex* and *Phaethon*.

5. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, position (character 29): (1 > 2) rostromedial to *cotylae quadratica squamosi et otici*. Paralleled in node 51, and in *Phaethon*.

6. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, size (character 30): (0 > 1) distinctly larger than *recessus tympanicus caudalis*. Paralleled in node 51, and in *Phaethon*.

7. *Os lacrimopalatinum* (character 78): (0 > 1) present. Paralleled in node 50.

Node 32 (3/–/–)

(((*Spheniscus magellanicus* + ((*Calonectris borealis* + *Puffinus gravis*) + (*Thalassarche melanophris* + *T*. *chlororhynchos*))) + ((*Phoenicopterus chilensis* + ((*Ciconia maguari* + (*Mycteria americana* + *Jabiru mycteria*)) + (*Platalea ajaia* + (*Plegadis chihi* + *Theristicus caudatus* + *Eudocimus ruber*))) + ((*Scopus* + (*Balaeniceps* + ((Ardeidae + *Phaethon*) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*)))))))

Synapomorphies:

1. *Os parasphenoidale*, *laminae parasphenoidalis*, *tuberculum basilare (et processus medialis laminae parasphenoidales)* (character 14): (0 > 1) present. Reversed in node 41. Paralleled in node 51, and in *Phaethon*.

2*. (Principally) *Regio frontalis*, *facies dorsualis*, *fossa glandulae nasalis* (character 22): (1 > 0) present. Reversal of synapomorphy 2 of node 30. Reversed in node 42.

3*. *Os lacrimale*, *processus descendens*, *incisura (aut foramen) ducti nasolacrimalis* (character 24): (1 > 0) present. Reversal of synapomorphy 3 of node 30. Reversed in nodes 35, 40, and 47. Paralleled in node 50, and in *Phaethon*.

4*. *Os lacrimale*, *processus descendens*, *foramina pneumatica* (character 25): (0 > 1) present. Reversed in node 54, and in *Spheniscus magellanicus*.

5*. *Rostrum maxillae*, *facies dorsalis rostri*, *sulci nasi* (character 40): (0 > 1) present. Reversed in *Phoenicopterus chilensis* and *Phaethon*.

Node 33 (58/56/11)

((*Podiceps major* + ((*Spheniscus magellanicus* + ((*Calonectris borealis* + *Puffinus gravis*) + (*Thalassarche melanophris* + *T. chlororhynchos*))) + ((*Phoenicopterus chilensis* + ((*Ciconia maguari* + (*Mycteria americana* + *Jabiru mycteria*)) + (*Platalea ajaia* + (*Plegadis chihi* + *Theristicus caudatus* + *Eudocimus ruber*))) + ((*Scopus* + (*Balaeniceps* + ((Ardeidae + *Phaethon*) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*))))))

Synapomorphies:

1. *Os parasphenoidale*, *rostrum parasphenoidale*, *processus basypterigoideus* (character 12): (0 > 1) present (0). Reversed in node 36.

2*. *Regio squamosalis*, *processus suprameaticus* (character 19): (0 > 1) present. Reversed in nodes 31 and 53, and in *Balaeniceps rex* and *Phaethon*. Paralleled in nodes 34, and in *Anhinga anhinga*.

3. *Pars rostralis orbitae*, *os ectethmoidale* (character 31): (0 > 1) near-absent. Reversed in nodes 35, 38, 47, and 54.

4. *Partes medialis et caudalis orbitae*, *fonticulus interorbitalis et foramen opticum*, conformation (character 34): (0 > 1) confluent with each other. Reversed in nodes 34 and 52.

5. *Saeptum nasale (nasi) osseum* (character 47): (0 > 1) absent. Reversed in nodes 34 and 41, and in *Plegadis chihi*. Paralleled in *Phaethon*.

6. *Os palatinum*, *pars choanalis*, *lamellae ventralis* (character 53): (0 > 1) present. Reversed in node 51, and in *Spheniscus magellanicus*, *Scopus umbretta*, and *Phaethon*. Paralleled in node 52.

7*. *Os palatinum*, *pars pterygoidea*, *facies parasphenoidalis*, *crista dorsalis palatina* (character 56): (0 > 1) present. Reversed in nodes 40 and 46. Paralleled in *Pelecanus thagus*.

8. *Pes pterygoidei*, *lamella dorsalis* (character 58): (0 > 1) present. Reversed in nodes 40 and 46. Paralleled in *Pelecanus thagus*

9. *Os quadratum*, *processus mandibularis*, *condylus medialis*, *facies articularis*, superficial shape (character 63): (0 > 1) concave. Reversed in node 39, and in *Platalea ajaia*.

Node 34 (95/95/20)

(*Thalassarche melanophris* + *T. chlororhynchos*)

Synapomorphies:

11. *Occiput*, *prominentia cerebellaris*, shape (character 4): (1 > 0) slight elevation with a distinguishable *linea (aut crista) medialis*. Reversal of synapomorphy 2 of node 31.

2*. *Os parasphenoidale*, *tuba auditiva (pharyngotympanica)*, *facies rostroventralis*, conformation (character 16): (0 > 1) tubes lacking lateral osseous walls. Paralleled in nodes 42, 48, and 51.

3*. *Regio squamosalis*, *fossa musculorum temporalium*, depth (character 18): (0 > 1) *pars ventralis fossae* as shallow as *pars dorsalis*. Reversal of synapomorphy 3 of node 31.

4*. *Regio squamosalis*, *processus suprameaticus* (character 19): (0 > 1) near-absent. Reversal of synapomorphy 4 of node 31. Paralleled in node 33.

5. *Os lacrimale*, *processus descendens et pes*, length (character 26): (0 > 1) extending towards *archus jugalis*. Paralleled in node 42, and in *Podiceps major*.

6. *Pars rostralis orbitae*, *ossa ectethmoidale et lacrimale*, conformation (character 32): (0 > 1) separated from each other. Paralleled in node 38.

7. *Partes medialis et caudalis orbitae*, *fonticulus interorbitalis et foramen opticum*, conformation (character 34): (1 > 0) separated from each other. Reversal of synapomorphy 4 of node 33. Paralleled in node 52.

8. *Pars caudalis orbitae*, *fonticulus orbitocranialis* (character 35): (0 > 1) absent. Paralleled in nodes 42 and 52.

9. *Rostrum maxillae*, *facies ventralis rostri*, *sulcus paratomialis*, rostral extension (character 38): (1 > 0) towards *apex rostri maxillae*. Paralleled in nodes 38 and 53.

10. *Saeptum nasale (nasi) osseum* (character 47): (1 > 0) present. Reversal of synapomorphy 5 of node 33. Paralleled in node 41, and in *Plegadis chihi*.

Node 35 (64/63/19)

((*Calonectris borealis* + *Puffinus gravis*) + (*Thalassarche melanophris* + *T. chlororhynchos*))

Synapomorphies:

1*. *Os lacrimale*, *processus descendens*, *incisura (aut foramen) ducti nasolacrimalis* (character 24): (0 > 1) near-absent. Reversion of synapomorphy 3 of node 32. Paralleled in nodes 30, 40, and 47.

2. *Ossa frontale et lacrimale*, *junctura (naso-) frontolacrimalis*, type (character 27): (0 > 1) syndesmosis. Paralleled in node 51.

3. *Pars rostralis orbitae*, *os ectethmoidale* (character 31): (1 > 0) present. Reversal of synapomorphy 3 of node 33. Paralleled in node 38, 47, and 54.

4*. *Rostrum maxillae, facies ventralis rostri, sulcus paratomialis* (character 37): (0 > 1) present. Paralleled in node 40.

5. *Rostrum maxillae*, *facies dorsalis rostri*, *apex (terminus) rostri*, shape (character 39): (0 > 1); hamulate. Paralleled in node 40.

6. *Os maxillare*, *pons-maxillaro jugalis* (character 44): (0 > 1) present.

7. *Os quadratum, basis processus orbitalis, facies (ventro-) medialis, foramen pnematicus* (character 62): (0 > 1) present. Paralleled in node 40.

8. *Ramus mandibulae*, *facies dorsalis*, *sulcus paratomialis* (character 68): (0 > 1) present. Paralleled in node 39.

9. *Ramus mandibulae*, *pars intermedia*, *margo ventralis*, shape (lateral perspective) (character 70): (0 > 1) straight relative to *margo ventralis partis caudalis mandibulae*. Paralleled in nodes 45, 48, and 51, and in *Podiceps major*.

10. *Fossa articularis quadratica*, *processus retroarticularis mandibulae* (character 74): (0 > 1) near-absent. Paralleled in node 42.

11. *Ramus mandibulae*, *pars caudalis*, *fenestra rostralis mandibulae* (character 75): (0 > 1) present. Paralleled in node 45, and in *Phaethon* and *Phalacrocorax brasilianus*.

Node 36 (97/97/33)

(*Calonectris borealis* + *Puffinus gravis*)

Synapomorphies:

1*. *Occiput*, *condylus occipitalis* (caudal perspective), shape (character 3): (1 > 0) circular. Reversal of synapomorphy 1 of node 31.

2. *Regio supraoccipitalis*, *foramina efferens ramorum occipitalium arteriarum ophtalmicum externarum*, position (character 6): (0 > 1) at or very near to *crista nuchalis transversa*. Paralleled in node 54.

3. *Os parasphenoidale*, *rostrum parasphenoidale*, *processus basypterigoideus* (character 12): (1 > 0) present. Reversal of synapomorphy 1 of node 33.

4. (*Principally*) *Regio parietalis*, *axis medialis cranii*, *crista (linea) nuchalis sagittalis* (character 21): (0 > 1) present. Paralleled in nodes 48 and 53, and in *Podiceps major*.

Node 37 (1/–/–)

((*Phoenicopterus chilensis* + ((*Ciconia maguari* + (*Mycteria americana* + *Jabiru mycteria*)) + (*Platalea ajaia* + (*Plegadis chihi* + *Theristicus caudatus* + *Eudocimus ruber*))) + ((*Scopus* + (*Balaeniceps* + ((Ardeidae + *Phaethon*) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*))))))

Synapomorphies:

1. *Pars medialis orbitae*, *saeptum interorbitale osseum*, *fonticulus interorbitalis* (character 33): (0 > 1) absent. Reversed in nodes 38 and 53.

2. *Ossa maxillares*, *processus palati*, conformation (character 45): (0 > 1) fused with each other along *axis medialis*. Paralleled in *Dendrocygna viduata*.

3. *Zona feloxoria craniofacialis*, conformation (character 67): (1 > 0) *indistinct jugum*. Reversal of synapomorphy 6 of node 30.

4*. *Ramus mandibulae*, *pars symphisialis*, length (character 72): (0 > 1) more than one-third of the total length of *mandibula*. Reversed in node 41, and in *Platalea ajaia*.

Node 38 (2/–/–)

(*Phethon* + Ardeidae)

Synapomorphies:

1. *Pars rostralis orbitae*, *os ectethmoidale* (character 31): (1 > 0) present. Reversal of synapomorphy 3 of node 33. Paralleled in nodes 35, 47, and 54.

2. *Pars rostralis orbitae*, *ossa ectethmoidale et lacrimale*, conformation (character 32): (0 > 1) separated from each other. Paralleled in node 34.

3. *Pars medialis orbitae*, *saeptum interorbitale osseum*, *fonticulus interorbitalis* (character 33): (1 > 0) present (0). Reversal of synapomorphy 1 of node 37. Paralleled in node 53.

4*. *Rostrum maxillae*, *facies ventralis rostri*, *sulcus paratomialis*, rostral extension (character 38): (1 > 0) towards *apex rostri maxillae*. Paralleled in nodes 34 and 53.

5*. *Rostrum maxillae*, *facies dorsalis rostri*, *apex (terminus) rostri*, shape (character 39): (1 > 0) decurved. Reversal of synapomorphy 5 of node 40. Paralleled in node 52, and in *Mycteria americana*.

6. *Os maxillare*, *terminus caudalis cristae tomialis*, '*processus* P2' (character 43): (0 > 1); present. Paralleled in node 45, and in *Dendrocygna viduata*.

7*. *Apertura nasalis ossea* (character 46): (1 > 0) present. Reversal of synapomorphy 6 of node 40.

8. *Os palatinum*, *pars choanalis*, conformation (character 51): (1 > 0) separated from each other along *planum medianum*. Reversal of synapomorphy 4 of node 41.

9*. *Os quadratum*, *processus mandibularis*, *condylus lateralis*, *sulcus intercondylaris*, *foramina pneumatica* (character 65): (1 > 0) absent (0). Reversal of synapomorphy 11 of node 40. Paralleled in node 53.

Node 39 (1/–/–)

((Ardeidae + Phaethon) + ((*Balaeniceps* + (Ardeidae + *Phaethon*) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*))))))

Synapomorphies:

1. *Regiones occipitalis et squamosalis*, *cristae laminae externae cranii* (character 5): (0 > 1) absent (0); present (1)

2. *Arcus jugalis*, *axis craniocaudalis*, position (character 59): (1 > 0) approximately aligned with *planum palati ossei*. Reversal of synapomorphy 7 of node 42.

3. *Os quadratum*, *processus mandibularis*, *condylus medialis*, *facies articularis*, superficial shape (character 63): (1 > 0) convex. Reversal of synapomorphy 9 of node 33. Paralleled in *Platalea ajaia*.

4. *Os quadratum*, *processus mandibularis*, *condylus medialis*, *(sub-) condylus pterygoideus*, position (lateral perspective) (character 64): (0 > 1) dorsal to *cotyla quadratojugalis*. Reversed in node 50, and in *Anhinga anhinga*.

5. *Zona feloxoria craniofacialis*, conformation (character 67): (0 > 2) distinct *sulcus* bordered by *eminentia ossea*. Paralleled in *Mycteria americana*.

6*. *Ramus mandibulae*, *facies dorsaalis*, *sulcus paratomialis* (character 68): (0 > 1) present. Reversed in *Pelecanus thagus*. Paralleled in node 35.

Node 40 (7/0/–)

((*Balaeniceps* + (Ardeidae + *Phaethon*) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*)))))

Synapomorphies:

1*. *Os parasphenoidale*, *tuba auditiva (pharyngotympanica)*, *facies rostroventralis*, conformation (character 16): (1 > 0) tubes completely (or nearly so) ossified. Reversal of synapomorphy 1 of node 42. Reversed in nodes 48 and 51.

2*. *Os lacrimale*, *processus descendens*, *incisura (aut foramen) ducti nasolacrimalis* (character 24): (0 > 1) near-absent. Reversal of synapomorhy 3 of node 32. Reversed in node 50, and in *Phaethon*. Paralleled in nodes 30, 35, and 45.

3*. *Pars caudalis orbitae*, *area muscularis aspera*, '*processus* P1' (character 36): (1 > 0) absent. Reversal of synapomorphy 5 of node 42. Reversed in *Pelecanus thagus*.

4. *Rostrum maxillae*, *facies ventralis rostri*, *sulcus paratomialis* (character 37): (0 > 1) present. Reversed in node 48, and in *Anhinga anhinga*. Paralleled in node 35.

5*. *Rostrum maxillae*, *facies dorsalis rostri*, *apex (terminus) rostri*, shape (character 39): (0 > 1) hamulate. Reversed in nodes 38 and 52. Paralleled in node 35.

6*. *Apertura nasalis ossea* (character 46): (0 > 1) near-absent. Reversed in node 38.

7. *Os palatinum*, *pars lateralis*, *angulus (processus) caudolateralis* (character 54): (0 > 1) absent. Reversed in node 51. Paralleled in node 54, and in *Podiceps major* and *Spheniscus magellanicus*.

8. *Os palatinum*, *pars pterygoidea*, *facies parasphenoidalis*, *crista dorsalis palatina* (character 56): (1 > 0) absent. Reversal of synapomorphy 7 of node 33. Reversed in *Pelecanus thagus*. Paralleled in node 46.

9. *Pes pterygoidei*, *lamella dorsalis* (character 58): (1 > 0) absent. Reversal of synapomorphy 8 of node 33. Reversed in *Pelecanus thagus*. Paralleled in node 46.

10. *Os quadratum*, *basis processus orbitalis*, *facies (ventro-) medialis*, *foramen pnematicus* (character 62): (0 > 1) present. Reversed in node 48, and in *Anhinga anhinga*. Paralleled in node 35.

11*. *Os quadratum*, *processus mandibularis*, *condylus lateralis*, *sulcus intercondylaris*, *foramina pneumatica* (character 65): (0 > 1) present. Reversed in nodes 38 and 53.

Node 41 (1/–/–)

((*Scopus* + (*Balaeniceps* + (Ardeidae + *Phaethon*)) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*))))))

Synapomorphies:

1. *Os parasphenoidale*, *laminae parasphenoidalis*, *tuberculum basilare (et processus medialis laminae parasphenoidales)* (character 14): (1 > 0) near-absent. Reversal of synapomorphy 1 of node 32. Reversed in node 51, and in *Phaethon*.

2. *Saeptum nasale (nasi) osseum* (character 47): (1 > 0) present. Reversal of synapomorphy 5 of node 33. Paralleled in node. 34. Reversed in *Phaethon*.

3. *Fossa antorbitalis*, *fenestra premaxillaris* (character 49): (0 > 1) present. Reversed in node 48.

4. *Os palatinum*, *pars choanalis*, conformation (character 51): (0 > 1) joined with each other along *planum medianum*. Reversed in node 38.

5*. *Ramus mandibulae*, *pars symphisialis*, length (character 72): (1 > 0) less than one-third of the total length of *mandibula*. Reversal of synapomorphy 4 of node 37. Paralleled in *Platalea ajaia*.

Node 42 (13/–/–)

((Ciconiidae + Threskiornithidae) + (*Scopus* + (*Balaeniceps* + (Ardeidae + *Phaethon*)) + (*Pelecanus* + (*Fregata* + (*Sula* + (*Phalacrocorax* + *Anhinga*)))))))

Synapomorphies:

1*. *Os parasphenoidale*, *tuba auditiva (pharyngotympanica)*, *facies rostroventralis*, conformation (character 16): (0 > 1) tubes lacking lateral osseous walls. Reversed in node 40. Paralleled in nodes 34, 48, and 51.

2*. (Principally) *Regio frontalis*, *facies dorsualis*, *fossa glandulae nasalis* (character 22): (0 > 1) absent. Reversal of synapomorphy 2 of node 32. Paralleled in node 30.

3. *Os lacrimale*, *processus descendens et pes*, length (character 26): (0 > 1) towards *archus jugalis*. Reversed in node 51, and in *Balaeniceps rex*. Paralleled in node 34, and in *Podiceps major*.

4. *Pars caudalis orbitae*, *fonticulus orbitocranialis* (character 35): (0 > 1) absent. Reversed in nodes 48 and 51. Paralleled in node 34.

5*. *Pars caudalis orbitae*, *area muscularis aspera*, '*processus* P1' (character 36): (0 > 1) present. Reversed in node 40. Paralleled in *Pelecanus thagus*.

6. *Rostrum maxillae*, *facies ventralis rostri*, *fenestra ventromedialis* (character 42): (0 > 1) absent. Reversed in node 46.

7. *Arcus jugalis*, *axis craniocaudalis*, position (character 59): (0 > 1) distinctly perpendicular to *planum palati ossei*. Reversed in node 39.

8. *Fossa articularis quadratica*, *processus retroarticularis mandibulae* (character 74): (0 > 1) near-absent. Reversed in nodes 47 and 54. Paralleled in node 35.

Node 43 (19/–/–)

(*Mycteria americana* + *Jabiru mycteria*)

Synapomorphy:

1. *Regio frontalis*, *facies dorsalis*, superficial shape (character 2): (0 > 1) planar. Paralleled in node 53, and in *Platalea ajaia* and *Balaeniceps rex*.

Node 44 (47/47/13)

(*Ciconia maguari* + (*Mycteria americana* + *Jabiru mycteria*)): Ciconiidae

Synapomorphies:

1*. *Rostrum maxillae*, *facies dorsalis rostri*, *apex (terminus) rostri*, shape (character 39): (0 > 2) straight. Reversed in *Mycteria americana*. Paralleled in node 48, and in *Anhinga anhinga*.

2. *Rostrum maxillae*, *margo tomialis* exclusive of *apex (terminus) rostri* (lateral view), conformation (character 41): straight. Paralleled in node 48, and in *Podiceps major*, *Scopus umbretta*, and *Anhinga anhinga*.

3. *Ramus mandibulae*, *pars intermedia*, *facies medialis (lingualis)*, *fossa medialis* (character 71): (0 > 1) present. Paralleled in nodes 48 and 51, and in *Scopus umbretta*.

Node 45 (13/0/–)

((*Ciconia maguari* + (*Mycteria americana* + *Jabiru mycteria*)) + (*Platalea ajaia* + (*Plegadis chihi* + *Theristicus caudatus* + *Eudocimus ruber*)))

Synapomorphies:

1. *Os maxillare*, *terminus caudalis cristae tomialis*, '*processus* P2' (character 43): (0 > 1) present. Paralleled in node 38, and in *Dendrocygna viduata*.

2*. *Ramus mandibulae*, *pars intermedia*, *margo ventralis*, shape (lateral perspective) (character 70): (0 > 1) straight relative to *margo ventralis partis caudalis mandibulae*. Reversed in node 46. Paralleled in nodes 35, 48, and 51, and in *Podiceps major*.

3. *Ramus mandibulae*, *pars caudalis*, *fenestra rostralis mandibulae* (character 75): (0 > 1) present. Paralleled in node 35, and in *Phaethon* and *Phalacrocorax brasilianus*.

Node 46 (81/81/25)

(*Plegadis chihi* + *Theristicus caudatus* + *Eudocimus ruber*)

Synapomorphies:

1. *Rostrum maxillae*, *facies ventralis rostri*, *fenestra ventromedialis* (character 42): (1 > 0) present. Reversal of 6 synapomorphy of node 42.

2. *Os palatinum*, *pars pterygoidea*, *facies parasphenoidalis*, *crista dorsalis palatine* (character 56): (1 > 0) absent. Reversal of synapomorphy 7 of node 33. Paralleled in node 40.

3. *Pes pterygoidei*, *lamella dorsalis* (character 58): (1 > 0) absent. Reversal of synapomorphy 8 of node 33. Paralleled in node 40.

4*. *Ramus mandibulae*, *pars intermedia*, *margo ventralis*, shape (lateral perspective) (character 70): (1 > 0) decurved relative to *margo ventralis partis caudalis mandibulae*. Reversal of synapomorphy 2 of node 45.

Node 47 (62/61/13) Node 47

(*Platalea ajaia* + (*Plegadis chihi* + *Theristicus caudatus* + *Eudocimus ruber*)): Threskiornithidae

Synapomorphies:

1. *Regio supraoccipitalis*, *fonticulus occipitalis* (character 7): (0 > 1) present. Paralleled in *Dendrocygna viduata* and *Phoenicopterus chilensis*.

2. *Os parasphenoidale*, *(ala parasphenoidalis) processus lateralis laminae parasphenoidales*, caudal extension (character 15): up to *processus paraoccipitalis ossis exocipitales*. Paralleled in nodes 48 and 53.

3*. *Os lacrimale*, *processus descendens*, *incisura (aut foramen) ducti nasolacrimalis* (character 24): (0 > 1) near-absent. Paralleled in nodes 30, 35 and 40.

4. *Pars rostralis orbitae*, *os ectethmoidale* (character 31): (1 > 0) present. Reversal of synapomorphy 3 of node 33. Paralleled in nodes 35, 38, and 54.

5. *Arcus jugalis, juncura maxillo-arcuatilis*, position (character 60): (0 > 1) dorsal to *terminus caudalis tomium maxillae*. Paralleled in node 48, and in *Dendrocygna viduata* and *Scopus umbretta*.

6. *Os quadratum*, *corpus (et processus oticus)*, *facies caudomedialis*, *foramen pnematicus* (character 61): (0 > 1) present. Paralleled in node 48, and in *Dendrocygna viduata* and *Anhinga anhinga*.

7. *Rostrum (symphysis) mandibulae*, *fascies dorsalis*, surface shape (character 69): (0 > 1) planar. Paralleled in *Balaeniceps rex*, *Phaethon*, *Ardea cocoi*, and *Anhinga anhinga*.

8*. *Fossa articularis quadratica*, *processus retroarticularis mandibulae* (character 74): (1 > 0) present. Reversal of synapomorphy 8 of node 42. Paralleled in node 54.

Node 48 (99/98/100)

(*Ardea cocoi* + *Ixobricus involucris* + *Egretta thula*): Ardeidae

Synapomorphies:

1. *Occiput*, *condylus occipitalis* (caudal perspective), shape (character 3): (0 > 1) bilobate. Paralleled in nodes 31 and 50, and in *Dendrocygna viduata* and *Ciconia maguari*.

2. *Regiones frotalis et laterosphenoidalis*, ‘second *processus postorbitalis*’ (character 10): (0 > 1) present. Paralleled in node 54.

3. *Os parasphenoidale*, *rostrum parasphenoidale*, *pars ventrocaudalis rostri*, shape (character 11): (0 > 1) lateromedially compressed. Paralleled in node 55.

4. *Os parasphenoidale*, *lamina parasphenoidalis*, conformation (character 13): (0 > 1) rostrally free from *os basisphenoidale*. Paralleled in node 53.

5. *Os parasphenoidale*, *(ala parasphenoidalis) processus lateralis laminae parasphenoidales*, caudal extension (character 15): (0 > 1) up to *processus paraoccipitalis ossis exocipitales*. Paralleled in nodes 47 and 53.

6*. *Os parasphenoidale*, *tuba auditiva (pharyngotympanica)*, *facies rostroventralis*, conformation (character 16): (0 > 1) tubes lacking lateral osseous wall. Reversal of synapomorphy of 1 node 40. Paralleled in nodes 34, 42, and 51.

7. *Regio squamosalis*, *fossa musculorum temporalium*, depth (character 18): (0 > 1) *pars ventralis fossae* distinctly deeper than *pars dorsalis*. Paralleled in nodes 31 and 51.

8. (*Principally*) *Regio parietalis*, *axis medialis cranii*, *crista (linea) nuchalis sagittalis* (character 21): (0 > 1) present. Paralleled in nodes 36 and 53, and in *Podiceps major*.

9. *Pars caudalis orbitae*, *fonticulus orbitocranialis* (character 35): (1 > 0) present. Reversal of synapomorphy 4 of node 42. Paralleled in node 51.

10. *Rostrum maxillae*, *facies ventralis rostri*, *sulcus paratomialis* (character 37): (1 > 0) absent. Reversal of synapomorphy 4 of node 40. Paralleled in *Anhinga anhinga*.

11*. *Rostrum maxillae*, *facies dorsalis rostri*, *apex (terminus) rostri*, shape (character 39): (0 > 2) straight. Paralleled in node 44, and in *Anhinga anhinga*.

12. *Rostrum maxillae*, *margo tomialis* exclusive of *apex (terminus) rostri* (lateral view), conformation (character 41): (0 > 1) straight. Paralleled in node 44, and in *Podiceps major*, *Scopus umbretta*, and *Anhinga anhinga*.

13. *Fossa antorbitalis*, *fenestra premaxillaris* (character 49): (1 > 0) absent. Reversal of synapomorphy 3 of node 41.

14. *Os palatinum*, *pars maxillaris*, *processus rostralis*, length (character 50): (0 > 1) distinctly longer than *pars choanalis*. Paralleled in node 51, and in *Spheniscus magellanicus*.

15. *Arcus jugalis, juncura maxillo-arcuatilis*, position (character 60): (0 > 1) dorsal to *terminus caudalis tomium maxillae*. Paralleled in node 47, and in *Dendrocygna viduata* and *Scopus umbretta*.

16. *Os quadratum*, *corpus (et processus oticus)*, *facies caudomedialis*, *foramen pnematicus* (character 61): (0 > 1) present. Paralleled in node 47, and in *Dendrocygna viduata, Phoenicopterus chilensis*, and *Anhinga anhinga*.

17. *Os quadratum*, *basis processus orbitalis*, *facies (ventro-) medialis*, *foramen pnematicus* (character 62): (1 > 0) absent. Reversal of synapomorphy 10 of node 40. Paralelled in *Anhinga anhinga*.

18. *Os quadratum*, *processus orbitalis*, length (character 66): (0 > 2) longer than *processus oticus*. Paralleled in node 50, and in *Phoenicopterus chilensis*.

19. *Zona feloxoria craniofacialis*, conformation (character 67): (2 > 1) distinct, transverse *lamina*. Paralleled in nodes 30 and 50, and in *Platalea ajaia* and *Scopus umbretta*.

20. *Ramus mandibulae*, *pars intermedia*, *margo ventralis*, shape (lateral perspective) (character 70): (0 > 1) straight relative to *margo ventralis partis caudalis mandibulae*. Paralleled in nodes 35, 45, and 51, and in *Podiceps major*.

21. *Ramus mandibulae*, *pars intermedia*, *facies medialis (lingualis)*, *fossa medialis* (character 71): (0 > 1) present. Paralleled in nodes 44 and 51, and in *Scopus umbretta*.

Node 49 (4/–/–)

(Pelecanidae + (Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae)))): ‘Steganopodes’

Synapomorphies:

1*. *Regio supraoccipitalis*, *foramina efferens venarum occipitalium externarum* (character 8): (0 > 1) present. Reversed in node 50. Paralleled in *Scopus umbretta*.

2. *Regio frontalis*, *facies orbitalis (ventralis)*, *pars rostromedialis*, *impressio glandulae nasalis* (character 23): (0 > 1) present.

3. *Conchae nasalis osseae* (character 48): (0 > 1) near-absent.

4*. *Vomer* (character 57): (0 > 1) absent. Reversed in node 50.

5*. *Os suprajugale* (character 77): (0 > 1) present.

Node 50 (95/95/100)

(*Fregata magnificens* + *F*. *minor*): Fregatidae

Synapomorphies:

1. *Occiput*, *condylus occipitalis* (caudal perspective), shape (character 3): (0 > 1) bilobate. Paralleled in nodes 31 and 48, and in *Dendrocygna viduata* and *Ciconia maguari*.

2*. *Regio supraoccipitalis*, *foramina efferens venarum occipitalium externarum* (character 8): (1 > 0) present. Reversal of synapomorphy 1 of node 49.

3. *Os lacrimale*, *processus descendens*, *incisura (aut foramen) ducti nasolacrimalis* (character 24): (1 > 0) present. Reversal of synapomorphy 2 of node 40. Paralleled in *Phaethon*.

4*. *Vomer* (character 57): (1 > 0) present. Reversal of synapomorphy 4 of node 51.

5. *Os quadratum*, *processus mandibularis*, *condylus medialis*, *(sub-) condylus pterygoideus*, position (lateral perspective) (character 64): (1 > 0) aproximately coplanar to *cotyla quadratojugalis*. Reversal of synapomorphy 4 of node 39. Paralleled in *Anhinga anhinga*.

6*. *Os quadratum*, *processus orbitalis*, length (character 66): (1 > 2) longer than *processus oticus*. Paralleled in node 49, and in *Phoenicopterus chilensis*.

7. *Zona feloxoria craniofacialis*, conformation (character 67): (2 > 1) distinct, transverse *lamina*. Paralleled in nodes 30 and 48, and in *Platalea ajaia* and *Scopus umbretta*.

8. *Ramus mandibulae*, *pars caudalis*, *fossa aditus canalis neurovascularis*, shape (character 73): (0 > 1) short, dorsoventrally narrow. Paralelled in *Platalea ajaia*, *Balaeniceps rex*, and *Anhinga anhinga*.

9. *Os lacrimopalatinum* (character 78): (0 > 1) present. Paralleled in node 31.

Node 51 (35/27/7) Node 51

(Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae))): 'Suliformes'

Synapomorphies:

1. *Os parasphenoidale*, *laminae parasphenoidalis*, *tuberculum basilare (et processus medialis laminae parasphenoidales)* (character 14): (0 > 1) present. Reversal of synapomorphy 1 of node 41. Paralleled in node 32, and in *Phaethon*.

2*. *Os parasphenoidale*, *tuba auditiva (pharyngotympanica)*, *facies rostroventralis*, conformation (character 16): (0 > 1) tubes lacking lateral osseous wall. Reversal of synapomorphy 1 of node 40. Paralleled in nodes 42 and 48.

3. *Regio squamosalis*, *fossa musculorum temporalium*, depth (character 18): (0 > 1) *pars ventralis fossae* distinctly deeper than *pars dorsalis*. Reversed in *Anhinga anhinga*. Paralleled in nodes 31 and 48.

4. *Os lacrimale*, *processus descendens et pes*, length (character 26): (1 > 0) extending up to *archus jugalis*. Reversal of synapomorphy 3 of node 42. Paralleled in *Balaeniceps rex*.

5. *Ossa frontale et lacrimale*, *junctura (naso-) frontolacrimalis*, type (character 27): (0 > 1) syndesmosis. Paralleled in node 35.

6. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, position (character 29): (1 > 2) rostromedial to *cotylae quadratica squamosi et otici*. Reversed in *Anhinga anhinga*. Paralleled in node 35, and in *Phaethon*.

7*. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, size (character 30): (0 > 1) distinctly larger than *recessus tympanicus caudalis*. Reversed in node 54. Paralleled in node 35, and in *Phaethon*.

8*. *Pars caudalis orbitae*, *fonticulus orbitocranialis* (character 35): (1 > 0) present. Reversal of synapomorphy 4 of node 42. Reversed in node 52. Paralleled in node 48.

9*. *Os palatinum*, *pars maxillaris*, *processus rostralis*, length (character 50): (0 > 1) distinctly longer than *pars choanalis*. Reversed in *Fregata minor*. Paralleled in node 48, and in *Spheniscus magellanicus*.

10*. *Os palatinum*, *pars choanalis*, *lamellae ventralis* (character 53): (1 > 0) near-absent. Reversal of synapomorphy 6 of node 33. Reversed in node 52. Paralleled in *Spheniscus magellanicus*, *Scopus umbretta*, and *Phaethon*.

11*. *Os palatinum*, *pars lateralis*, *angulus (processus) caudolateralis* (character 54): (0 > 1) present. Reversal of synapomorphy 7 of node 40. Reversed in node 54.

12*. *Os palatinum*, *pars pterygoidea*, *processus pterygoideus* (character 55): (1 > 0) near-absent. Reversal of synapomorphy 5 of node 30. Reversed in node 54. Paralleled in *Phaethon*

13*. *Os quadratum*, *processus orbitalis*, length (character 66): (0 > 1) shorter than *processus oticus*.

14. *Ramus mandibulae*, *pars intermedia*, *margo ventralis*, shape (lateral perspective) (character 70): (0 > 1) straight relative to *margo ventralis partis caudalis mandibulae*. Paralleled in nodes 35, 45, and 48, and in *Podiceps major*.

15*. *Ramus mandibulae*, *pars intermedia*, *facies medialis (lingualis)*, *fossa medialis* (character 71): (0 > 1) present. Reversed in node 52. Paralleled in nodes 44 and 48, and in *Scopus umbretta*.

Node 52 (92/92/100)

(*Sula variegata* + *S*. *leucogaster*): Sulidae

Synapomorphies:

1. *Partes medialis et caudalis orbitae*, *fonticulus interorbitalis et foramen opticum*, conformation (character 34): (1 > 0) separated from each other. Reversal of synapomorphy 4 of node 33. Paralleled in node 34.

2*. *Pars caudalis orbitae*, *fonticulus orbitocranialis* (character 35): (0 > 1) absent. Reversal of synapomorphy 8 of node 51. Paralleled in nodes 34 and 42.

3. *Rostrum maxillae*, *facies dorsalis rostri*, *apex (terminus) rostri*, shape (character 39): (1 > 0) decurved. Reversal of synapomorphy 5 of node 40. Paralleled in node 38, and in *Mycteria americana*.

4*. *Os palatinum*, *pars choanalis*, *lamellae ventralis* (character 53): (0 > 1) present. Reversal of synapomorphy 10 of node 51. Paralleled in node 33.

5*. *Ramus mandibulae*, *pars intermedia*, *facies medialis (lingualis)*, *fossa medialis* (character 71): (1 > 0) absent. Reversal of synapomorphy 15 of node 51.

Node 53 (84/83/28)

(Sulidae + (Phalacrocoracidae + Anhingidae)): ‘Suloidea’

Synapomorphies:

1. *Regio frontalis*, *facies dorsalis*, superficial shape (character 2): (0 > 1) planar. Paralleled in node 43, and in *Platalea ajaia* and *Balaeniceps rex*.

2. *Os parasphenoidale*, *rostrum parasphenoidale*, *pars ventrocaudalis rostri*, shape (character 11): (0 > 1) lateromedially compressed. Paralleled in node 48.

3. *Os parasphenoidale*, *(ala parasphenoidalis) processus lateralis laminae parasphenoidales*, caudal extension (character 15): (0 > 1) up to *processus paraoccipitalis ossis exocipitales*. Paralleled in nodes 47 and 48.

4. *Regio exoccipitalis*, *processus paraoccipitalis*, *apex (terminus) processus*, orientation (character 17): (0 > 1) caudal to *occiput*.

5*. *Regio squamosalis*, *processus suprameaticus* (character 19): (1 > 0) near-absent. Reversal of synapomorphy 2 of node 33. Reversed in *Anhinga anhinga*. Paralleled in node 31, and in *Balaeniceps rex* and *Phaethon*.

6*. (Principally) *Regio parietalis*, *axis medialis cranii*, *crista (linea) nuchalis sagittalis* (character 21): (0 > 1) present. Reversed in *Anhinga anhinga*. Paralleled in nodes 36 and 48, and in *Podiceps major*.

7. *Ossa frontale et lacrimale (et nasale), junctura (naso) frontolacrimalis*, position (character 28): (0 > 1) ventrocaudal to *zona flexoria craniofacialis*. Paralleled in *Podiceps major*.

8. *Pars medialis orbitae*, *saeptum interorbitale osseum*, *fonticulus interorbitalis* (character 33): (1 > 0) present. Reversal of synapomorphy 1 of node 37. Paralleled in node 38.

9. *Rostrum maxillae*, *facies ventralis rostri*, *sulcus paratomialis*, rostral extension (character 38): (1 > 0) towards *apex rostri maxillae*. Paralleled in nodes 34 and 38.

10. *Os palatinum*, *pars choanalis*, *lamellae dorsalis* (character 52): (0 > 1) near-absent. Paralleled in *Spheniscus magellanicus*.

11. *Os quadratum*, *processus mandibularis*, *condylus lateralis*, *sulcus intercondylaris*, *foramina pneumatica* (character 65): (0 > 1) absent. Reversal of synapomorphy 11 of node 40. Paralleled in node 38.

Node 54 (92/92/100)

(*Phalacrocorax brasilianus* + *Anhinga anhinga*)

Synapomorphies:

1. *Cranium*, dorsoventral depth (character 1): (0 > 1) less than bilateral width.

2. *Regio supraoccipitalis*, *foramina efferens ramorum occipitalium arteriarum ophtalmicum externarum*, position (character 6): (0 > 1) at or very near to *crista nuchalis transversa*. Paralleled in node 36.

3. (Principally) *Regio ossis laterosphenoidalis*, *processus postorbitalis* (character 9): (0 > 1) absent.

4. *Regiones frotalis et laterosphenoidalis*, 'second *processus postorbitalis*' (character 10): (0 > 1) present. Paralleled in node 48.

5. *Os parasphenoidale*, *lamina parasphenoidalis*, conformation (character 13): (0 > 1) rostrally free from *os basisphenoidale*.

6. *Ossa squamosalis et prooticum*, *cotylae quadratica squamosi et otici*, conformation (character 20): (2 > 1) juxtaposed to each other.

7. *Os lacrimale*, *processus descendens*, *foramina pneumatica* (character 25): (1 > 0) absent (0). Reversal of synapomorphy 4 of node 32. Paralleled in *Spheniscus magellanicus*.

8*. *Partes ossea meatus acusticus externi*, *recessus tympanicus dorsalis*, size (character 30): (1 > 0) similar to *recessus tympanicus caudalis*. Reversal of synapomorphy 7 of node 51.

9. *Pars rostralis orbitae*, *os ectethmoidale* (character 31): (1 > 0) present. Reversal of synapomorphy of 3 node 33. Paralleled in nodes 35, 38, and 47.

10*. *Os palatinum*, *pars lateralis*, *angulus (processus) caudolateralis* (character 54): (0 > 1) absent. Reversal of synapomorphy 11 of node 51. Paralleled in node 40, and in *Spheniscus magellanicus* and *Podiceps major*.

11*. *Os palatinum*, *pars pterygoidea*, *processus pterygoideus* (character 55): (1 > 0) near-absent. Reversal of synapomorphy 12 of node 51. Paralleled in node 30.

12. *Fossa articularis quadratica*, *processus retroarticularis mandibulae* (character 74): (1 > 0) present. Reversal of synapomorphy 8 of node 42. Paralleled in node 47.

13. *Os nuchale* (character 76): (0 > 1) present.

DISCUSSION

The ‘waterbird assemblage’: Natatores (*sensu* Livezey and Zusi 2007) or Aequornithes (*sensu* G. Mayr 2010)

The phylogenetic relationships within the so-called ‘waterbird assemblage’ have been (or should be) the subject of controversy due to different results obtained with phenotypic- and molecular-based studies. The analysis of Ericson et al. (2006), based on 5,007 base pairs from five nuclear gene regions recovered an unresolved clade comprising Gaviidae, Spheniscidae, (Diomedeida + (Procellariidae + Hydrobatidae)), Ciconiidae, (Threskiornithidae + Ardeidae + Scopidae + Balaeniciptidae + Pelecanidae), and (Fregatidae + (Sulidae + (Phalacrocorax + Anhingidae))). Subsequently to this, Hackett et al. (2008), in an analysis using 52,383 of 19 nuclear gene loci, retrieved a similar but better resolved topology. In their analysis, Gaviidae was placed sister to a clade formed by two sister-groups: one including Spheniscidae and Procellariiformes, the other Ciconiidae sister to ((Ardeidae + Threskiornithidae) + (Pelecanidae + (Scopidae + Balaeniciptidae)) + (Fregatidae + (Sulidae + (Phalacrocorax + Anhingidae)))). Similar results have been also found in other three analyses, the first incorporating their data to 31 new loci (Kimball et al. 2013); the second combining insertion/deletion mutations (referred to as ‘gap-characters’) with nucleotide sequences (Yuri et al. 2013), and the third using a whole genome approach (Jarvis et al. 2014).

The *c*. 2,000 phenotypic characters-based inference of Livezey and Zusi (2007) recovered a 'waterbird clade' similar to that of molecular-based analyses in terms of constituent taxa, albeit including Podicipedidae, Phoenicopteridae, and Phaethontidae. Topologically, Livezey's and Zusi's (2007) clade was divided into two sister groups: the first comprising (Gaviidae + Podicipedidae) plus (Spheniscidae + Procellariiformes), and the second (Balaeniciptidae + (Phaethonthidae + (Fregatidae + (Pelecanidae + (Sulidae + (Phalacrocorax + Anhingidae)))))) plus (Ardeidae + (Scopidae + (Threskiornithidae + (Ciconiidae + Phoenicopteridae))))). A similar topology was proposed by Smith (2010), the differences referring to the positions of Phaethontidae, Scopidae, Balaeniciptidae, and Pelecanidae.

The sister-taxon/taxa to the 'waterbird clade' vary (-ies) among the molecular-based hypotheses, and obviously between these and the study of Livezey and Zusi (2007). In the hypothesis by Ericson et al. (2006), the 'waterbird clade' was placed in a polytomy with ((Psophidae + (Aramidae + Gruidae)) + (Ralidae + Heliornithidae)), Musophagidae, Cuculidae, and Otidae. The other most recent, molecular-based hypotheses placed Musophagidae (Hackett et al. 2008, Yuri et al. 2013), (Aramidae + (Gruidae + Rallidae)) (Kimball et al. 2013) or (Phaethontidae + Eurypygidae) (Jarvis et al. 2014) as sister-taxon to the 'waterbird clade'. In the hypothesis of Livezey and Zusi (2007), the 'waterbird clade' was placed sister to a diverse 'landbird clade', named by them as 'Terrestrornithes', which encompass a variety semi-aquatic, predatory, and perching birds.

At least with respect to the constituent taxa, the present hypothesis is more congruent with those by Livezey and Zusi (2007) in the sense that in includes both Phoenicopteridae and Phaethontidae (but not Podicipedidae) as members of the clade. However, despite some (but significant) congruencies with previous hypotheses derived from both molecular and phenotypic data, there are some important differences as well. For example, a close relationship between Phaethontidae and Ardeidae, and between these taxa and the 'Steganopodes' clade (*i.e.*, that comprising Pelecanidae, Fregatidae, Sulidae, Phalacrocoracidae, and Anhingidae), have not been previously proposed. Nevertheless, even such a 'novelty' shares some degree of congruence with previous hypotheses.

Unlike the study by Livezey and Zusi (2007: 16, table 2), which was unable to identify a synapomorphy for his 'waterbird clade', the monophyly of the group as recovered herein is supported by 1 unambiguous synapomorphy plus 4 according to ACCTRAN. Among them, the presence of *sulci nasi* (character 40) is noteworthy because these furrows occurs in almost all species within the clade—but *Phoenicopterus chilensis* and *Phaethon*—, thus potentially qualifying as 'key innovation', which is defined by Heard and Hauser (1995: 52) as 'an evolutionary change in individual traits(s) that is causally linked to an increased diversification rate in the resulting clade (*for which it is a synapomorphy* [italics ours]). Key innovations may, therefore, be viewed as a synapomorphy that did not, or did not significantly, revert to previous state among descent species (Endress 2001). However, the functional significance of *sulci nasi* remains to be elucidated (Mayr 2010).

Regarding again the relationships within the ‘waterbird clade’, the studies by Hackett et al. (2008) and Yuri et al. 2013, recovered three major groupings: the first consisted of Gaviidae, sister to a clade containing the following: (Spheniscidae + Procellariiformes) and ((Ciconiidae + (Pelecanidae + (Scopidae + Balaenicipitidae)) + (Ardeidae + Threskiornithidae)) plus (Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae))). In the phenotype-based hypotheses, Phoenicopteridae is embedded within a similarly-composed clade as sister to Ciconiidae (Livezey and Zusi 2007) or (Ciconiidae + Ardeidae + Threskiornithidae) (Smith 2010).

The present hypothesis is thus more similar to the molecular-based studies with regard to the within-group relationships. The main differences refer to the arrangement of Pelecanidae and Threskiornithidae, and of course, the presence of Phaethontidae (see below).

The ‘pelagic assemblage’: Procellariimorphae (*sensu* Livezey and Zusi 2007) or Austrodyptornithes (*sensu* Yuri et al. 2013)

The monophyly of a clade composed of Spheniscidae plus Procellariiformes was proposed in several molecular-based studies (Hackett et al. 2008, Yuri et al. 2013, Jarvis et al. 2014), and in the phenotypic hypotheses by Livezey and Zusi (2007). The more discrepant results were those obtained by Smith (2010). He found Spheniscidae sister to a Podicipedidae plus Gaviidae clade. The present hypothesis is thus equivalent to the proposals of most previously analyses, irrespective of the type of data used for estimation.

Within the ‘marine assemblage’, a monophyletic Procellariiformes (Oceanitidae, Diomedeidae, Hydrobatidae, Procellariidae, and Pelecanoididae) has been congruently supported by both molecular- and phenotypic-based inferences; however, within-group relationships vary among different studies (*e.g.*, Nunn and Stanley 1998, Hackett et al. 2008, Livezey and Zusi 2007).

Podicipedidae and Phoenicopteridae

Molecular-based hypotheses invariably recovered a monophyletic (Podicipedidae + Phoenicopteridae), which falls not in the ‘waterbird clade’ but within the large Metaves clade (Ericson et al. 2006, Hackett et al. 2008, Kimball et al. 2013, Yuri et al. 2013, Jarvis et al. 2014). This clade, originally proposed Fain and Houde (2004) and lately adopted by Ericson et al. (2006) and Hackett et al. (2008), is now considered the sister to Coronaves (*sensu* Fain and Houde 2004), which is the clade wherein the ‘waterbird clade” is embedded. Metaves is divided into two groupings: the first is formed by (Eurypygidae + Rhynochetidae) sister to Apodidae, Aegothelidae, Caprimulgiformes, Hemiprocnidae, Podargidae, and Trochilidae. The other contains Phaethontidae, Pteroclididae, Columbiformes, Mesitornithidae, Podicipedidae, and Phoenicopteridae (see above under ‘Nodes 33 and 37’).

In phenotypic analyses, however, Podicipedidae grouped with Gaviidae in a clade sister to either (Spheniscidae + Procellariiformes) (Livezey and Zusi 2007) or Spheniscidae (Smith 2010). G. Mayr and Clark (2003) and G. Mayr (2004), respectively, recovered (Podicipedidae + Phoenicopteridae) in a clade with Procellariidae and Speniscidae, and with Gaviidae and Spheniscidae.

In the present hypothesis, *Podiceps major* (Podicipedidae) and *Phoenicopterus chilesis* (Phoenicopteridae) are, respectively, sister to and embedded with, the 'waterbird clade'. This position of *P. major*, near to but not included in the 'waterbird clade' is relatively more concordant with molecular studies (but see discussion under 'Node 32'), although it should be noted that none representative of Gaviidae was included in the present analysis.

As commented above, the most recent molecular-based analyses recovered Phoenicopteridae in a clade other than the 'waterbird clade' (Ericson et al. 2006, Hackett et al. 2008, Kimball et al. 2013, Yuri et al. 2013, Jarvis et al. 2014). In the studies of Livezey and Zusi (2007) and Smith (2010), Phoenicopteridae was found within the 'waterbird clade' but at different positions. Livezey and Zusi (2007) recovered (Phoenicopteridae + Ciconiidae) sister to Threskiornithidae. The study by Smith (2010) includes two main analyses: one using extant and fossil taxa, the other using extant taxa only. In the first, Phoenicopteridae was placed sister to a polytomy consisting of Ciconiidae, Ardeidae, and

Threskiornithidae, whilst in the second, it falls within an unresolved 'waterbird clade'.

According to the present hypothesis, Phoenicopteridae is sister to a large clade including Ciconiidae, Ardeidae, Threskiornithidae, Scopidae, Balaeneciptidae, Phaethonthidae, Pelecanidae, Fregatida, Sulida, Phalacrocoracidae, and Anhingidae. This position, however, is tentative, as it has no congruence with previous hypotheses.

The wading birds and allies: storks, ibises, shoebill, and hamerkop

The most recent molecular-based analyses recovered Ciconiidae as siter to ((Pelecanidae + (Scopidae + Balaenicipitidae) + (Ardeidae + Threskiornithidae)) plus (Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae))) (Hackett et al. 2008, Yuri et al. 2013). In the phenotype-based studies, Ciconiidae either grouped with Phoenicopteridae in a clade sister to Threskiornithidae (Livezey and Zusi 2007) or formed a clade with Ardeidae and Threskiornithidae (Smith 2010). A monophyletic (Ciconiidae + Threskiornithidae) has not been previously proposed, although pre-cladistic classifications invariably placed Threskiornithidae near to Ciconiidae and Ardeidae (*e.g.*, Fürbringer 1888, Wetmore 1960).

A closer phylogentic relationship of *Balaeniceps rex*, the sole member of Balaenipitidae, to Pelecanidae has long been proposed by Gould (1851: 2), who wrote: '[t]his is evidently a Grallatorial [*i.e.*, long-legged wading] type of *Pelecanidae* [*sic*]; at least such is the conclusion to which I am directed after a careful examination and comparison of it with *Pelecanus*, *Grus*, *Ardea* and *Cancroma* [= *Cochlearius*; Ardeidae], to none of which genera is it so nearly allied, except in general contour, as to *Pelecanus*.' This hypothesis received a significant boost by the comparative anatomy studies of Cottan (1957). Similarly to *Balaeniceps rex*, the phylogenetic affinities of *Scopus umbretta* (Scopidae) have been a subject of controversy. Pre-cladistic hypotheses placed it closer to either Ardeidae or Balaeniciptidae (*e.g.*, Parker 1862, Beddard 1884).

A closer relationship between Scopidae, Balaeniciptidae, and Pelecanidae has been proposed in molecular analyses. Specifically, in the studies of Hackett et al. (2008) and Yuri et al (2013), Scopidae grouped with Balaeniciptidae and Pelecanidae in a clade sister to (Ardeidae + Threskiornithidae). This clade is now named 'Pelecaniformes' (*e.g.*, Chesser et al. 2010). In the two afore-cited studies, this modified 'Pelecaniformes' was placed sister to 'Suliformes'; *i.e.*, (Fregatidae + (Sulidae + (Phalacrocoracidae + Anhingidae))).

Phenotype-based analyses, however, yielded different results. Livezey and Zusi (2007) found a topologically pectinate clade that contains Balaenicipitidae and the (Phaethontidae + Steganopodes), whereas Smith (2010) recovered a clade comprising Balaenicipitidae, Pelecanidae, Fregatidae, Sulidae, †Plotopteridae Howard, 1969, Anhingidae, †Borvocarbo Mayr, 2007, Phalacrocoracidae, and Anhingidae.

The presence of *Phaethon* notwithstanding (see below), the present proposal is more congruent with the molecular-based hypotheses in that it places Scopidae, Balaenicipitidae, Ardeidae and Pelecanidae phylogenetically closer to each other than to Phoenicopteridae and Ciconiidae. Topologically, however, it is more congruent with the hypothesis by Smith (2010), particularly with regard to the positions of both Balaenicipitidae and Scopidae relative to Steganopoes.

Phaethontidae

Perhaps the most controversial taxon within or related to the ‘waterbird clade’ is Phaethontidae. This taxon has been traditionally, although not consistently, placed in Pelecaniformes (del Hoyo et al. 1992, Nelson 1996); however, the most recent molecular-based analyses agree that its closer phylogenetic affinities probably lay with Metaves, specifically with Pteroclididae, Columbiformes, Mesitornithidae, Podicipedidae, and Phoenicopteridae. More recently, the genome-based analysis by Jarvis et al. (2004) recovered (Eurypygidae + *Phaethon*) sister to which they called ‘a core waterbird assemblage’; *i.e.*, a clade comprising Gaviidae sister to ((Pelecanidae + (Ardeidae + (Threskiornithidae + (Phalacrocoracidae))) plus (Procellariidae + Spheniscidae)).

Phenotype-based analyses invariably placed Phaethontidae within the ‘waterbird clade’, although at different positions. In the analysis by Livezey and Zusi (2007), Phaethontidae was sister to (Pelecanidae + (Fregatidae + Sulidae + (Phalacrocoracidae + Anhingidae))) in a monophyletic Pelecaniformes. In contrast, Bourdon et al. (2005) and Smith (2010) recovered it together †*Prophaethon* Andrews, 1899 and †*Lithoptila* Bourdon et al., 2005, in a clade sister to Procellariiformes. In the analysis by Smith (2010), when the fossil taxa were excluded, Phaethontidae remained as sister-taxon to Procellariiformes.

As already mentioned, a closer relationship between Phaethontidae and Ardeidae was not previously proposed. However, considering the present hypothesis (see also comments under 'Node 49') and those by Bourdon et al. (2005), Livezey and Zusi (2007), Smith (2010) and Jarvis et al. (2004), it would not be unreasonable to put forward a suggestion that Phaethontidae is more closely related to the 'waterbird clade' than to Metaves. Jarvis et al. (2004: 1,327–28) even stated that 'core waterbirds were sister to a fully supported clade (Phaethontimorphae) containing tropicbirds and the sunbittern [Eurypygidae] . . . We did not include Phaethontimorphae in the core waterbirds because their relationship had relatively low 70% BS [Bootstrap Support], although their aquatic (tropicbirds) and semiaquatic (sunbittern) lifestyles are consistent with a waterbird grouping, and multiple analyses presented below group them with 100% BS. The problems of phylogenetic relationships of Phaethontidae will be touched in the next section.

The 'totipalmate birds': Steganopodes and Suliformes

Among the members of the 'waterbird clade', the so-called 'totipalmate birds' (Pelecaniformes, as traditionally conceived) is perhaps the most controversial group with respect to its monophyly. There is now evidence sufficient to propose that *Phaethon* very likely does not belong to this assemblage (*e.g.*, Bourdon et al. 2005, Hackett et al. 2008, Smith 2010, this work), although a better-supported hypothesis regarding its closer phylogenetic relationship remains to be determined.

Strictly speaking, *Phaethon* was originally placed near to, but not together with, the other 'totipalmate birds'. Linnaeus (1758: 122) erected the order Anseres for waterbirds in which all, or most *digiti pedis* are united together by *telae interdigitales*. He diagnosed *Pelecanus* (p. 132) as having '*Nares lineares, obliteratae . . . Pedes digitis omnibus quatuor fimul palmatis*' and described five species, *viz*. *P. Onocrotalus*, *P. Aquilus* (= *Fregata aquila*). *P. Carbo* (= *Phalacrocorax carbo*), *P. Bassanus* (= *Morus bassanus*) and *P. Piscator* (= *Sula sula*). As it can be seen from the above quotation, all these species had in common the closed nares and, importantly, 'all four' *digiti pedis* united together by *telae intergitales*; *i.e.*, *pedes stegani aut totipalmati* (the 'totipalmate feet').

Linnaeus also proposed (p. 134) *Phaethon* to include his *P*. *aethereus* and *P*. *demersus*, the latter being not a tropicbird, but the penguin currently known as *Eudyptes chrysocome* (J.R. Forster, 1781) (*fide* Sharpe and Ogilvie-Grant 1898); therefore, of no direct relevance to the present discussion. Anyway, *Phaethon* was diagnosed as having '*Nares oblongae, postice membrana femitecta*. *Digit postici antrorsum versi*'. Linnaeus made no explicit reference to *telae interdigitales*; however, in the description of *P*. *aethereus* itself, he stated (p. 134) '*digito postico adnato . . . digito quarto etiam membrane affixo*'; *i.e.*, *digitus I (hallux)* much reduced and united to *digitus II* by *tela interdigitalis*, thus suggesting totipalmaty.

Since then, the 'totipalmate birds' were considered to form a taxon at the order, suborder, or family levels, 'defined' by the possession of *pedis totipalmti*. That is best exemplified by Beddard's (1898: 402, footnote 1) statement: '[t]his one feature [*pes totipalmatus*] is sufficient to define the group.' This notion has been propagated into the 20th century by Sibley and Ahlquist (1972: 65): 'The only obvious anatomical character shared by all members of the Pelecaniformes and not found in other groups is the totipalmate feet'.

However, the question whether the putative families of Pelecaniformes (Phalacrocoracidae, Anhingidae, Sulidae, Pelecanidae, Fregatidae, and Phaethontidae) are phylogenetically more closely-related *inter s*e than any of them is not a recent one; rather, since the second half of the 19^{th} century not a few authors doubted that this grouping reflected 'natural' relationships. Mirvart (1878: 354), for example, wrote: 'besides the four genera [*Phalacrocorax*, *Plotus* (= *Anhinga*), *Sula*, and *Pelecanus*] described, the two genera *Fregata* and *Phaethon* are usually classed with them to constitute the group of the Steganopodes. But, from the point of view here adopted (that of the postcranial part of the axial skeleton only), I have found it impossible to detect characters which seem to me good and sufficient to unite such steganopodal group together.' Actually, *contra* Sibley and Ahlquist (1972, 1990), *pedes totipalmati* has never been unanimously viewed as a character 'sufficient' to unite those families. Furthermore, as it can be seen from the above statement by Mirvart, doubts on the 'validity' of the order has arisen in large part due to Fregatidae and Phaethontidae, both of which have been often considered to include ‘too divergent’ or ‘aberrant’ forms of Pelecaniformes (*e.g.*, Beddard 1898, Shufeldt 1902, Lanham 1947).

The monophyly of Pelecaniformes has been consistently challenged by molecular data, firstly by Sibley’s and Ahlquist’s (1990) DNA-DNA hybridization ‘phenetics’ approach and lately by molecular-based cladistics (*e.g.*, Cracraft et al. 2004, Fain and Houde 2004, Ericson et al. 2006, Hackett et al. 2008). However, it should be remembered that at least one molecular-based proposal (Kennedy and Spencer 2004) has supported the group's monophyly.

As commented in the introduction, the relatively few phenotype-based analyses confirmed or denied the monophyly the traditional of Pelecaniformes. In the hypothesis of Cracraft (1985), Pelecaniformes (*i.e.*, [*Phaethon* + Steganopodes]) was supported by 12 synapomorphies, seven of which were non-homoplastic. However, Cracraft’s results should be viewed with caution, not because of ‘unconvincing synapomorphies’ as augmented by G. Mayr (2003), but because of the rather small sampling of outgroup taxa. Cracraft (1985) included only Gaviidae, Podicipedidae, Spheniscidae, and Procellariiformes as outgroup taxa, thus disregarding the previous postulated hypotheses of closer relationships between ‘Pelecaniformes’ and Ardeidae, Ciconiidae, Scopidae, and Balaenicipitidae.

Mayr (2003), in an analysis aimed at identifying the closer phylogenetic relationships of *Balaeniceps rex*, recovered a Steganopodes clade with the following relationship: (Fregatidae + (Pelecanidae (Sulidae + (Phalacrocorax + Anhingidae)))). Bourdon et al. (2005) essentially reached the same result. In both studies, Phaethontidae was placed outside the clade of the 'totipalmate birds'. Livezey and Zusi (2007) also recovered a 'traditional' Pelecaniformes, with Balaenicipitidae as its sister taxon. In the analysis by Smith (2010), Fregatidae was placed sister to (Sulidae + (Phalacrocorax + Anhingida))), but only when the fossil frigatebird *Limnofregata* Olson, 1977 was included in the analysis; analysis with extant taxa only recovered the same relationships as those recovered elsewhere (Mayr 2003, Bourdoun et al. 2005, Livezey and Zusi 2007).

The present analysis recovered a monophyletic Steganopodes, but contrary to most previous phenotype-based studies, with Pelecanidae sister to a Suliformes clade; *i.e.*, (Fregatidae + (Sulidae + (Phalacrocorax + Anhingida))). As commented under 'wading birds', the clade which includes Balaenicipitidae, Scopidae, and Steganopodes, as proposed herein is, more congruent with the molecular-based hypotheses (*e.g.*, Ericson et al. 2006, Hackett et al. 2008, Yuri et al. 2013) than with most phenotype-based ones. Furthermore, it agreed with some earlier, pre-cladistic proposals that suggested that Phaethontidae was not directly related to the other 'totipalmated birds'. The main incongruence between this and those molecular-based hypotheses lies in the placement of Pelecanidae as sister to a Suliformes clade. In the studies of Hackett et al. (2008) and Yuri et al. (2013), Suliformes was recovered as sister to a 'Pelicaniformes' clade, which includes, besides Pelecanidae, Scopidae, Balaenicipitidae, Ardeidae, and Threskiornithidae.

Concluding remarks

> ‘Only when they must choose between competing theories do scientists behave like philosophers’
>
> —Thomas Kuhn, *The Structure of Scientific Revolutions*, 1962

When in face of two (or more) contradictory hypotheses of phylogenetic relationships, scientist may, or should, ask to him/herself: ‘How do I decide which one to accept?’ For a long time, it was argued that the hypothetic-deductive model of Austrian-born British philosopher Karl Popper could be applicable to the cladistic inference (*e.g.*, Pinna 1991, Kluge 1999).

According to Popper (2001 [1959]), science proceeds not by the simple observation of facts, but by the interests of the observer in knowing a given reality for which his/her background is no longer satisfactory. Thus, starting by selecting the object to be observed; and, finding the insufficiency in the reference knowledge base, the observer may formulate a hypothesis from which consequences are deduced, and then tested by experiment. Here, the hypothesis is not verified in terms of its ‘truth’ or ‘falsehood’; instead, the observer should make all possible efforts to refute it, thus allowing for the establishment and development of new background knowledge. This is Popper’s ‘falsifiability’ criterion of science. It should be stressed that, for Popper (2001 [1959]), a hypothesis is falsifiable if it prohibits at least one event that are not prohibited by the background knowledge.

Recently, Vogt (2008; see also Rieppel 2008) argued that Popper's the hypothetico-deductive method and use of falsification in cladistics is not feasible or even appropriate. That is, the hypothesis derived from the analysis of taxon/character matrix—the cladogram—is not falsiable because it does not prohibit the occurrence of convergent evolution, thus allowing for both apomorphies and homoplasies as explanations for the relationships of a given group (Vogt 2008). Naturally, the same reasoning can be applied to the analysis of a multiple sequence alignment.

Nevertheless, it should be mentioned that the impossibility of falsifying cladograms does not mean they are not scientific. Cladistic hypotheses are statements about the phylogenetic relationships among a group of organisms represented by the best option given the data available, but subject to confrontation with additional evidence, particularly those drawn from different sources. Therefore, as pointed out by Santos and Capellari (2009), cladograms can (and should) be compared against each other to find congruencies among them. The idea of such a comparison is, also according to Santos and Capellari (2009), similar to Hennig's (1966, 1968 [1955]) method of 'reciprocal illumination', in which two sorts of data are complementary to each other, and has the potential to enlighten one another. If, for example, two (or more) cladograms are congruent, in the sense of depicting the same (or almost the same) relationships, they have a better explanatory value, when compared to other contradictory cladograms. On the other hand, in case of no, or little, congruence among cladograms, then the differences should be reconciled through reanalysis of existing data and/or the analysis of new characters/DNA sequences. Santos and Capellari (2009, quoting Mickevich and Lipscomb 1991) rightly noted that reciprocal illumination is the process through which 'perceptual errors' are recognized and corrected.

It still should be noted that even such a comparison would not be conclusive. Congruences and conflicts between cladograms based on different datasets differences can be the result of idiosyncrasies or other factors influencing taxon sampling and outgroup selection, and of course, the methods of analysis used (*e.g.*, Hillis and Wiens 2000). Usually, conflicts are resolved in favour of those hypotheses with higher 'measures of clade support'. It follows, however, from arguments given above, that such an interpretation is, nothing but tautological. Furthermore, Grant and Kluge (2008: 1063) argued that 'degree of support does not provide a rational basis for greater confidence or disbelief in a group as more or less accurate, reliable, probable, or worthy of formal taxonomic recognition.'

When compared to other previous phenotype-based hypotheses (*e.g.*, Cracraft 1985, Livezey and Zusi 2007), the hypothesis by Smith (2010), and particularly the present one, have a considerable degree of congruence with molecular-based hypotheses. There are still, however, persistent discrepancies, especially with respect to the relationships within the more inclusive clades. That said, one may (or should) conclude that the alleged polyphyly of ‘Steganopodes’ (= ‘Pelecaniforme’s to the exclusion of *Phaethon*); *i.e.*, that Pelecanidae belongs to a different clade that includes Balaenicipitidae and Scopidae (as recovered by molecular-based phylogenies), is at best contentious—except for those who idiosyncratically prefer one hypothesis over another.

On the side of the phenotypic approach, a large part of that said ‘perceptual errors’ is likely to be found on the process of delineating the character statements. Therefore, from a practical perspective, in the analysis of Livezey and Zusi (2007), and consequently that of Smith (2010), there are several ‘chimerical’ character-statements in which the neomorphic state ‘absent’ is mixed with the transformational states, and transformational characters wherein variable is imprecisely defined and/or its qualifier is missing. For example, the character-statement ‘Quadrate, intercondylar sulcus of mandibular process a deep, parabolic (“U-shaped”) channel with sides (craniocaudal perspective) subdiagonal (typically parallel) and directly opposite each other and dorsally foveate (ventral perspective): absent (0); present (1)’ (Smith’s character 38; taken from Livezey and Zusi 2006b: character 529) was constructed as neomorphic in form, though actually it would be more accurately described as a transformational character. In this particular case, what Smith (2010) coded as ‘absent’, in opposition to the ‘state 1’ is likely an overlooked variation in the shape and/or conformation of that structure, which may includes at least a few other states.

In this context, and following the logic proposed by Sereno (2007), which, if not the best, is at least the less subjective, the *c*. 2,000 character-statements used by Livezey and Zusi (2007) could be critically reviewed, if necessary, adjusted, and used to construct a new hypothesis of phylogenetic relationships among taxa within, and related to, the 'waterbird clade', including Steganopodes. Such a new hypothesis may eventually prove to be more congruent with those molecular-based hypotheses, though possible conflicts still have to be settled as part of a 'checking-correcting-rechecking' spiral.

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RESUMO

A sistemática do "clado das aves aquáticas", especialmente aquela das ditas "aves totipalmadas" (Pelecaniformes), constitui-se num misto de congruências e conflitos entre as abordagens fenotípica e molecular na análise das relações filogenética entre seus membros. Neste trabalho, as relações filogenéticas dentro do 'clado das aves aquáticas' é avaliada a partir da análise de 78 caracteres osteológicos e 29 táxons terminais sob o método do ajuste (peso) implícito dos caracteres. No geral, a presente hipótese é mais congruente com as hipóteses baseadas na evidência molecular do que naquelas baseadas em caracteres fenotípicos, pelo menos relações filogenéticas dentro dos grupos. As principais diferenças se referem às posições de Pelecanidae, Threskiornithidae, and Phaethontidae, este último considerado como o táxon mais controverso dentro do "clado das aves aquáticas", ou próximo deste. Quanto às "aves totipalmadas", a presente análise recuperou Fregatidae como grupo irmão de (Sulidae + (Phalacrocoracidae + (Anhigidae) e Pelecanidae como seu grupo irmão, em um grupo monofilético chamado 'Steganopodes'. A legada polifilia de "Steganopodes"; *i.e.*, que Pelecanidae pretence a outro clado juntamente com Balaenicipitidae and Scopidae, como recuperado pelas análises moleculares; é, no mínimo, controversa. Por causa disso, esse conflito deve ser resolvido por meio da reanalise dos dados ora disponíveis e/ou pela análise de novos caracteres/sequências de ADN.

Palavras-chave: Aequornithes, cladística, Steganopodes, Suliformes, aves aquáticas.

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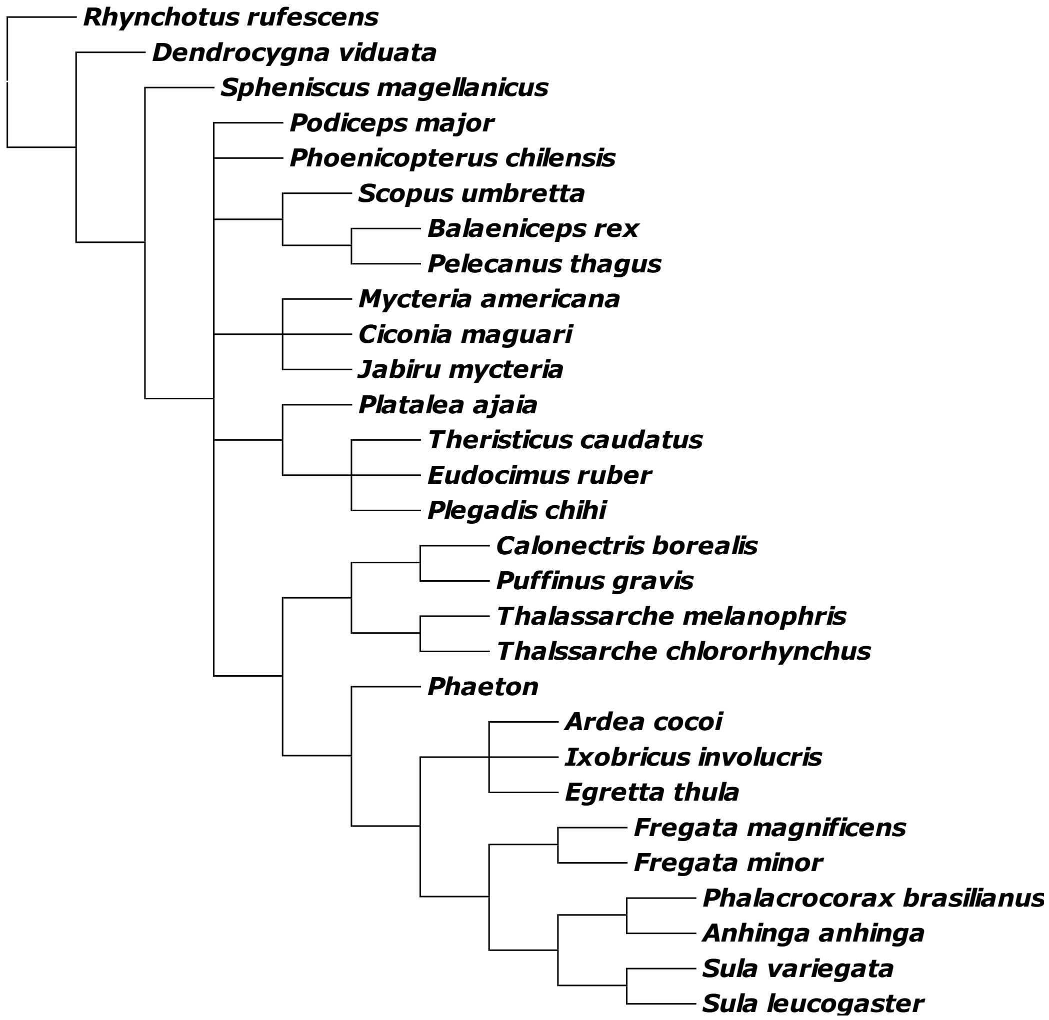

Figure 1 - The strict consensus tree of six equally most parsimonious trees obtained from analysis under equal weights.

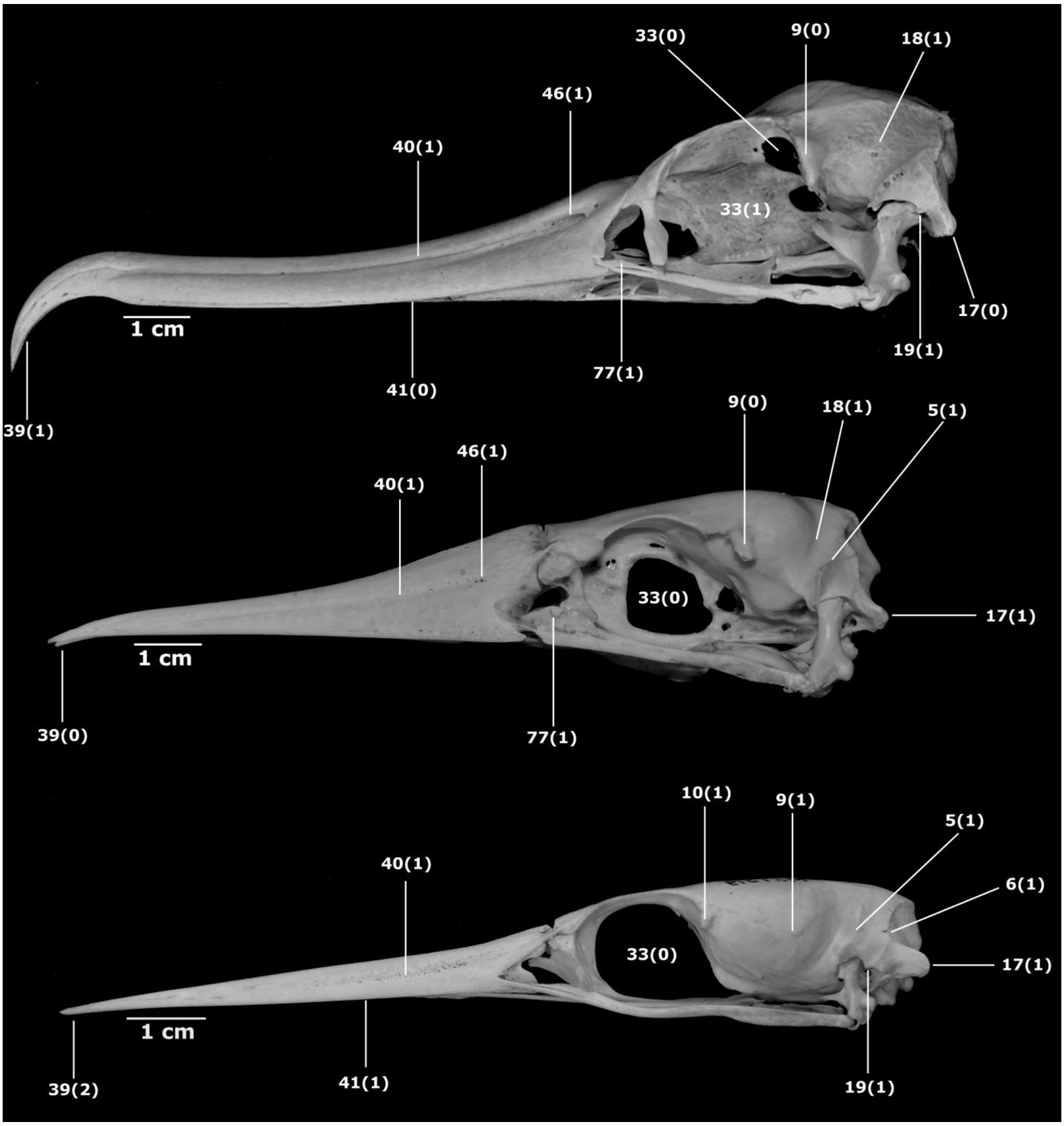

Figure 2 – Lateral views of the skulls of *Fregata magnificens*, *Sula leucogaster*, and *Anhinga anhinga*.

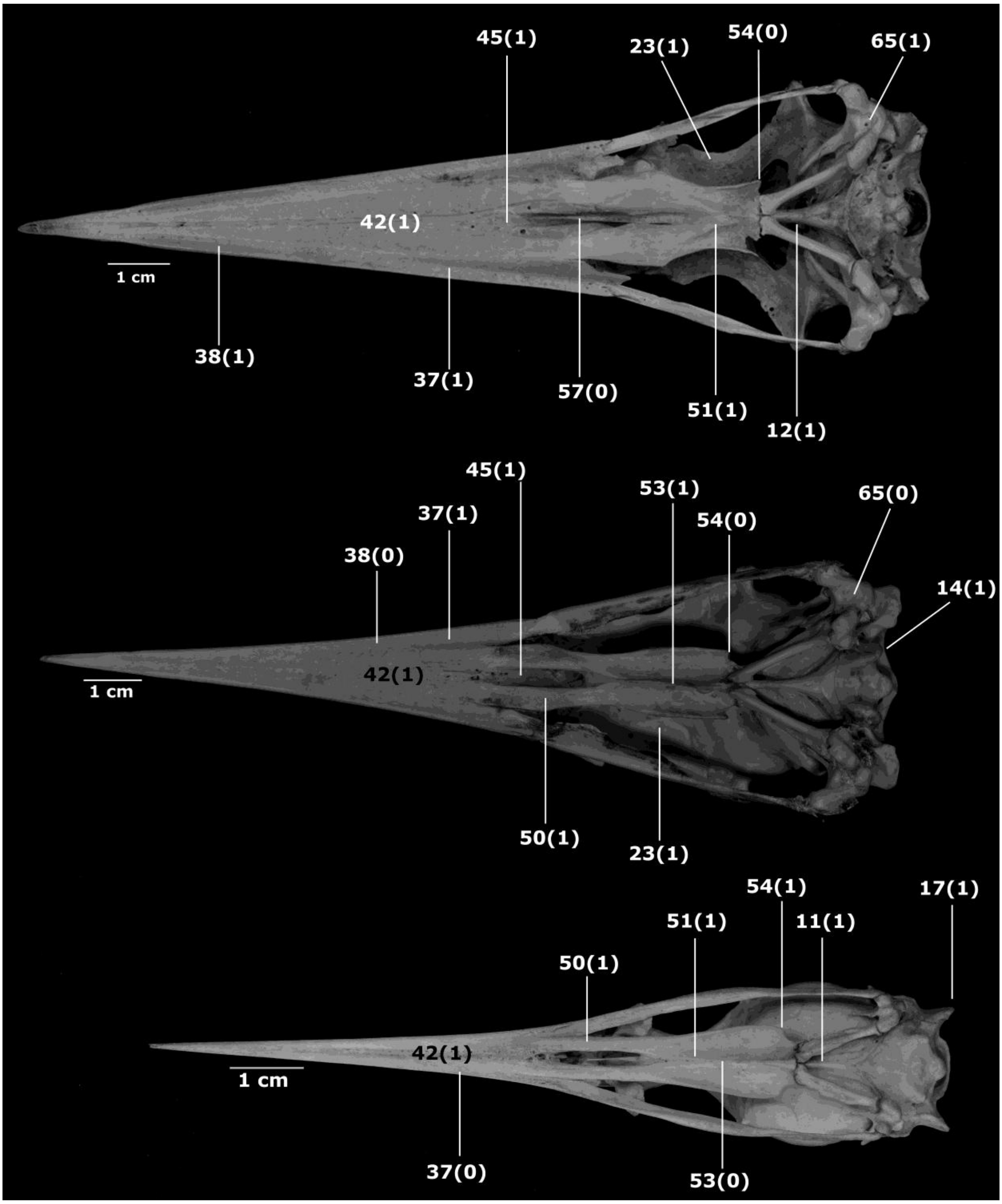

Figure 3 – Ventral views of the skulls of *Fregata magnificens*, *Sula leucogaster*, and *Anhinga anhinga*.

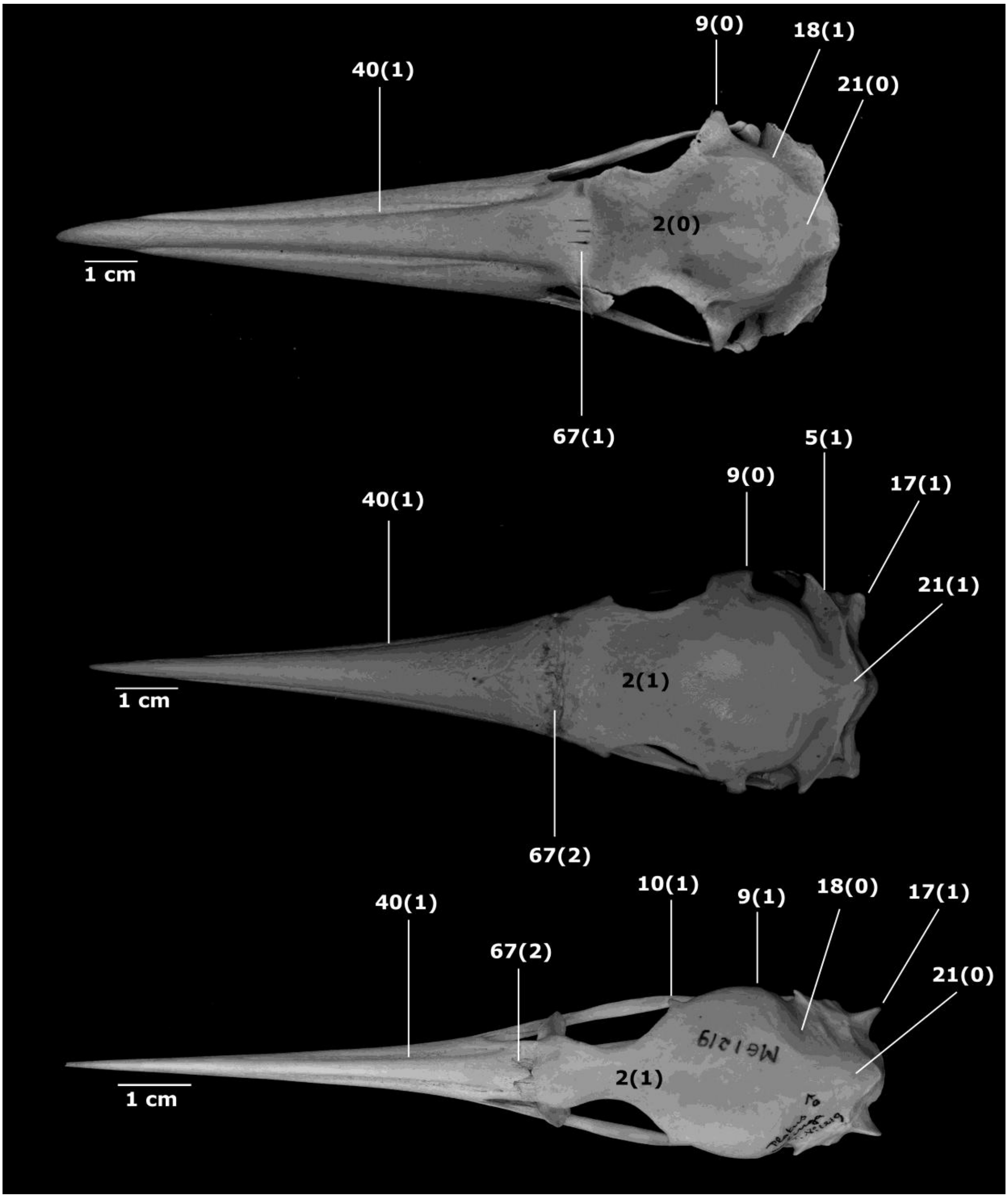

Figure 4 – Dorsal views of the skulls of *Fregata magnificens*, *Sula leucogaster*, and *Anhinga anhinga*.

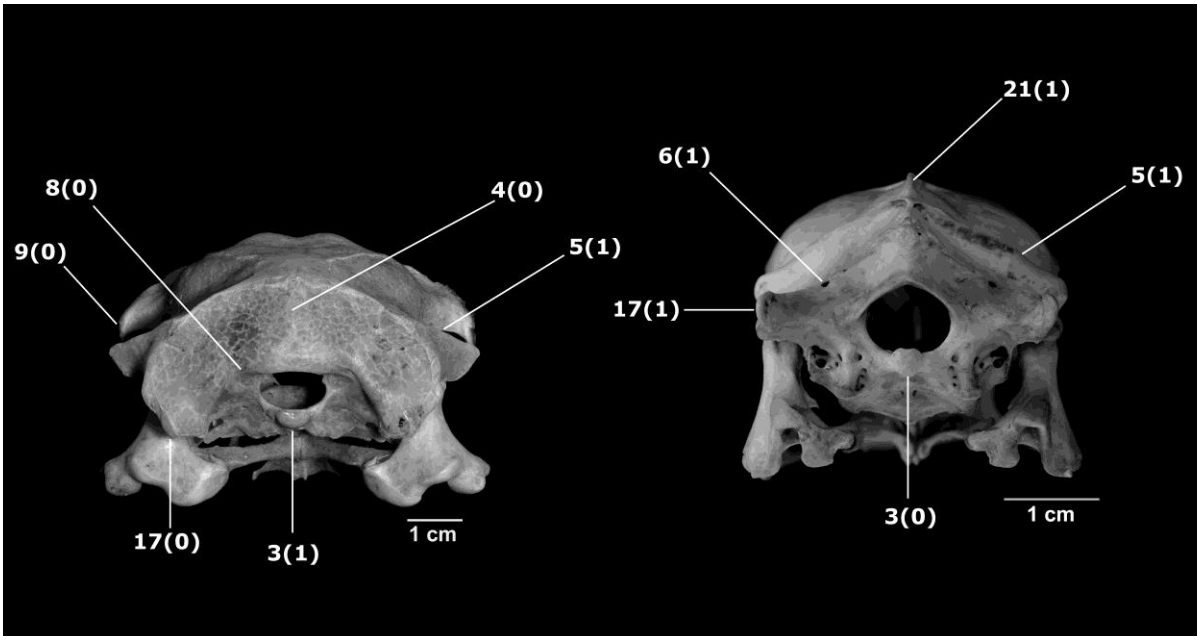

Figure 5 – Occipital views of the skulls of *Fregata magnificens*, and *Anhinga anhinga*.

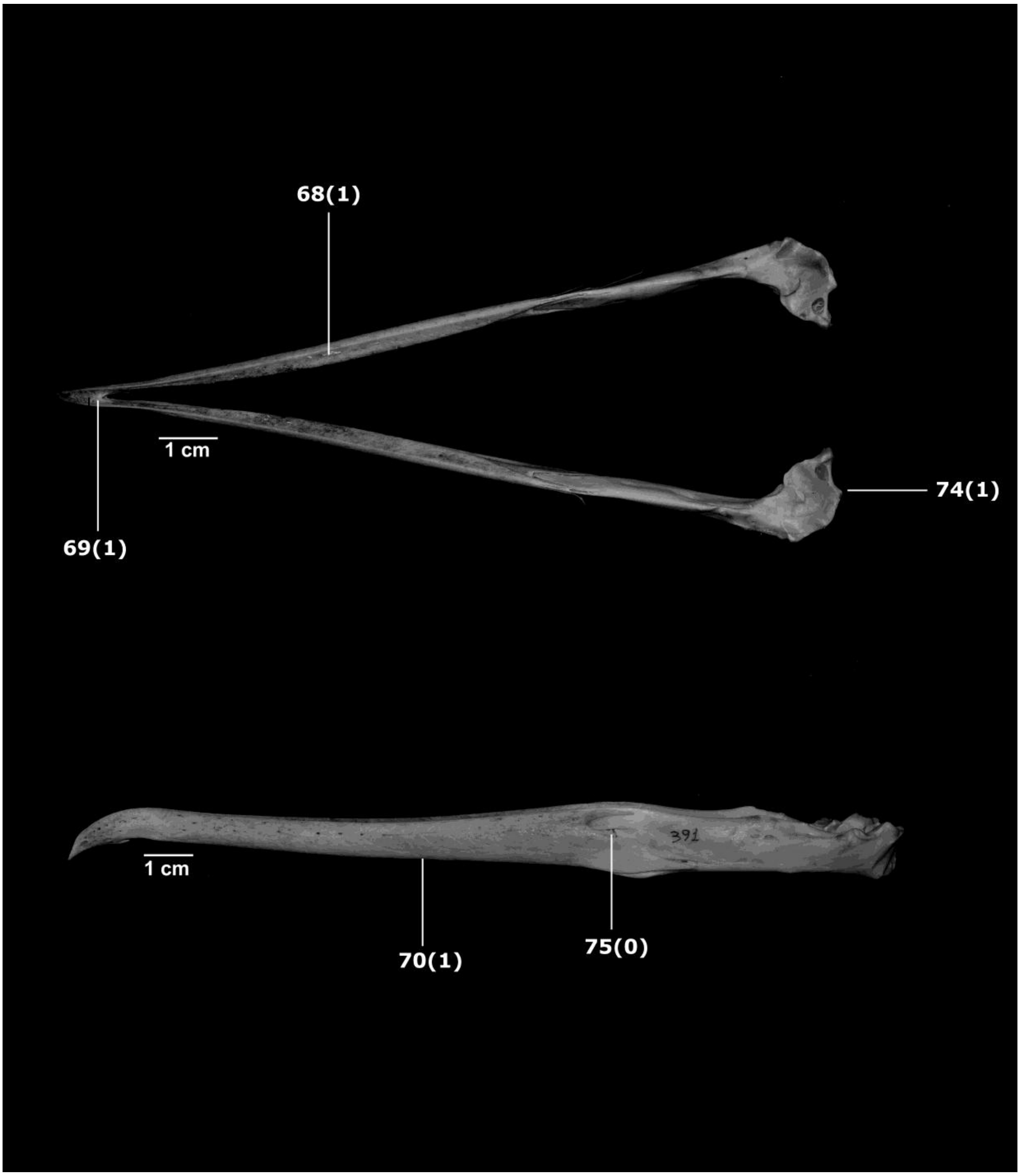

Figure 6 – Dorsal and lateral views of the mandible (*mandibula*) of *Fregata magnificens*

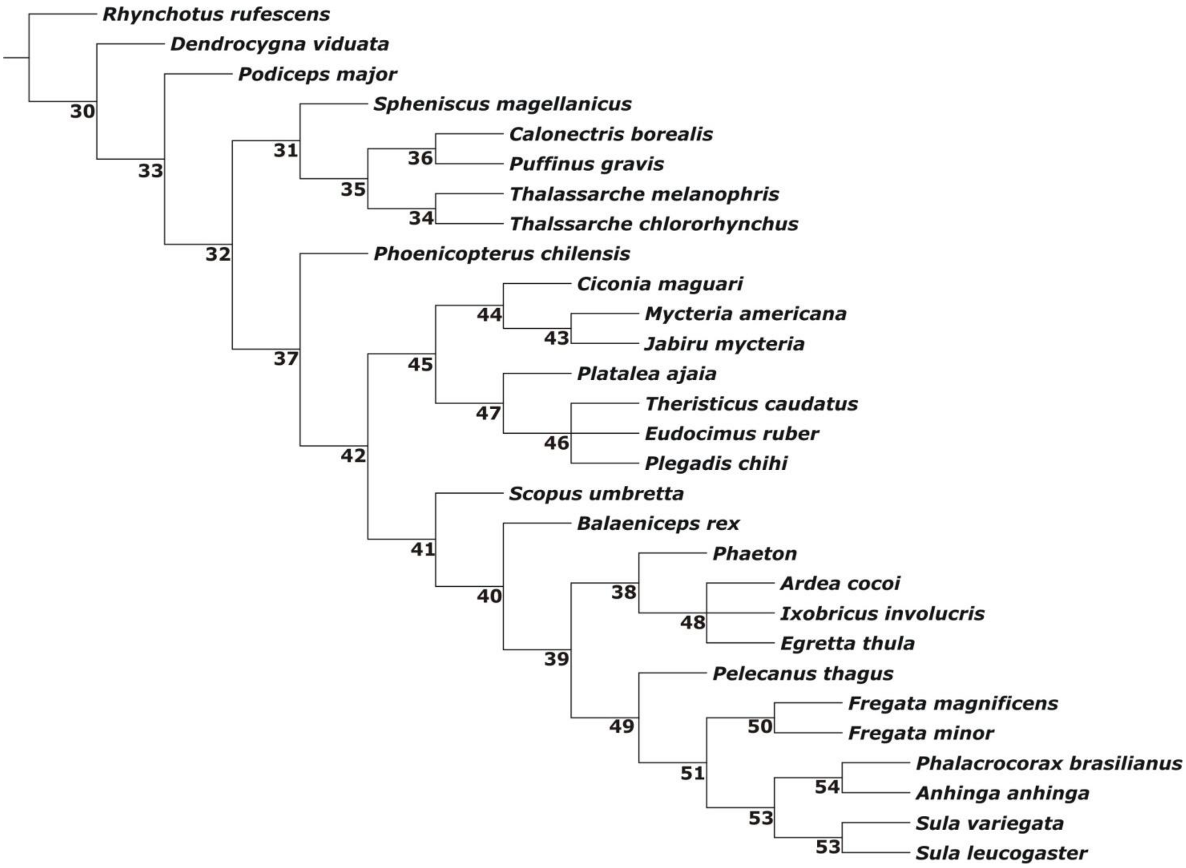

Figure 7 - Final hypothesis of phylogenetic between outgroup and ingroup taxa. The numbers of nodes correspond to those listed in the section ‘Results’, subsection ‘parsimony analysis’.

TABLE I

Results of implied weight analysis with different constants of concavity, *K*. Cladograms used to construct the final hypothesis are those shaded in grey (see Table II). Ci = consistency index, and RI = retention index.

Values of *K*	N° of cladograms	Steps	Tree Fit	Adjusted homoplasy	CI	RI
K0 = 2.3059	1	275	44.34	33.66	0.309	0.671
K1 = 2.4980	1	275	45.53	32.47	0.309	0.671
K2 = 2.7069	1	275	46.73	31.27	0.309	0.671
K3 = 2.9348	1	275	47.93	30.07	0.309	0.671
K4= 3.1843	1	271	49.15	28.85	0.314	0.671
K5 = 3.4588	1	271	50.39	27.61	0.314	0.678
K6 = 3.7622	1	270	51.63	26.37	0.315	0.680
K7 = 4.0993	1	269	52.90	25.10	0.316	0.682
K8 = 4.4761	1	267	54.18	23.82	0.318	0.685
K9 = 4.9000	1	267	55.47	22.53	0.318	0.685
K10 = 5.3804	1	267	56.78	21.22	0.318	0.685
K11 = 5.9294	1	267	58.08	19.92	0.318	0.685
K12 = 6.5629	1	267	59.40	18.60	0.318	0.685
K13 = 7.3020	1	267	60.73	17.27	0.318	0.685
K14 = 8.1754	1	264	62.09	15.91	0.322	0.690
K15 = 9.2235	1	264	63.46	14.54	0.322	0.690
K16= 10.5046	1	264	64.85	13.15	0.322	0.690
K17 = 12.1059	1	264	66.24	11.76	0.322	0.690
K18 = 14.1647	1	264	67.65	10.35	0.322	0.690
K19 = 16.9098	1	264	69.08	8.92	0.322	0.690
K20 = 20.7529	1	264	70.52	7.48	0.322	0.690

TABLE II

Pairwise SPR distances for the 21 fittestet cladograms resulting from the analysis under implied weights with different constants of concavity, K (see Table I). Cladograms used to contruct the final hypothesys 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	–	1	1	1	5	5	4	5	5	6	5	4	6	5	8	8	7	9	9	8	8
1	1	–	1	2	5	5	4	5	5	5	5	5	5	5	8	8	7	9	9	8	8
2	1	1	–	2	4	4	3	4	4	6	4	5	6	4	7	5	6	9	9	8	8
3	1	2	2	–	5	5	5	6	6	6	6	5	5	6	8	9	8	8	9	9	9
4	5	5	4	5	–	0	3	4	3	3	3	4	4	3	6	8	7	8	7	8	8
5	5	5	4	5	0	–	3	4	3	3	3	4	4	3	6	8	7	8	7	8	8
6	4	4	3	5	3	3	–	3	3	5	3	4	5	3	7	7	6	8	8	7	7
7	5	5	4	6	4	4	3	–	2	4	2	3	4	2	6	6	5	7	7	6	6
8	5	5	4	6	3	3	3	2	–	2	0	1	2	0	6	6	5	7	7	6	6
9	6	5	6	6	3	3	5	4	2	–	2	2	1	2	6	7	7	6	5	6	6
10	5	5	4	6	3	3	3	2	0	2	–	1	2	0	6	6	5	7	7	6	6
11	4	5	5	5	4	4	4	3	1	2	1	–	2	1	7	5	6	7	7	6	6
12	6	5	6	5	4	4	5	4	2	1	2	2	–	2	7	7	7	5	6	6	6
13	5	5	4	6	3	3	3	2	0	2	0	1	2	–	6	6	5	7	7	6	6
14	8	8	7	8	6	6	7	6	6	6	6	7	7	6	–	2	1	2	1	2	2
15	8	8	5	9	8	8	7	6	6	7	6	5	7	6	2	–	1	2	2	1	1
16	7	7	6	8	7	7	6	5	5	7	5	6	7	5	1	1	–	2	2	1	1
17	9	9	9	8	8	8	8	7	7	6	7	7	5	7	2	2	2	–	1	1	1
18	9	9	9	9	7	7	8	7	7	5	7	7	6	7	1	2	2	1	–	1	1
19	8	8	8	9	8	8	7	6	6	6	6	6	6	6	2	1	1	1	1	–	0
20	8	8	8	9	8	8	7	6	6	6	6	6	6	6	2	1	1	1	1	0	–
Total	110	110	100	120	98	98	98	91	**79**	90	**79**	85	92	79	104	105	96	114	112	104	104

APPENDIX 1

List of studied specimens.

Institutional abbreviations: **USNM**, United States National Natural History Museum, Smithsonian Institution, Whashington, DC; **FMNH**, Field Museum of Natural History, Chicago; **MVZ**, Museum of Vetebrate Zoology, Berkeley; **MPEG**, Museu Paraense Emílio Goeldi, Belém; **MNRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; **MZUSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo; **MCEMAV**, Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Sul; **UFRGS**, Centro de Estudos Costeiros, Limnológicos e Marinhos do Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Imbé; and **MCN**, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre.

Rhynchotus rufescens MCN 0680, 0682, 0683, 0687, 0689; *Dendrocygna viduata* UFRGS, MCN; *Spheniscus magellanicus* UFRGS 066, 216, MCN 0038, 0444; *Thalassarche melanophris* UFRGS 208; *Thalassarche clororhynchos* UFRGS; *Calonectris borealis* UFRGS; *Puffinus gravis* UFRGS; *Podiceps major* UFRGS, MCN 00664; *Phoenicopterus chilensis* MCN; *Mycteria americana* MCN 0608; *Ciconia maguari* MCN 0073; *Jabiru mycteria* MCN 0043; *Theristicus caudatus* UFRGS 254; *Eudocimus ruber* MCN 0063; *Plegadis chihi* MCN; *Platalea ajaia* MCN 0128; *Ixobrychus involucris* UFRGS 253, MCN 0465; *Ardea cocoi* MCN 0129, 0154; *Egretta thula* UFRGS, MCN; *Scopus umbretta* USNM 431497; *Pelecanus thagus* UFRGS (unnumbered).

APPENDIX 1 (cont.)

Fregata magnificens MZUSP 88433, 88434, MCEMAV 9, 10, 11, 48, 49, 182, 186, 215, 222, 223, 225, 240; UFRGS 386; *Fregata minor* FMNH, MVZ, MNRJ; *Sula variegata* UFRGS (unnumbered); *Sula leucogaster* MCEMAV 247, 248, 319, 320; UFRGS 001, 384, 385; *Phalacrocorax brasilianus* UFRGS 083, 149, 383; *Anhing anhinga* MPEG 492, 01219.

APPENDIX 2

Taxon/character matrix used in the cladistc analysis

Taxon/character	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**
Rhynchotus rufescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dendrocygna viduata	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Spheniscus magellanicus	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0
Thalassarche melanophris	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Thalssarche chlororhynchus	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Calonectris borealis	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
Puffinus gravis	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
Podiceps major	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Phoenicopterus chilensis	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0
Phaeton sp.	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Mycteria americana	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Ciconia maguari	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Jabiru mycteria	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Theristicus caudatus	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1
Eudocimus ruber	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1
Plegadis chihi	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1
Platalea ajaia	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1
Ardea cocoi	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1
Ixobricus involucris	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1
Egretta thula	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1
Scopus umbretta	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Balaeniceps rex	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Pelecanus thagus	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0
Fregata magnificens	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0
Fregata minor	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0
Sula variegata	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1
Sula leucogaster	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1
Phalacrocorax brasilianus	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1
Anhinga anhinga	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1

APPENDIX 2 (cont.)

Taxon/character	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Rhynchotus rufescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dendrocygna viduata	0	0	0	0	2	0	1	0	1	0	—	0	0	1	0
Spheniscus magellanicus	0	0	1	0	2	0	0	0	0	0	0	0	0	2	1
Thalassarche melanophris	1	0	0	1	2	0	0	0	1	1	1	1	0	2	1
Thalssarche chlororhynchus	1	0	0	1	2	0	0	0	1	1	1	1	0	2	1
Calonectris borealis	0	0	1	0	2	1	0	0	1	1	0	1	0	2	1
Puffinus gravis	0	0	1	0	2	1	0	0	1	1	0	1	0	2	1
Podiceps major	0	0	0	1	2	1	1	0	1	0	1	0	1	1	0
Phoenicopterus chilensis	0	0	0	1	2	0	0	0	0	1	0	0	0	1	0
Phaeton sp.	0	0	0	0	2	0	1	0	0	1	1	0	0	2	1
Mycteria americana	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0
Ciconia maguari	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0
Jabiru mycteria	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0
Theristicus caudatus	1	0	0	1	2	0	1	0	1	1	1	0	0	1	0
Eudocimus ruber	1	0	0	1	2	0	1	0	1	1	1	0	0	1	0
Plegadis chihi	1	0	0	1	2	0	1	0	1	1	1	0	0	1	0
Platalea ajaia	1	0	0	1	2	0	1	0	1	1	1	0	0	1	0
Ardea cocoi	1	0	1	1	2	1	1	0	1	1	1	0	0	1	0
Ixobricus involucris	1	0	1	1	2	1	1	0	1	1	1	0	0	1	0
Egretta thula	1	0	1	1	2	1	1	0	1	1	1	0	0	1	0
Scopus umbretta	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0
Balaeniceps rex	0	0	0	0	2	0	1	0	1	1	0	0	0	1	0
Pelecanus thagus	0	0	0	1	2	0	1	1	1	1	1	0	0	1	0
Fregata magnificens	1	0	1	1	2	0	1	1	0	1	0	1	0	2	1
Fregata minor	1	0	1	1	2	0	1	1	0	1	0	1	0	2	1
Sula variegata	1	1	1	0	2	1	1	1	1	1	0	1	1	2	1
Sula leucogaster	1	1	1	0	2	1	1	1	1	1	0	1	1	2	1
Phalacrocorax brasilianus	1	1	1	0	1	1	1	1	1	0	0	1	1	2	0
Anhinga anhinga	1	1	0	1	1	0	1	1	1	0	0	1	1	1	0

APPENDIX 2 (cont.)

Taxon/character	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**
Rhynchotus rufescens	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0
Dendrocygna viduata	0	0	0	0	0	0	0	—	x	0	0	0	1	0	1
Spheniscus magellanicus	1	—	0	1	0	0	0	—	0	1	0	0	0	0	0
Thalassarche melanophris	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0
Thalssarche chlororhynchus	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0
Calonectris borealis	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0
Puffinus gravis	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0
Podiceps major	1	—	0	1	0	0	0	—	0	0	1	0	0	0	0
Phoenicopterus chilensis	1	—	1	—	0	0	0	—	0	0	0	0	0	0	1
Phaeton sp.	0	1	0	1	1	0	1	0	0	0	0	1	1	0	1
Mycteria americana	1	—	1	—	1	1	0	—	0	1	1	1	1	0	1
Ciconia maguari	1	—	1	—	1	1	0	—	2	1	1	1	1	0	1
Jabiru mycteria	1	—	1	—	1	1	0	—	2	1	1	1	1	0	1
Theristicus caudatus	0	0	1	—	1	1	0	—	0	1	0	0	1	0	1
Eudocimus ruber	0	0	1	—	1	1	0	—	0	1	0	0	1	0	1
Plegadis chihi	0	0	1	—	1	1	0	—	0	1	0	0	1	0	1
Platalea ajaia	0	0	1	—	1	1	0	—	x	1	0	1	1	0	1
Ardea cocoi	0	1	0	1	0	0	0	—	2	1	1	1	1	0	1
Ixobricus involucris	0	1	0	1	0	0	0	—	2	1	1	1	1	0	1
Egretta thula	0	1	0	1	0	0	0	—	2	1	1	1	1	0	1
Scopus umbretta	1	—	1	—	1	1	0	—	0	1	1	1	0	0	1
Balaeniceps rex	1	—	1	—	1	0	1	1	1	1	0	1	0	0	1
Pelecanus thagus	1	—	1	—	1	1	1	1	1	1	0	1	0	0	1
Fregata magnificens	1	—	1	—	0	0	1	1	1	1	0	1	0	0	1
Fregata minor	1	—	1	—	0	0	1	1	1	1	0	1	0	0	1
Sula variegata	1	—	0	0	1	0	1	0	0	1	0	1	0	0	1
Sula leucogaster	1	—	0	0	1	0	1	0	0	1	0	1	0	0	1
Phalacrocorax brasilianus	0	0	0	1	0	0	1	0	1	1	0	1	0	0	1
Anhinga anhinga	0	0	0	1	0	0	0	—	2	1	1	1	0	0	1

APPENDIX 2 (cont.)

Taxon/characters	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
Rhynchotus rufescens	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0
Dendrocygna viduata	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Spheniscus magellanicus	0	1	0	0	1	0	1	0	1	1	1	0	1	0	0
Thalassarche melanophris	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
Thalssarche chlororhynchus	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
Calonectris borealis	0	1	0	0	0	0	0	1	0	1	1	0	1	0	0
Puffinus gravis	0	1	0	0	0	0	0	1	0	1	1	0	1	0	0
Podiceps major	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0
Phoenicopterus chilensis	0	1	0	0	0	0	0	1	0	1	1	0	1	0	0
Phaeton sp.	0	1	0	1	0	0	0	0	1	0	—	0	0	0	0
Mycteria americana	0	1	0	0	0	0	0	1	0	1	1	0	1	1	0
Ciconia maguari	0	1	0	0	0	0	0	1	0	1	1	0	1	1	0
Jabiru mycteria	0	1	0	0	0	0	0	1	0	1	1	0	1	1	0
Theristicus caudatus	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1
Eudocimus ruber	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1
Plegadis chihi	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1
Platalea ajaia	0	1	0	0	0	0	0	1	0	1	1	0	1	1	1
Ardea cocoi	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1
Ixobricus involucris	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1
Egretta thula	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1
Scopus umbretta	0	0	0	1	0	1	0	0	0	1	1	0	1	1	1
Balaeniceps rex	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0
Pelecanus thagus	1	0	1	1	0	1	0	1	1	1	1	1	1	0	0
Fregata magnificens	1	0	1	1	1	1	0	0	0	0	—	0	0	0	0
Fregata minor	1	0	1	1	0	1	0	0	0	0	—	0	0	0	0
Sula variegata	1	0	1	1	1	1	1	1	0	0	—	1	0	0	0
Sula leucogaster	1	0	1	1	1	1	1	1	0	0	—	1	0	0	0
Phalacrocorax brasilianus	1	0	1	1	1	1	1	0	1	1	0	1	0	0	0
Anhinga anhinga	1	0	1	1	1	1	1	0	1	1	0	1	0	0	0

APPENDIX 2 (cont.)

Taxon/character	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**
Rhynchotus rufescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dendrocygna viduata	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Spheniscus magellanicus	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Thalassarche melanophris	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1
Thalssarche chlororhynchus	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1
Calonectris borealis	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1
Puffinus gravis	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1
Podiceps major	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0
Phoenicopterus chilensis	1	0	1	0	0	2	0	0	2	0	0	1	—	0	0
Phaeton sp.	0	1	0	1	0	0	2	1	1	0	0	0	0	1	1
Mycteria americana	0	0	1	0	0	0	2	0	0	1	1	1	0	1	1
Ciconia maguari	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1
Jabiru mycteria	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1
Theristicus caudatus	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1
Eudocimus ruber	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1
Plegadis chihi	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1
Platalea ajaia	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1
Ardea cocoi	1	0	0	1	0	2	1	1	1	1	1	0	0	1	0
Ixobricus involucris	1	0	0	1	0	2	1	1	0	1	1	0	0	1	0
Egretta thula	1	0	0	1	0	2	1	1	0	1	1	0	0	1	0
Scopus umbretta	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Balaeniceps rex	0	1	1	0	1	0	0	0	1	2	0	0	1	1	0
Pelecanus thagus	0	1	0	1	1	0	2	0	0	0	0	0	0	1	0
Fregata magnificens	0	1	0	0	1	2	1	1	0	1	1	0	1	1	0
Fregata minor	0	1	0	0	1	2	1	1	0	1	1	0	1	1	0
Sula variegata	0	1	0	1	0	1	2	1	0	1	0	0	0	1	0
Sula leucogaster	0	1	0	1	0	1	2	1	0	1	0	0	0	1	0
Phalacrocorax brasilianus	0	1	0	1	0	1	2	1	0	1	1	0	0	0	1
Anhinga anhinga	1	0	0	0	0	1	2	1	1	1	1	0	1	0	0

APPENDIX 2 (cont.)

Taxon/character	**76**	**77**	**78**
Rhynchotus rufescens	0	0	0
Dendrocygna viduata	0	0	0
Spheniscus magellanicus	0	0	1
Thalassarche melanophris	0	0	1
Thalssarche chlororhynchus	0	0	1
Calonectris borealis	0	0	1
Puffinus gravis	0	0	1
Podiceps major	0	0	0
Phoenicopterus chilensis	0	0	0
Phaeton sp.	0	?	0
Mycteria americana	0	0	0
Ciconia maguari	0	0	0
Jabiru mycteria	0	0	0
Theristicus caudatus	0	0	0
Eudocimus ruber	0	0	0
Plegadis chihi	0	0	0
Platalea ajaia	0	0	0
Ardea cocoi	0	0	0
Ixobricus involucris	0	0	0
Egretta thula	0	0	0
Scopus umbretta	0	0	0
Balaeniceps rex	0	?	0
Pelecanus thagus	0	?	0
Fregata magnificens	0	1	1
Fregata minor	0	1	1
Sula variegata	0	1	0
Sula leucogaster	0	1	0
Phalacrocorax brasilianus	1	1	0
Anhinga anhinga	1	1	0

Capítulo 3

Considerações finais

Quando em face de duas, ou mais, hipóteses de relacionamentos filogenéticos para determinado grupo, o sistemata certamente se pergunta: 'qual delas aceitar?' Por muito tempo, argumentou-se que o modelo hipotético-dedutivo do filósofo austríaco Karl Pooper seria perfeitamente aplicável à inferência cladística (*e.g.*, PINNA, 1991). Para Popper (2001 [1959]) a busca de conhecimento não se dá por meio da simples observação de fatos, mas pelo interesse que um observador tem em conhecer uma determinada realidade que seu quadro de referências já não satisfaz. Assim, partindo-se da seleção do objeto a ser observado; e, constatada a insuficiência do quadro de referências, o observador formula uma hipótese geral da qual se deduzem consequências que permitem a possibilidade de um experimento. Neste ponto, não é preciso verificar a fim de atribuir significado; *i.e.*, optar pela "verdade" ou "falsidade" da hipótese, mas a tentativa e de refutá-la, o que permite o estabelecimento de um "novo conhecimento" e de seu desenvolvimento. Esse é o critério de "falseabilidade" de Popper (2001 [1959]). E vale lembrar ainda que, para Popper (2001 [1959]), uma hipótese é passível de ser falseada se ela proibir a ocorrência de, pelo menos, um evento ou observação anteriormente não proibido no quadro de referências do conhecimento.

Mais recentemente, Vogt (2008; veja também RIEPPEL, 2008) apresentou argumentos contrários à aplicação do modelo hipotético-dedutivo, e consequentemente do o critério de 'falseabilidade', às hipóteses cladísticas. Nos cladogramas gerados a partir da análise de uma matriz de dados não se proíbem a ocorrência da evolução convergente. Em outras palavras, em uma análise, quando uma hipótese de homologia primária não é congruente com as demais, ela não é refutada no sentido popperiano do termo, mas é adequada à topologia do cladograma, permitindo, com isso, que tanto apomorfias quando homoplasias sirvam como explicações para as relações de parentesco de um dado grupo (Vogt 2008). O mesmo raciocínio aplica-se, naturalmente, aos alinhamentos múltiplos de sequências das análises moleculares.

É preciso ressaltar que a impossibilidade de verificação e "falseação" dos cladogramas, não significa dizer que os estes não são objetos de investigação científica. Cladogramas, especialmente aqueles gerados a partir de diferentes evidências, podem (e devem) ser comparados uns com os outros a fim de identificar possíveis congruências. Esse tipo de comparação é, segundo Santos e Capellari (2009), semelhante ao princípio da iluminação recíproca de Hennig (1966, 1968 [1955]), segundo o qual uma determinada hipótese é avaliada a partir do seu grau de concordância com outras hipóteses geradas a partir de outros tipos de evidência. Dessa forma, clagoramas congruentes no sentido de apresentarem as mesmas, ou quase as mesmas, relações de parentescos têm um maior poder explanatórios. Ao contrário, no caso de não haver congruência, então as diferenças precisam ser reconciliadas por meio da reanálise dos dados existentes e, principalmente, análise de novos conjuntos de caracteres e/ou marcadores moleculares.

A partir do exposto, e comparando-se as hipóteses ora disponíveis na literatura (*e.g.*, LIVEZEY; ZUSI, 2007; HACKETT et al., 2008; SMITH 2010) com a proposta deste trabalho, conclui-se que esta é um pouco mais congruente com as hipóteses derivadas de dados moleculares, particularmente no que se refere às aves totipalmadas. Contudo, há diferenças consideráveis, mormente quanto aos clados mais inclusivos. Fica claro (ou pelo menos deveria ficar) que, a polifia das aves Pelecaniformes, ao menos no que diz respeito a Pelecanidae, não é tão óbvia quanto parece. Mais duvidoso é o posicionamento de *Phaethon*, já que há incongruências entre hipóteses geradas, tanto baseadas em dados semelhantes, como também em evidências diferentes (*i.e.*, fenotípica *vs*. molecular). Nesse sentido, qualquer investigação que vise a elucidação das relações filogenéticas desse táxon deve, necessariamente, incluir em sua análise, não somente táxons pertencentes ao "clado das aves aquáticas", mas também aqueles do clado Metaves, particularmente Columbiformes, Gruiformes e Eurypygiformes.

Para Mickevich e Lipscomb (1991), a iluminação recíproca é o processo pelo qual os "erros perceptuais" são identificados e corrigidos. Nas análises baseadas na evidência fenotípica, boa parte de tais erros está, certamente, no processo de delineação dos caracteres. Nesse contexto, no conjunto de quase 2.000 caracteres de Livezey e Zusi (2006) há vários exemplos dos ditos "caracteres quiméricos" (*i.e.*, aqueles em que o estado neomórfico "ausente" e combinado a estados transformacionais) e caracteres transformacionais cujos estados estão definidos de forma pouco precisa e/ou cujos qualificadores estão ausentes. Não que a lógica de Sereno (2007) seja monolítica; porém, ela se constitui numa proposta relativamente objetiva e, portanto, menos propensa a idiossincrasias. Seria oportuno, então, revisar os caracteres de Livezey e Zusi (2006) e, se necessário, emendá-los para corrigir quaisquer erros. Assim uma nova hipótese de relações filogenéticas para o "clado das aves aquáticas" poderia ser gerada. Tal revião não impede que novos sistemas de caracteres sejam explorados; aliás, isso é mais do que desejado.

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Anexo 1

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Anexo 2

Glossário nomenclatural

Aegothelidae. Família monogenérica que inclui Aegotheliformes e que, tradicionalmente, pertencia à ordem Caprimulgiformes. Estudos recentes indicam uma relação filogenética mais próxima de Apodiformes.

Aequornithes. Clado nomeado por Mayr (J. Zoolog. Syst. Evol. Res. 49: 58-76, 2010) e que inclui as ordens Gaviiformes, Sphenisciformes, Procellariiformes, Ciconiiformes, Suliformes e Pelecaniformes.

Anatidae. Família pertencente à ordem Anseriformes e que inclui os inclui patos, cisnes e gansos.

Anhingidae. Família pertencente à ordem Suliformes (anteriormente Pelecaniformes), que inclui *Anhinga* (biguatinga).

Aramidae. Família pertencente à ordem Gruiforme, cujo único represente vivente é *Aramus guarauna* (carão).

Ardeidae. Família pertencente à ordem Pelecaniformes (anteriormente Ciconiiformes), que inclui as garças e socós.

Apodidae. Família pertencente à ordem Apodiformes, que inclui os andorinhões.

Austrodyptornithes. Clado nomeado por Yury et al. (Biology 2: 419-44, 2013), que inclui as ordens Sphenisciphormes e Procellariiformes.

Balaeniciptidae. Família monogenérica pertencente à ordem Pelecaniformes (anteriormente Ciconiiformes), que inclui *Balaeniceps rex* ("cegonha"-bico-de-sapato).

Caprimulgiformes. Ordem que inclui cinco famílias, cujos representantes são geralmente conhecidos como bacuraus.

Ciconiidae. Única família da ordem Ciconiiformes, que inclui as cegonhas.

Ciconiiformes. Ordem que atualmente inclui apenas a família Ciconiidae; mas, anteriormente incluía, ainda, Ardeidae, Balaeniciptidae, Threskiornithidae e Scopidae.

Columbiformes. É uma ordem, cujos únicos representantes viventes são as Columbidae (pombas e afins).

Coronaves. Clado originalmente proposto por Fain e Houde (Evolution 58: 2558–2573, 2004), que inclui, além do ‘clado das aves aquáticas’, as aves Charadriiformes (batuíras, maçaricos, gaivotas e afins) e as aves estritamente terrestres. É o clado irmão de Metaves.

Diomedeidae. Família pertencente à ordem Procellariiformes, que inclui os albatrozes.

Eurypygidae. Família monogenérica, que inclui apenas *Eurypyga helias* (pavãozinho-do-pará).

Fregatidae. Família pertencente à ordem Suliformes (anteriormente Pelecaniformes), que inclui dois gêneros: *Fregata* e †*Limnofregata*.

Gaviiformes. Família constituída por aves do Hemisfério Norte, conhecidas em língua inglesa como “loons”. Inclui apenas uma família vivente: Gaviidae.

Gaviidae. Veja Gaviiformes.

Gruidae. Família pertencente à ordem Gruiformes, que inclui os grous.

Hemiprocnidae. Família monogenérica, que inclui *Hemiprocne*. São filogeneticamente próximas a Apodidae.

Hydrobatidae. Família (às vezes subfamília) pertencente à ordem Procellariiformes, que inclui os gêneros *Hydrobates* e *Oceanodroma*.

Metaves. Clado originalmente proposto por Fain e Houde (Evolution 58: 2558–2573, 2004), que inclui Apodidae, Aegothelidae, Caprimulgiformes, Columbiformes, Eurypygidae, Hemiprocnidae, Mesitornithidae, Phoenicopteridae, Phaethontidae, Podargidae, Podicipedidae, Pteroclididae e Rhynochetidae e Trochilidae.

Natatores. Clado proposto por Livezey e Zusi (Zool. J. Linnean. Soc. 149: 1-95, 2007), cuja composição é semelhante a Aequornithes, mas inclui, ainda, Phaethontidae, Phoenicopteridae e Podicipedidae.

Neornithes. Clado (ou subclasse) que inclui todas as linhagens de aves viventes.

Oceanitidae. Família (às vezes subfamília) pertencente à ordem Procellariiformes, que inclui os gêneros *Oceanites*, *Garrodia*, *Pelagodroma*, *Fregetta* e *Nesofregetta*.

Odontopterygiformes. Ordem que inclui vários gêneros de aves fósseis.

Pelecanidae. Família monogenérica pertencente à ordem Pelecaniformes, que inclui os pelicanos.

Pelecaniformes. Ordem que tradicionalmente incluía Anhingidae, Fregatidae, Phaethontidae, Phalacrocoracidae, Sulidae e Pelecanidae.

Atualmente, porém, inclui Pelecanidae e mais Ardeidae, Balaenicipitidae, Scopidae e Threskiornitidae.

Phalacrocoracidae. Família pertencente à ordem Suliformes (Pelecaniformes, na sistemática tradicional), que inclui os biguás e afins.

Phaethontidae. Família cujas relações filogenéticas ainda são pouco definidas. Pertencia à ordem Pelecaniformes; mas, atualmente, está alocada na sua própria ordem monotípica: Phaethontiformes.

Phaethontimorphae. Clado proposto por Jarvis et al. (Science 346: 1320-1331, 2014), que inclui Phaethontidae e Eurypygidae.

Phoenicopteridae. Família que inclui os flamingos. Atualmente, está alocada na sua própria ordem monotípica: Phoenicopteriformes.

Plotopteridae. Família fóssil alocada na ordem Pelecaniformes, como tradicionalmente conhecida, ou mais recentemente, em Suliformes.

Podargidae. Família pertencente à ordem Caprimulgiformes encontrada na Ásia e Australásia.

Podicipedidae. Única família da ordem Podicipediformes; inclui os mergulhões.

Procellariidae. Família pertencente à ordem Procellariiformes, que inclui os pretréis e afins.

Procellariiformes. Ordem que inclui os albatrozes, petréis e afins.

Pteroclididae. Família que inclui aves da Ásia Central, conhecidas em língua inglesa como “Sandgrouse”. Atualmente, está alocada na sua própria ordem monotípica: Pterocliformes.

Rhynochetidae. Família que inclui duas espécies, *Rhynochetos jubatus* e †*R. orarius*, ambas endêmica da Nova Caledônia.

Scopidae. Família monogenérica que inclui uma espécie, *Scopus umbretta*, da África e península Arábica. Anteriormente alocada na ordem Ciconiiformes; mas, atualmente, na Pelecaniformes.

Steganopodes. Clado proposto originalmente por Cracraft (Auk 102: 834-853 1985), que inclui Anhingidae, Fregatidae, Pelecanidae, Phalacrocoracidae e Sulidae.

Spheniscidae. Única família da ordem Sphenisciformes, a qual inclui os pinguins.

Sulida. Veja Suloidea.

Sulidae. Família pertencente à ordem Suliformes (Pelecaniformes, na sistemática tradicional), que inclui os atobás.

Suloidea. Clado proposto originalmente por Cracraft (Auk 102: 834-853 1985), que inclui Anhingidae, Phalacrocoracidae e Sulidae.

Terrestrornithes. Clado proposto por Livezey e Zusi (Zool. J. Linnean. Soc. 149: 1-95, 2007), que inclui batuíras, maçaricos, gaivotas, trinta-réis e afins, bem como a maioria das aves-de-rapina e dos pássaros.

Threskiornithidae. Família ora pertencente à ordem Pelecaniformes (anteriormente Ciconiiformes), que inclui os ibises, colhereiros e afins.

Tinamidae. Família que inclui inhambus ou "codornas" da região Neotropical e é alocada na sua própria ordem monotípica: Tinamiformes.

Trochilidae. Família que inclui os beija-flores e, atualmente, é alocada na ordem Apodiformes.