# PHYLOGENY OF THE PHALACROCORACIDAE[1]

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*Abstract.* I undertook a phylogenetic analysis of the Recent taxa of Phalacrocoracidae using qualitative osteological characters. The family comprises two subfamilies. The Phalacrocoracinae (cormorants) comprise four genera of all-dark, littorine species: *Microcarbo* (microcormorants), *Compsohalieus* (marine cormorants), *Hypoleucos* (mesocormorants), and *Phalacrocorax* (macrocormorants). The Leucocarboninae (shags) comprise five genera of variably plumaged, littorine, and pelagic species: *Leucocarbo* (guano shags), *Notocarbo* (blue-eyed shags), *Nesocarbo* (Campbell Island Shag), *Euleucocarbo* (New Zealand blue-eyed shags), and *Stictocarbo* (cliff shags). The relationship of the anhingas (Anhingidae) to the Phalacrocoracidae remains problematical and unresolved. Additional analyses using cranial or postcranial characters produced comparable results, with the greatest divergence obtained when only crania were compared. I discuss the nature of homoplasy in the family: cormorants are characterized by convergences, shags by reversals. Plumage patterns have functional correlates, but phylogenetic history may be the ultimate factor.

*Key words: Phalacrocoracidae; Anhingidae; Phalacrocoracinae; Leucocarboninae; cormorants; phylogenetics; systematics; osteology.*

## INTRODUCTION

Since the very first attempts to reconstruct the phylogeny of the Class Aves, there has been little controversy over which taxa comprised the Phalacrocoracidae. More pertinent at the time was determining the relationships of the family within Pelecaniformes, and that of the order to the rest of birds. The most widely accepted phylogeny was by Wetmore (1934), who positioned the family between the Sulidae and Anhingidae at the "primitive end" of the avian phylogeny. Little effort was expended by systematists before or after this to determine relationships within the cormorants.

The Phalacrocoracidae have been considered to comprise approximately 30 species in one to five genera; the most recent treatment recognizes 29 species in one genus (Dorst and Mougin 1979). There has been little consensus among authorities on the status of certain species and higher-order relationships within the family, possibly because of sporadic and incomplete systematic treatments and changing concepts of species and genera. Although cormorants are found worldwide, and are usually abundant members of the littorine avifauna, in the past century there have been only a few attempts at a family-wide treat-

ment (Sharpe 1899, Peters 1931, von Boetticher 1937, van Tets 1976, Dorst and Mougin 1979); incomplete treatments dealing with regional faunas, selected species groups, or collection holdings were more common (Ogilvie-Grant 1898; Hutton 1903; Hall 1920; Mathews and Iredale 1921; Falla 1932, 1937; van Tets 1965). Most recently, Cracraft (1985) investigated the systematic relationships among Pelecaniformes, and confirmed the monophyly of the family.

The classification generally followed in the northern hemisphere is of a single genus *Phalacrocorax* (cf. Dorst and Mougin 1979), sometimes supplemented by the monotypic genus *Nannopterum* for the Flightless Cormorant of the Galápagos (cf. Sharpe 1899, Witherby et al. 1940). Other taxonomies often remove the microcormorants (sensu van Tets 1976) from *Phalacrocorax* into the genus *Haliaetor* [sic] (cf. Peters 1931). In the southern hemisphere, *Phalacrocorax* is partitioned further by the use of *Leucocarbo* and *Stictocarbo* for various shags of the southern oceans (cf. Falla 1932, 1937).

An ancillary (and essentially trivial) issue has been whether the anhingas (darters) constitute a distinct family or are a subfamily of the Phalacrocoracidae. Peters (1931), Olson (1985), Becker (1986), and others considered their differences to be sufficient for family standing (i.e., Anhingidae), while Dorst and Mougin (1979), Cracraft (1985), and many others found their similarities

with the Phalacrocoracidae to be great enough to restrict it to a subfamily (i.e., Anhinginae).

The first worldwide treatment was by Sharpe (1899), who, without indicating methodology or characters used, placed all forms from the early Miocene to the Recent into *Phalacrocorax,* reserving separate genera for an Eocene taxon *Actiornis* spp., the Galapagos Cormorant (*Nannopterum harrisi*), and the extinct Pallas's Cormorant (*Pallasicarbo perspicillatus*). Because he listed the latter species also in *Phalacrocorax,* this gave it the notable distinction of belonging to two genera simultaneously.

Peters (1931) followed a traditional linear arrangement of species placed into two genera (*Phalacrocorax, Halietor*), but without justification or methodology. Von Boetticher (1936) considered certain aspects of external morphology (e.g., rectrix number, abdomen color, etc.) and biogeography, and clustered all of the extant forms by general similarity into three genera and 10 subgenera. He later revised this taxonomy (von Boetticher 1937) and altered species allocations, generic and subgeneric names, and proposed a resolution of the blue-eyed shag complex (*Leucocarbo* s.l.) of the southern hemisphere.

Systematists studying southern hemisphere Phalacrocoracidae have been faced with a greater diversity of species than elsewhere in the world, and perhaps as a direct result of this, have proposed a variety of taxonomies (cf. Mathews and Iredale 1913, Falla 1937, and others). Of these, only van Tets (1976) considered all extant species. Using similarities in external morphology and behavior, he apportioned all members of this family into two genera (*Phalacrocorax, Leucocarbo*) with three subgenera in the former, and two in the latter genus.

Most recently, Dorst and Mougin (1979), following Peters (1931), lumped all extant species into a single genus *Phalacrocorax.* Assessments of possible specific and superspecific affinities were given by footnote but without justification. Neither Dorst and Mougin nor Peters presented an explicit phylogeny of the family, but listed species in a linear arrangement, "in taxonomic sequence" (Peters 1931:iv, Mayr and Cottrell 1979:vi).

To date, no attempt has been made to present anything other than a linear arrangement of species and only van Tets (1976) gave distinct characters to delineate higher-order relationships. I undertook a phylogenetic analysis of Recent Phalacrocoracidae and Anhingidae using 137 osteological characters. I present a hypothetical evolutionary tree for the family, and discuss its implications for classification, morphological convergence, and plumage patterns.

This article is dedicated to the memory of Ralph W. Schreiber, friend and teacher, who encouraged me early on to study Pelecaniformes, and supported my continuing research on cormorants with insight and humor. His sudden death diminishes us all.

## METHODS

### TAXA AND SPECIMENS

I studied skeletons of all Recent taxa of Phalacrocoracidae, except for the Indian Cormorant, *Hypoleucos fuscicollis,* and some of the island forms of *Notocarbo atriceps* found in Antarctic waters (e.g., *N. a. melanogenis, N. a. purpurascens,* etc.), of which no specimens are readily available (Wood and Schnell 1986). In taxa known to be particularly variable or encompassing many subspecies, I studied as many forms as possible. In all, I examined 226 specimens of 36 putative species of cormorants, shags, and anhingas (Table 1). Except for certain New Zealand shags (*Nesocarbo campbelli, Euleucocarbo chalconotus, E. colensoi, E. onslowi, E. ranfurlyi:* one skeleton each), three microcormorants (*Microcarbo coronatus, M. niger, M. pygmaeus:* one skeleton each), and the extinct Spectacled or Pallas's Cormorant (*Compsohalieus perspicillatus:* unassociated skeletal elements), I examined at least two specimens of each species.

### ANALYSIS OF CHARACTERS

I used 137 osteological characters for the phylogenetic analysis (Appendix 1); less than one-fourth of these have been described or defined previously, but most are illustrated without identification in references accompanying the character descriptions. Where possible, anatomical descriptions follow Howard (1929) and Owre (1967); in many cases, however, suitable names for features could not be determined through these sources, and characters were described instead by appearance or location. In some taxa previously considered to be of subspecific rank (e.g., *E. chalconotus, N. bransfieldensis, Stictocarbo featherstoni*), I found sufficient diagnostic characters (autapomorphies) to discriminate them as species (see McKitrick and Zink 1988). In the
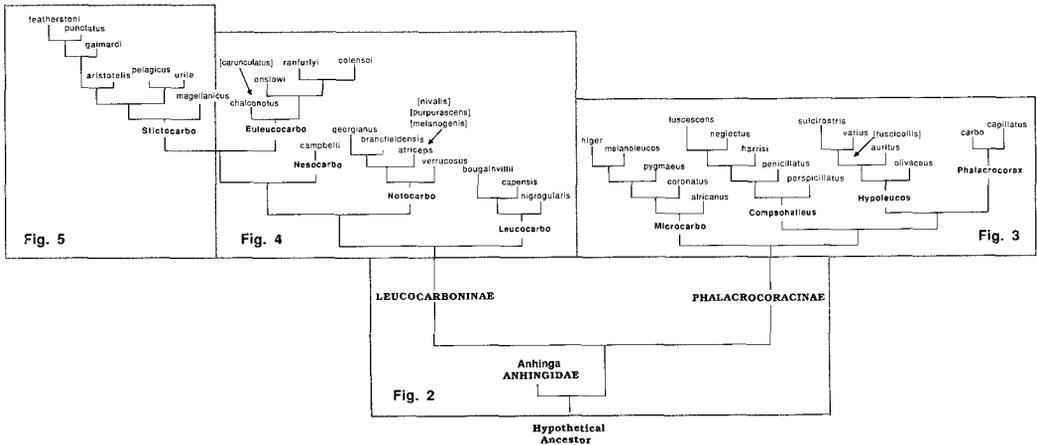
FIGURE 1.    General tree of the Recent species of Phalacrocoracidae (CI = 0.678, length = 227 steps). Character changes are given in the indicated figures which follow. Species names in brackets indicate presumptive placement where no specimens were available for study.

case of *N. atriceps* and *albiventer,* two taxa currently considered specifically distinct, I was unable to discover any diagnostic osteological characters. For this analysis, therefore, they were treated together under the senior synonym, *atriceps.* Members of two genera of cormorants (*Hypoleucos, Phalacrocorax*) showed substantial geographic variation in osteology within currently recognized species; in these cases, I used specimens of the nominal taxon (e.g., *H. olivaceus olivaceus, P. carbo carbo,* etc.).

I used only qualitative osteological characters in this analysis because little is known at present about behavior, life histories, and the intrataxon variation in external morphology for approximately half of the extant species. In addition, it is not possible at present to establish polarities and states with many of these nonosteological characters.

Each of the characters I used was a discrete trait for which at least two discrete states could be defined. I made no attempt to develop an exhaustive list of diagnostic characters for each species.

DERIVATION OF TREES

I determined polarities of each character by comparison with selected taxa—*Sula* and *Morus* (Sulidae), *Pelecanus* (Pelecanidae), *Fregata* (Fregatidae), *Diomedea* (Diomedeidae), and *Spheniscus* (Spheniscidae)—each proposed as an outgroup to the Phalacrocoracidae (Cracraft 1985). I used

these outgroups and the method of Maddison et al. (1984) to construct a hypothetical ancestor to root the evolutionary tree. I found no differences in tree topology of the Phalacrocoracidae using actual outgroup taxa or a hypothetical ancestor, although I obtained the most parsimonious solution using the latter. Transformation series were treated as linear, except in four cases where I was unable to determine linearity with confidence. These (8, 60, 62, 97) I treated as unordered characters. To test the effect of these assumptions about the probable evolution of character states on tree stability, I performed subsequent analyses treating all characters as unordered.

The trees were derived using the PAUP program (Swofford 1984), and I used the method of search described by Livezey (1986). The search for most parsimonious trees was accomplished using the multiple parsimony (MULPARS) and alternate swapping between global and local search (ALT) options. The accelerated transformation (ACCTRAN) optimization, which minimizes reversals within a tree, was used to position characters. Results of analysis using delayed transformation (DELTRAN), which minimizes parallel character states within a tree, did not alter topology; differences involved only the placement of nine characters (see below in Results).

See Appendix 1 for character descriptions and polarities, and Appendix 2 for the data matrix of character state codings for the hypothetical ancestor, anhingas, shags, and cormorants. A list
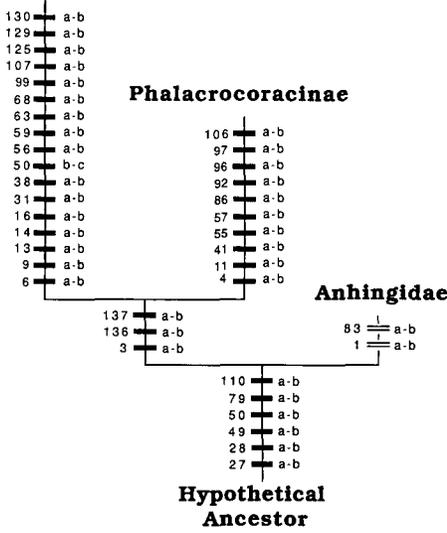
FIGURE 2. Partial tree of the character changes at the subfamily level. Solid lines represent derived character transformations; parallel lines, transformations convergent elsewhere in the tree. The number to the left of the character state symbol is the character number described in Appendix 1; the letter sequence to the right is the character state transformation.

of species and specimens examined is available from the author.

## RESULTS

I found one tree using the characters and polarities given in Appendix 1. The tree illustrated (Figs. 1–5) has a length of 227 steps, and a CI of 0.678. The normalized $F$-ratio was 0.266, with four out of 137 characters unordered. Separate analyses using DELTRAN and ACCTRAN optimizations (see Methods) differed only in the relative placement of nine characters (3, 27, 28, 49, 50, 57, 110, 112, 135) in the basal portion of the tree; topologies did not differ between these runs. The tree illustrated here is the result of analyses using the ACCTRAN optimization.

ANHINGIDAE Ridgway, 1887
(anhingas, darters)

Two homoplasious synapomorphies support the monophyly of the Anhingidae (Fig. 2) and are convergent with features related to feeding and diving found in the Phalacrocoracidae (see Stolpe 1932, Owre 1967). Coding of eight characters (27, 28, 49, 50, 79, 80, 97, 100) were problematical in this group, possibly because I examined only five specimens of two putative species (A.
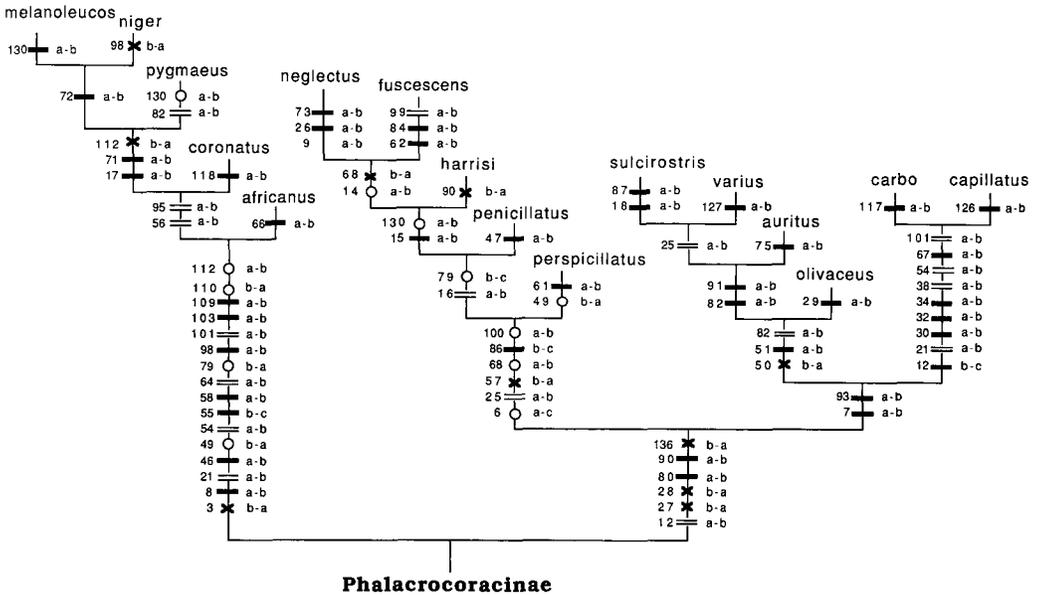


FIGURE 3. Partial tree of the character changes in the Phalacrocoracinae (cormorants). Solid lines represent unambiguously derived character transformations, parallel lines represent character transformations convergent to states found lower in the tree, crosses represent character transformations reversed to states found lower in the tree, and open circles represent complexly varying characters showing evidence of both convergence and reversal within the family. Symbol legends are described in Figure 2.
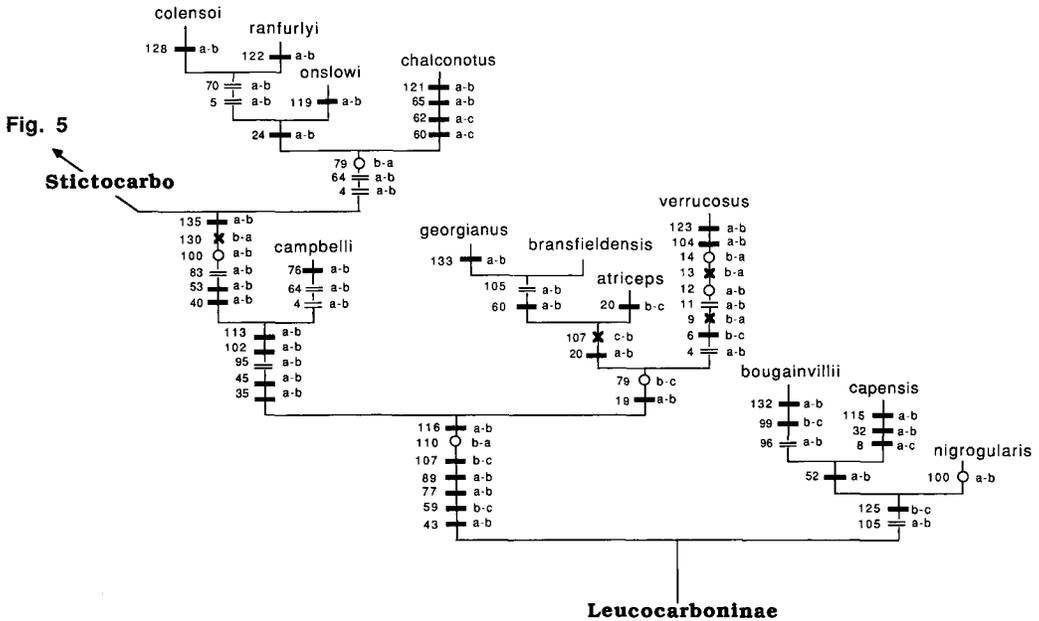
**FIGURE 4.**  Partial tree of the character changes in the Leucocarboninae (primitive shags). Symbols and legends are described in Figures 2 and 3.

*anhinga, A. novaehollandiae*). In some specimens, intermediate states for these characters were found; in other specimens, character states varied among supposed conspecifics. Because precise coding of these characters could not be determined with confidence, they were treated as polymorphic, i.e., both character states found within the group. In subsequent analyses, these characters were coded first as primitive and then as derived. In both cases, a single tree was found which differed only from that illustrated here in that the Anhingidae were placed between subfamilies of Phalacrocoracidae. In the former analysis, Anhingidae was the sister group to the shags; in the latter, to cormorants. Similar results were obtained using all characters unordered; otherwise, the trees were the same as in the primary analysis.

PHALACROCORACIDAE Bonaparte, 1855

Three synapomorphies, one of which (137: terminal hook to the bill) is unambiguous, reaffirms the monophyly of the family (Fig. 2) implied earlier by Cracraft (1985). I determined that the Phalacrocoracidae comprise two primary clades, which I treat here as subfamilies: the Phalacrocoracinae and Leucocarboninae. These subfamilies are referred to here as cormorants and shags,

respectively, and are supported by various other characters of plumage color, external morphology, and behavior (van Tets 1976; Siegel-Causey, unpubl.).
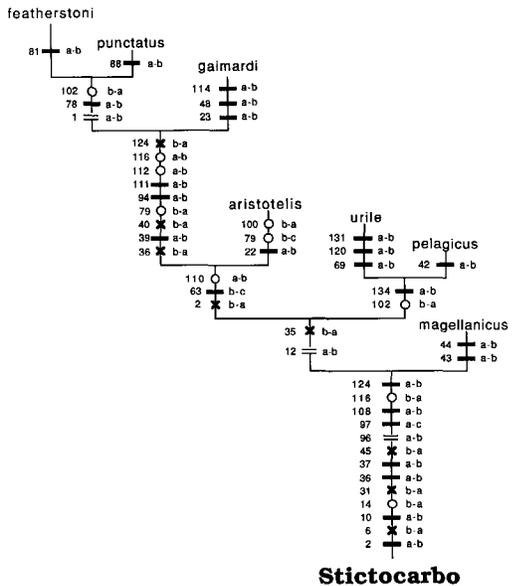


**FIGURE 5.**  Partial tree of the character changes in the continuation of the Leucocarboninae (cliff shags). Symbols and legends are described in Figures 2 and 3.

PHALACROCORACINAE Bonaparte, 1855 (cormorants)

Ten character state changes, six of them unambiguous synapomorphies (41, 55, 86, 92, 97, 106), support the monophyly of this subfamily (Fig. 2). Of the remaining synapomorphies, three (4, 11, 96) are convergent and one is reversed (57) farther up in the tree. The unambiguous synapomorphies relate to jaw musculature, distal wing flexibility and strength, and hind limb action (see Owre 1967), and correlate with an overall preference by cormorants for less sustained flight and feeding in deeper waters (Ainley 1984, Siegel-Causey 1985). My analysis confirms van Tets' (1976) implication that the cormorants constitute a monophyletic group.

*Microcarbo* Bonaparte, 1855 (microcormorants).—My analysis confirms the monophyly of this derived genus by 16 character changes (Fig. 3), six of which are unambiguous (8, 46, 55, 58, 103, 109). The unambiguously derived synapomorphies represent changes in cranial shape and terminal enervation of the mandible, coracoidal musculature, possible increased furcular movement, and hind limb musculature (see Owre 1967).

Large cormorants.—The remaining three genera of cormorants are united by six synapomorphies, one of which (80) is unambiguous, and relates to humeral rotation and more powerful flight capabilities (see Owre 1967). Other behavioral and morphological features (van Tets 1965, 1976) support this grouping.

*Compsohalieus* Ridgway, 1884 (marine cormorants).—Six synapomorphies, one of them unambiguous (86) and relating to distal wing flexibility (Owre 1967), establishes the monophyly of this genus of heavy-bodied, widely distributed cormorants (Fig. 3). Members of this genus are the deepest and strongest divers in the family (Ainley 1984, Siegel-Causey 1985); some of the characters (6, 68, 100) are convergent with those observed in shags and may represent similar adaptations to a pelagic habitat.

Continental cormorants.—This clade, constituting *Phalacrocorax* and *Hypoleucos*, comprises moderate to large cormorants breeding in the marine and aquatic littoral. Two unambiguous synapomorphies (7, 93) relating to bill shape and distal wing musculature (see Owre 1967) establish the monophyly of this group (Fig. 3); similarities in plumage (Ogilvie-Grant 1898, Palmer

1964) and behavior (van Tets 1965, 1976) lend additional validity for the clade.

*Hypoleucos* Reichenbach, 1852 (mesocormorants).—Three synapomorphies, one of which (51) is unambiguous and relates to adduction of the mandible (Owre 1967), establish the monophyly of this genus of entirely dark, medium-sized cormorants (Fig. 3). My analysis indicates that *H. olivaceus* is the earliest divergence within this genus and, together with *H. auritus,* are the only New World mesocormorants. As with *P. carbo,* all of the species I examined in this genus showed distinct intrataxon variation in character states. The Indian Cormorant, *H. fuscicollis,* is most likely a member of this genus; its plumage, behavior, and external morphology (Ogilvie-Grant 1898; Ali and Ripley 1968; van Tets, pers. comm.) indicate that its systematic position may lie between *H. auritus* and *H. varius.* Unfortunately, no skeletons exist of this species (Wood and Schnell 1986), so its phylogenetic position remains undetermined.

*Phalacrocorax* Brisson, 1760 (macrocormorants).—Two species, the Great Cormorant, *P. carbo,* and the Japanese Cormorant, *P. capillatus,* comprise this genus of large cormorants. Nine character changes, five of them unambiguous synapomorphies (12, 30, 32, 34, 67) and relating to palatal musculature, nasal glands, and flight (see Owre 1967), establish the monophyly of this genus (Fig. 3). Most of the synapomorphies are related to feeding and have been associated previously with a preference for shallower waters and a diet of upper-water fish (Kuroda 1922, Austin 1948, van Dobbin 1952, Ono 1980, Härkönen 1988).

LEUCOCARBONINAE, new name (shags)

Seventeen character changes, six of which are unambiguous synapomorphies (50, 59, 63, 107, 125, 129), establish the monophyly of this subfamily (Figs. 4, 5). These derived characters relate to jaw musculature, and strengthened humoral and femoral musculature (see Owre 1967). My analysis indicates the existence of five main clades, which I interpret as genera. All but one of these genera have been recognized previously, but species allocation among them has differed widely among authors. For convenience, the first four genera are referred to as "primitive shags."

*Leucocarbo* Bonaparte, 1857 (guano or trek shags).—My analysis establishes the monophyly

of this basal clade with two synapomorphies, one of which (125) is unambiguous and related to distal hind limb movement (Owre 1967) (Fig. 4). Some osteological characters (e.g., 6, 91) varied among the three specimens of *L. nigrogularis* that I examined, but most of the differences were found in one of them (BMNH 1964.39.2), a probable juvenile. The small number of available skeletons prevents knowing whether these differences were ontogenetic or represented normal variation within this form. No such variation was seen in *L. bougainvillii* or *L. capensis*.

The remaining genera in the Leucocarboninae are united by seven synapomorphies, four of which are unambiguous (43, 59, 77, 89) and related to jaw movement and wing action (see Owre 1967). The other three characters vary complexly within the subfamily, showing repeated reversals and convergences.

*Notocarbo*, n. gen. (blue-eyed shags).—This clade of at least four species is supported by one unambiguous synapomorphy (19) found on the mesethmoid, and one (79) homoplasious character on the humerus that is convergent with states observed in *Compsohalieus* (Fig. 4). Their possible functions are obscure. No pre-existing genus name is available for this clade so I propose *Notocarbo* (Noto- = G., "southern"; -carbo = L., coal, black: a generic root in the family) in light of their exclusively southern hemisphere distribution; I designate *N. atriceps atriceps* as the type species for this genus. The diagnostic character for the genus is osteological: the prefrontal process of the mesethmoid is broadly produced into an anteriorly directed triangular projection. External morphology of this group is similar to other primitive shags, and discrimination by such characters at present is problematical. The genus includes the South Georgia Shag (*N. georgianus*), the Antarctic Shag (*N. bransfieldensis*), the Imperial Shag (*N. atriceps*), and the Kerguelen Shag (*N. verrucosus*). Referred taxa are those currently considered as subspecies of *N. atriceps* or *albiventer*.

The remaining shags are united by five synapomorphies. The only unambiguous synapomorphy is the attachment of M. iliotrochanter on the femur (113), and relates to lessened mobility of that element (Owre 1967).

*Nesocarbo* Voisin, 1973 (Campbell Island Shag).—The Campbell Island Shag (*N. campbelli*), has long been considered closely related to the other shags of New Zealand and outlying islands, in particular, *E. colensoi* and *E. ranfurlyi* (Ogilvie-Grant 1898, 1905; Hutton 1903; Mathews and Iredale 1921; Falla 1932, 1937). My analysis showed *N. campbelli* to be osteologically distinctive (76) and a sister species to the New Zealand blue-eyed shags (Fig. 4), consistent with Voisin's (1973) designation of this form as a monotypic genus, *Nesocarbo*.

*Euleucocarbo* Voisin, 1973 (New Zealand blue-eyed shags).—My analysis confirmed the monotypy of this genus with three character state changes related to flight (see Owre 1967) (Fig. 4), all of which were homoplasious within shags and convergent with cormorants, *Microcarbo* in particular. The four taxa treated here are quite similar looking, and, as in the other primitive shags, convergent for many external features. Skeletal specimens are rare, and often misidentified (Siegel-Causey, unpubl. data). Because of this and the small number of reliable specimens, intrageneric relationships among this group should be considered tentative until more detailed work is possible.

*Stictocarbo* Bonaparte, 1855 (cliff shags).—The monophyly of this genus was confirmed by 13 character changes, four of which (10, 37, 97, 108) are unambiguous (Fig. 5) and related to prey capture and femoral abduction (see Owre 1967). The single most distinctive character in this clade is the degree of dorsoventral compression of the cranium (10). This feature is most exaggerated in the North American taxa, *S. pelagicus* and *S. urile*, where the dorsal surface of their crania is nearly planar. There are many convergences with cormorants in characters related to swimming, especially to the marine cormorants, *Compsohalieus* spp. Many of the synapomorphies expressed in this genus are associated with the hind limbs (e.g., 108, 116, 124) and related to their more upright resting posture (see Owre 1967).

The basal group of cliff shags (*S. magellanicus, S. pelagicus, S. urile, S. aristotelis*) are characterized by characters of the cranium and tibiotarsus (22, 43, 133) that are likely associated with foot flexion and feeding (see Owre 1967). The Red-legged Shag (*S. gaimardi*) of South America, and the Chatham Island and Spotted shags of New Zealand (*S. featherstoni* and *S. punctatus*), are the most derived Cliff Shags, and are distinguished from their congeners by 10 character changes, three of which (39, 94, 111) are un-

TABLE 1. A Linnaean classification of the Recent species of Phalacrocoracidae. Genera and subfamily limits were set using the conventions given in Wiley (1981). Fossil taxa, and Recent taxa of Anhingidae, are not included. * Species placement referred without examination; ** species extinct.

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Family Phalacrocoracidae Bonaparte, 1855
  Subfamily Phalacrocoracinae Bonaparte, 1855
    Genus *Microcarbo* Bonaparte, 1855
      *M. africanus* (Gmelin, 1789)
      *M. coronatus* (Wahlberg, 1855)
      *M. pygmaeus* (Pallas, 1773) [type by original designation]
      *M. niger* (Vieillot, 1817)
      *M. melanoleucos* (Vieillot, 1817)
    Genus *Compsohalieus* Ridgway, 1884
      *C. perspicillatus* (Pallas, 1811)**
      *C. penicillatus* (Brandt, 1837) [type by original designation]
      *C. harrisi* (Rothschild, 1898)
      *C. neglectus* (Wahlberg, 1855)
      *C. fuscescens* (Vieillot, 1817)
    Genus *Hypoleucos* Reichenbach, 1852
      *H. olivaceus* (Humboldt, 1805) [=*brasilianus* (Gmelin, 1789)]
      *H. auritus* (Lesson, 1831)
      *H. fuscicollis* (Stephens, 1826)*
      *H. varius* (Gmelin, 1789) [type by original designation]
      *H. sulcirostris* (Brandt, 1837)
    Genus *Phalacrocorax* Brisson, 1760
      *P. carbo* (Linnaeus, 1758) [type by tautonomy]
      *P. capillatus* (Temminck and Schlegel, 1850)
  Subfamily Leucocarboninae, new name
    Genus *Leucocarbo* Bonaparte, 1857
      *L. nigrogularis* (Ogilvie-Grant and Forbes, 1899)
      *L. capensis* (Sparrman, 1788)
      *L. bougainvillii* (Lesson, 1837) [type by subsequent designation]
    Genus *Notocarbo*, n. gen.
      *N. verrucosus* (Cabanis, 1875)
      *N. atriceps atriceps* (King, 1828) [type by original designation]
      *N. bransfieldensis* (Murphy, 1936)
      *N. georgianus* (Lönnberg, 1906)
    Genus *Nesocarbo* Voisin, 1973
      *N. campbelli* (Filhol, 1878) [type by monotypy]
    Genus *Euleucocarbo* Voisin, 1973
      *E. carunculatus* (Gmelin, 1789) [type by original designation]*
      *E. chalconotus* (Gray, 1845)
      *E. onslow* (Forbes, 1893)
      *E. colensoi* (Buller, 1888)
      *E. ranfurlyi* (Ogilvie-Grant, 1901)
    Genus *Stictocarbo* Bonaparte, 1855
      *S. magellanicus* (Gmelin, 1789)
      *S. pelagicus* (Pallas, 1811)
      *S. urile* (Gmelin, 1789)
      *S. aristotelis* (Linnaeus, 1761)
      *S. gaimardi* (Lesson and Garnot, 1828)
      *S. punctatus* (Sparrman, 1786) [type by subsequent designation]
      *S. featherstoni* (Buller, 1873)

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ambiguous (see also von Boetticher 1935). Functions of these characters are obscure, but they may be associated with bill flexion, distal wing movement, and stance (Owre 1967). One autapomorphy each establishes the Chatham Island and Spotted shags as distinct species (cf. McKitrick and Zink 1988) rather than subspecific forms of *S. punctatus* as was hypothesized earlier (Ogilvie-Grant 1905, Oliver 1930, Peters 1931, Fleming 1939, van Tets 1976).

## DISCUSSION

### TAXONOMIC CLASSIFICATION

My findings indicate a greater diversity of form in the family than previously recognized, and prompt a revision of the classification of the Phalacrocoracidae. Rather than submerge these differences with subgeneric groupings (cf. van Tets 1976), I have adopted Wiley's (1981) conventions for a hierarchial classification. I recognize two subfamilies in the Phalacrocoracidae, nine genera, and at least 35 species of cormorants and shags (Table 1).

Systematic treatments of the past have placed the anhingas in various taxonomic categories, from a genus in the Phalacrocoracidae (Ripley 1951, Ali and Ripley 1968) to a separate family (Becker 1986 and others). These efforts have dealt primarily with the question of higher-order rank, which ultimately is subjective. Yet undetermined are the phylogenetic relationships of the taxa comprising the Anhingidae, or their precise relationship with the Phalacrocoracidae; a more detailed survey of character and taxon variation in this group than was possible in this study is needed to resolve the problematical characters discussed earlier. Until then, the most prudent course is to consider the Anhingidae of equal rank to the Phalacrocoracidae.

Cormorants (Phalacrocoracinae) can be generalized as heavy-bodied, deep-feeding, flat- and tree-nesting birds with indifferent or labored flight. The most distinct genus of cormorants, perhaps of the entire family, are the microcormorants, *Microcarbo*. Unlike the rest of the family, which are the size of a goose or duck, microcormorants are nearer the size of a raven and have quite distinct behaviors in courtship, feeding, and reproduction (van Tets 1976). This group is one of the few in the family previously recognized as a distinct genus (e.g., Peters 1931); however, *Halietor* is the junior synonym of the equally used *Microcarbo* (e.g., von Boetticher

1937, van Tets 1976). Therefore, I use *Micro-carbo* to designate this genus.

Until recently (Crawford et al. 1982, Williams and Cooper 1983), *M. coronatus* was considered to be a subspecific form of *M. africanus*; in my results, unambiguous autapomorphies distinguish both, and *M. africanus* is distinguished from its sister species by two characters. *Microcarbo pygmaeus* and *M. niger* have often been considered conspecific (Ogilvie-Grant 1898, Deignan 1963), and in many accounts it is unclear which species is being discussed. My analysis supports the specific standing of *M. pygmaeus* and *M. niger*; less clear, however, is the relationship between *M. melanoleucos* and *M. niger,* but this may be a consequence of the few skeletons available.

Marine cormorants, *Compsohalieus* spp., are identified for the first time by this analysis; before, members were grouped with other cormorants or shags, but rarely did any of the previous systematic treatments associate any of them together. The constituent species are restricted to islands or coastlines adjacent to upwelling regions of temperate and tropical oceans. Although species (*C. penicillatus, C. fuscescens, C. neglectus*) may become locally abundant, most have strongly circumscribed distributions likely caused by factors related to breeding habitat, weak winter dispersal, and diet (Rand 1960, Palmer 1964, Thomson and Morley 1966, Cooper 1981, Ainley 1984, Siegel-Causey 1985). One of the species is flightless (*C. harrisi*). Another now extinct species, *C. perspicillatus,* may have been flightless (Greenway 1958), but osteological and morphological evidence is equivocal (Shufeldt 1915, Stegmann 1936). I did not include in this analysis the numerous autapomorphies associated with presumed or actual flightlessness which are detailed elsewhere (Stejneger 1885, Stejneger and Lucas 1889, Lucas 1895, Gadow 1902, Shufeldt 1915, Ono 1980).

Continental cormorants are entirely black, have broad geographic distributions, and, including certain microcormorants, are the only members of the family to inhabit the continental interiors. Mesocormorants, *Hypoleucos* spp., include two of the most common cormorants of the New World: the Olivaceous and Double-crested cormorants (*H. olivaceus, H. auritus*). These two species have complementary distributions extending from Tierra del Fuego to Canada, from the Atlantic and Caribbean shores to the Pacific, and with *Phalacrocorax carbo* are undoubtedly the most studied members of the family (see van Dobbin 1952, Palmer 1964, Siegel-Causey 1985). Recent studies indicate that geographic subdivision within the New World species is much greater than is currently recognized and that certain populations may be reproductively isolated (Siegel-Causey, in press). Less is known about the other members of this genus, especially the Indian Cormorant, *H. fuscicollis,* of which only rudiments of distribution and behavior have been reported.

Macrocormorants, *Phalacrocorax* spp., are among the largest extant species in the family. The Great Cormorant, *P. carbo,* is distributed over a vast area (eastern Canada to southern Africa, western Europe to China, and Australasia including some sub-Antarctic islands), and the present species definition includes forms that vary widely in certain character states (e.g., 82, 130). It is very likely that *P. carbo,* as currently recognized, is a superspecies defined by superficial similarities in plumage and external morphology (cf. Witherby et al. 1940, Palmer 1964, Marion 1983). For this analysis, I used specimens of the nominal subspecies to represent *P. carbo,* although subsequent work indicated that certain forms (e.g., *P. c. lucidus, P. c. maroccanus, P. c. novaehollandiae*) may be specifically distinct (Siegel-Causey, unpubl.). Little is known about *P. capillatus,* but its present distribution around the Japan Sea, close resemblance to East Asian populations of *P. carbo,* and behavior (Ogilvie-Grant 1898, Austin 1948, Yamamoto 1967, Ono 1980) suggest that it may be a population isolated during Pleistocene glaciations.

Shags (Leucocarboninae) can be characterized as compact, pelagic, flat- and cliff-nesting birds with fair flight abilities. The shags possess many homoplasious characters related to diving and strong flying, and as a group, are the strongest fliers and most pelagic of the family.

Guano shags, *Leucocarbo* spp., are more cormorant-like in external morphology compared to the other members of this subfamily. The exception is the Guanay, *L. bougainvillii,* whose overall external appearance is quite similar to members of the other genera of shags. The Socotra Shag, *L. nigrogularis,* is the most primitive form in this subfamily, and externally resembles the Cape Shag, *L. capensis,* in many features (Archer 1937, Ripley and Bond 1966, Gallagher and Woodcock 1980). Little is known about its biology, but information on its behavior and nesting habits (Gallagher and Rogers 1978; Gal-

lagher et al. 1984; van Tets, pers. comm.) lend support to its placement with the Leucocarboninae. The Cape Shag was regarded previously as having affinities with the Indian Cormorant (*H. fuscicollis*) and Socotra Shag (Peters 1931), the Great Cormorant, *P. carbo* (von Boetticher 1937), or Bank and Brandt's cormorants, *C. neglectus* and *C. penicillatus* (Dorst and Mougin 1979). Using overall similarity in courtship behavior, van Tets (1976) was the first to place this species within the shags (*Leucocarbo* s.l.). The Guanay is the most derived member of this genus and possesses the white abdomen and fleshy eye-ring of many of the other southern hemisphere shags. The Socotra, Cape, and Guanay shags are distinguished from all other shags by their preference to breed in very dense colonies, often in vast numbers on level ground, but other comparative aspects of behavior have been little studied.

Blue-eyed shags (actually, the eye-ring is bluish—the irides are generally dark), *Notocarbo* spp., seem to be more pelagic than the other genera of shags, and are found throughout coastal Fuego-Patagonia, Antarctica, and various sub-Antarctic islands (Watson 1975, Siegel-Causey 1986a). In addition to the species listed here, taxa currently regarded as subspecies are referred into this genus (i.e., *N. a. nivalis*, *N. a. melanogenis*, *N. a. purpurascens*). Skeletons were not available for these forms, so precise determination of rank and relationship is not yet possible.

It has been unclear in the past whether the two blue-eyed shags of South America (*atriceps, albiventer*) were conspecific or distinct species (see Lataste 1893, Devillers and Terschuren 1978). In a previous study on patterns of courtship behavior in various pairings between forms identified in the field as *atriceps* or *albiventer,* I detected no significant differences in type or sequence between forms (Siegel-Causey 1986a). The extent of variation within morphological, osteological, and behavioral characters is such that there are no diagnostic features to discriminate *atriceps* from *albiventer.* Therefore, I have treated both forms under the senior synonym, *N. atriceps.*

The Antarctic Shag (*N. bransfieldensis*) is massive (one of the largest shags extant) and is distinguished by at least four diagnostic characters (Siegel-Causey, unpubl.). They are resident on the Palmer Peninsula of Antarctica and islands along the Scotia Arc (Watson et al. 1971) and feed in nearshore waters (Bernstein and Maxson 1984, 1985). Subfossil evidence from Tierra del Fuego supports a broader distribution, possibly related to extensive postbreeding dispersal (Siegel-Causey, unpubl.). The South Georgia Shag (*N. georgianus*) is smaller and restricted to the Scotia Arc (Murphy 1936). The Kerguelen Shag (*N. verrucosus*) is smaller still, and appears to be restricted to the Kerguelen Archipelago (Paulian 1953, Voisin 1970). Previous records of this species on the Crozet Islands were misidentifications (Voisin, pers. comm.). The interspecific relationships with *Notocarbo* are tentative, and further study is proceeding to understand better their phylogeny and biogeography (Siegel-Causey, unpubl.).

Blue-eyed shags of the New Zealand waters (*Nesocarbo campbelli, Euleucocarbo* spp.) are externally quite similar (see Voisin 1973), but osteologically distinct from *Notocarbo.* All of these taxa have been regarded variously in the past as subspecific forms of *atriceps, albiventer, campbelli,* or *carunculatus* (see Buller 1895, Falla 1937, Falla and Stokell 1945, Voisin 1973). I was able to discern autapomorphic characters for each species examined, but a more detailed study of all of the shags of the Southern Ocean is essential for the resolution of relationships in these groups. All of these species were represented by only a single skeleton, so precise determination of relationship among them is problematical for the present.

The most derived genus of shags is cliff shags, *Stictocarbo* spp., comprising two groups of ecologically differentiated birds. The basal group of species (*S. magellanicus, S. pelagicus, S. urile, S. aristotelis*) are dark-colored, nest in a range of habitats from gentle slopes of islands to perpendicular cliff faces, and feed in the upper layers of marine coastal waters (Witherby et al. 1940, Lack 1945, Snow 1960, Siegel-Causey and Hunt 1981, Siegel-Causey 1986b). The most derived cliff shags (*S. gaimardi, S. punctatus, S. featherstoni*) are the only members of the family with gray plumage, and were recognized early on as being closely related (Murphy 1936). These shags are able to stand nearly upright when at rest, and are able to breed on the steepest cliffs (Forbes 1893, Koepcke and Koepcke 1953, Siegel-Causey 1987).

Sibley and Ahlquist (unpubl.) have evaluated the DNA-DNA hybridization of selected taxa of the Class Aves (the "tapestry") with the aim of elucidating the phylogeny of birds. Their

coverage of the Pelecaniformes, and Phalacrocoracidae in particular, is quite sketchy, so comparisons with their results and the phylogeny presented here is problematical. The Sibley and Ahlquist "tapestry" differs in that shags are intermixed with cormorants, but parallels my results in distinguishing members of *Microcarbo* from those of *Phalacrocorax* and *Hypoleucos*. It is difficult at present, however, to interpret their technique and results accurately (see Houde 1987), so meaningful comparisons are not yet possible.

## CRANIAL CHARACTERS

Previous avian osteologists have been concerned about problems inherent in using cranial characters (see Woolfenden 1961) that may represent functional accommodations for food gathering, defense, etc., rather than particular evidence of phylogenetic relationship. To test for the possibly confounding effects caused by the integration of cranial characters in this analysis, I analyzed the character subsets separately (i.e., cranial vs. postcranial characters). In general, the cranial and postcranial subsets were congruent with the entire data set. With two exceptions, in both analyses all species were grouped into genera identically as found in the analysis using all characters. Intrageneric relationships were not resolved within most genera in these character subsets, however, and the number of equally parsimonious trees was correspondingly large. Intergeneric relationships in the postcranial analysis (Fig. 6b) were identical to those found in the analysis of all characters except that the Anhingidae, Phalacrocoracinae, and Leucocarboninae were resolved only to a polytomy. The analysis employing exclusively cranial characters (Fig. 6a) produced a much different topology than in the other analyses.

Here, all except two species assignments (*C. perspicillatus, N. verrucosus*) were preserved, but generic relationships differed somewhat from the analysis using all characters. Although the order of genera is preserved within subfamilies, the Phalacrocoracinae are paraphyletic using this subset, and the primitive shags (*Leucocarbo* spp.) are polyphyletic.

It appears that the head is prone to convergence as earlier workers surmised, and postcranial characters are less prone to convergence. An analysis using cranial characters alone will allow only generic assignment for most taxa of cor-
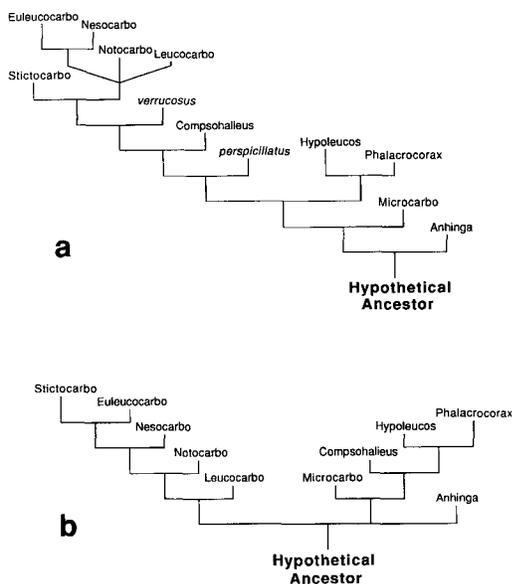
FIGURE 6. Strict consensus trees of segregated character analysis. (a) Cranial characters only ($n = 100$, normalized CF = 0.771, Rohlf's CI = 0.860, length = 86). Species relationships are polytomic, but generic assignments are unchanged from that shown in Figures 1–5, with the exception that *C. perspicillatus* and *N. verrucosus* are unassigned. (b) Postcranial characters only ($n = 100$, normalized CF = 0.771, Rohlf's CI = 0.686, length = 132). Species relationships are polytomic only in *Notocarbo* and *Euleucocarbo,* and all generic assignments are unchanged from that shown in Figures 1–5.

morants and shags. On the other hand, an analysis employing only postcranial characters will allow a fairly accurate generic assignment, and interspecific relationships will be resolved in selected genera (e.g., *Hypoleucos, Compsohalieus, Microcarbo, Nesocarbo, Stictocarbo*). Full resolution will obtain only in using a full complement of characters.

## HOMOPLASY

Considerable convergence and reversal of character states is evident in the tree (Figs. 1–5) and by the consistency of character change (Appendix 1). The extent to which some of these are related to errors in assessing homology is open to interpretation since anatomical studies in this family are rare and restricted to only a few taxa. The majority of convergences and reversals are associated with probable adaptations for flight and feeding (see Stolpe 1932, Owre 1967), and most involve the wing elements (56, 64, 68, 79), sternum, quadrate, and mandible (6, 13, 21, 38, 41,

49). Some of these characters co-occurred, possibly indicating functional adaptations to common ecological problems. This effect is particularly notable in comparisons between taxa, e.g., *Anhinga* and *Euleucocarbo* (83, 100), *Phalacrocorax* and *Microcarbo* (14, 45, 102, 116), and are supported in many cases by ecological associations (Fjeldså 1981, 1985).

Reversals were just as numerous, and perhaps are more problematic. In some cases of reversal (2, 13, 31, 40, 98, 124), the character change involved only a few taxa at a time, often as an autapomorphic condition. Such characters probably reflect a simple, readily activated genetic mechanism, as may be the case for many of the plumage characters of the shags (cf. Baker 1973, Jefferies and Parslow 1976, Birkhead 1984). The complex of repeated reversal of character states as evident within the Leucocarboninae (e.g., 6, 14, 100, 102, 107, 110, 116, 130) are more perplexing, although some seem amenable to biogeographic or ecological explanation (Siegel-Causey, unpubl.).

## PLUMAGE PATTERNS

Plumage patterns in seabirds have been hypothesized to be adaptive for thermoregulation (Hamilton and Heppner 1967, Heppner 1970), social communication (Armstrong 1971, Ward and Zahavi 1973), reproductive isolating mechanisms (Pierotti 1987), and foraging efficiency (Simmons 1972, Siegfried et al. 1975). The most recent scrutiny has been directed towards the latter two areas.

Pierroti (1987) examined the relationship between bill, face, and foot color among shags and cormorants grouped by areas of potential breeding sympatry to investigate whether external coloration served to reduce interspecific hybridization. If hybridization between species is more likely than that between members of different genera, as his study assumed, then the hybridization potential was overestimated because only a single genus was used for the family Phalacrocoracidae (e.g., his table 4, groups 2–5). Questions of rank aside, prereproductive isolating mechanisms such as incompatible courtship behavior, size, nesting and breeding preferences, etc., may have evolved much earlier before present species ever bred sympatrically.

Cairns (1986) surveyed the plumage color in 61 species of pursuit-diving seabirds, and postulated adaptive significance only in reference to

foraging efficiency. If the Phalacrocoracidae use plumage as a means to reduce detection by prey, then all-black species should feed near the bottom, white-bellied species near the top of the water column, and those with intermediate patterns (e.g., gray or light brown) highest of all. In contrast to such functional explanations, it can be useful to examine plumage patterns phylogenetically.

Cormorants (Phalacrocoracinae) are entirely black and feed near the bottom, or near the 1% incident light level (van Dobbin 1952, Ainley 1984, Cairns 1986, Härkönen 1988). The exception, *M. melanoleucos*, is polymorphic with some populations having white abdomens, and is believed to feed on shoaling sprat in the upper water layers (Falla and Stokell 1945, Thomson and Morley 1966). The relation of plumage color to feeding habitat, predicted by Simmons (1972), is not supported in the Leucocarboninae.

Shags have a greater diversity of plumage types than do cormorants. Two species of guano shags (*L. nigrogularis, L. capensis*) are entirely black, and feed in a similar manner as do cormorants but higher in the water column (Gallagher and Woodcock 1980, Furness and Cooper 1982). Most other shags (*L. bougainvillii, Notocarbo* spp., *Nesocarbo* spp., *Euleucocarbo* spp.) are black with white abdomens, and feed within the water column from benthic to surface layers (Murphy 1936, Kooyman et al. 1971, Serventy et al. 1971, Duffy 1983). The cliff shags vary in plumage, from black with white abdomens (*S. magellanicus*), to all-black (*S. aristotelis, S. pelagicus, S. urile*), to light gray (*S. gaimardi, S. punctatus, S. featherstoni*). Less is known about their feeding habits, but they appear to have broad preferences in feeding similar to other shags (Falla and Stokell 1945, Lack 1945, Cawkell and Hamilton 1961, Ainley et al. 1981). In shags, plumage patterns track the phylogeny, with the most primitive taxa being entirely black, the blue-eyed shags (s.l.) with white abdomens, and the most derived cliff shags with gray plumage. In the Leucocarboninae, functional adaptation such as camouflage seems less important in determining plumage patterns than does phylogenetic history.

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# APPENDIX 1

## DESCRIPTION OF CHARACTERS

The 137 characters used in this analysis are numbered and grouped anatomically. Character states are lettered and correspond to the changes shown in Figures 2–4. Plesiomorphic conditions are designated "a" and derived character states are ordered alphabetically. Character transformation series were assumed linear; characters followed by "U" were analyzed as unordered. References indicate depictions of characters, but most are illustrated without identification. Taxa with problematic state determinations are listed in parentheses after the corresponding character. Consistency indices (CI) follow each character. Anatomical terminology follows Howard (1929) and Owre (1967).

### SKULL

1. Temporal crests: (a) separated at midline; (b) meet sagittally. CI = 0.5.
2. Temporal and nuchal crests: (a) separated at midline by sagittal crest; (b) meet sagittally, without sagittal crest. (Ono 1980: fig. 1–3a) CI = 0.05.
3. Sagittal crest: (a) produced at midline; (b) absent or obsolete. CI = 0.5.
4. Postorbital process: (a) simple and small; (b) excavated posterolaterally. (Shufeldt 1902: pl. VI, fig. 25) CI = 0.33.
5. Postorbital process: (a) produced into triangular tuberosity; (b) connected by strong lateral shelf to attachment of M. protractus pterygoideus. (Shufeldt 1902: pl. IV, fig. 14) CI = 0.5.
6. Second postorbital (temporal) process: (a) absent or miniscule; (b) prominent, oriented on dorsoventral surface; (c) prominent, oriented on lateralmost surface. (Dullemeijer 1951a: fig. 1b) CI = 0.4 (variable in *nigrogularis*).
7. Nasal prominence: (a) proximalmost width is greater than half the width of the ventral surface of maxilla; (b) is less than half the width. (Ono 1980: fig. 1–2,–3) CI = 1.0.
8. Nasal shelf of premaxillary: (a) dorsally convex; (b) excavated; (c) planar. CI = 1.0. U
9. Maxillary: (a) nostril groove superficial; (b) deeply excavated. (Pycraft 1898: pl. 8, fig. 3) CI = 0.33.
10. Cranium: (a) approximately long as deep; (b) dorsoventrally compressed. (Ono 1980: fig. 1–2,–3) CI = 1.0.
11. Frontal: (a) preorbital length is subequal to width; (b) length is much greater than sagittal width. CI = 0.5.
12. Nasal gland depression on ventral surface of frontal: (a) small, barely extending into orbit; (b) moderate, not longer than half the length of the frontal; (c) large, reaching posterior margin of orbit. (Technau 1936: figs. 14 and 23) CI = 0.5.
13. Nasal gland depression: (a) shallow; (b) strongly excavated. CI = 0.5.
14. Nasal gland depression: (a) medially restricted to midline; (b) extends laterally to edge of orbit. (Technau 1936: pl. IV, fig. 2) CI = 0.25.
15. Nasal gland depression: (a) posterior margin linear; (b) posterior margin distinctly serrate. (Siegel-Causey, in press) CI = 1.0.
16. Mesethmoid: (a) unfenestrated; (b) fenestrated by one or more foramina. (Shufeldt 1902: pl. IV) CI = 0.5.
17. Prefrontal (lachrymal) process of mesethmoid: (a) with posterior and/or anterior accessory flanges; (b) without accessory flanges. (Shufeldt 1888: fig. 1) CI = 1.0.
18. Prefrontal (lachrymal) process of mesethmoid: (a) simple, unconnected; (b) superiorally connected to internal surface of orbit by strong lateral flange. (Pycraft 1898: Pl. 8, fig. 3) CI = 1.0.
19. Prefrontal (lachrymal) process of mesethmoid: (a) anterior surface normally produced, often into a thin spine; (b) broadly produced into a triangular projection. CI = 1.0.
20. Palatine process of prefrontal (lachrymal): (a) anteroventral surface produced; (b) surface excavated into distinct cup; (c) ventral surface deeply excavated. CI = 1.0.
21. Attachment of M. depressus mandibulus: (a) by distinct fossa; (b) laterally produced. (Owre 1967: fig. 50) CI = 0.5.
22. Attachment of M. protractus pterygoideus: (a) fossa emarginate; (b) fossa with strongly produced anterior ridge. CI = 1.0.
23. Attachment of M. rectus capitus: (a) posterior; (b) anterior to vagus foramen. (Shufeldt 1902: pl. VI, fig. 29) CI = 1.0 (variable in *atriceps*).
24. Attachment of M. pterygoideus ventralis fasciculus: (a) oriented in line with lateral edge of basitemporal plate; (b) oriented sagittally to lateral edge. (Owre 1967: fig. 52) CI = 1.0.
25. Eustachian canal: (a) lateralmost margin of anterior edge closed or nearly so; (b) lateralmost margin is broadly open. (Cracraft 1985: fig. 2) CI = 0.5.
26. Basitemporal plate: (a) lateral edge between eustachian canal and attachment of M. rectus capitus not prominent; (b) lateral edge is strongly produced. (Dullemeijer 1951c: fig. 19) CI = 1.0.
27. Foramen trigeminalis prooticus: (a) posterior; (b) anterior to upper tympanic recess. (Saiff 1978: fig. 2) CI = 0.5 (variable in *Anhinga*).
28. Foramen trigeminalis prooticus: (a) smaller; (b) larger than upper tympanic recess. CI = 0.5 (variable in *Anhinga*).
29. Upper tympanic recess: (a) open; (b) with accessory transverse strut. CI = 1.0.
30. Upper tympanic recess: (a) extends between quadrate articular surfaces; (b) restricted to posterior margin of articular surfaces. (Saiff 1978: fig. 2) CI = 1.0.
31. Palatine: (a) with well-defined lateral angles; (b) are laterally rounded. (Cottam 1957: fig. 1c) CI = 0.5.
32. Palatine: (a) distinctly narrowed posteromedially into abrupt neck at pterygoidal articulation; (b) pterygoidal articulation is broad. (Shufeldt 1902: pl. VI, figs. 27 and 29) CI = 1.0.

33. Palatine: (a) articulate simply with pterygoids; (b) with strong posterodorsal process. CI = 1.0.

34. Palatine: (a) ventral surface planar; (b) strongly concave. (Pycraft 1898: pl. 7, fig. 3) CI = 1.0.

35. Supraoccipital condyle (articulation of occipital style): (a) anterior; (b) posterior to occipital condyle. CI = 0.5.

QUADRATE

36. Quadrate: (a) pneumatic; (b) apneumatic. CI = 0.5.

37. Orbital process: (a) separate from supraorbital process; (b) juncture to shaft is excavated medially into a deep fossa bounded by a strong ridge running superiorly to supraorbital process. (Dullemeijer 1951b: fig. 12) CI = 1.0.

38. Supraorbital process: (a) reduced or obsolete; (b) strongly produced. (Lowe 1926: fig. 3) CI = 0.5.

39. Supraorbital process: (a) conical; (b) lateral shelf. CI = 1.0.

MANDIBLE

40. Caudal fossa: (a) entire; (b) bisected by distinct vertical ridge. (Dullemeijer 1951b: fig. 16) CI = 0.5.

41. Attachment of M. adductus mandibulae externus profundus: (a) absent, reduced, or indistinct; (b) produced into robust tuberosity on dorsomedial surface of external articular process. (Owre 1967: fig. 54d) CI = 1.0.

42. Attachment of M. adductus mandibulae externus superficialis: (a) absent, reduced, or indistinct; (b) expressed as strong transverse ridge. (Dullemeijer 1951a: fig. 3b) CI = 1.0.

43. Attachment of M. adductus mandibulae internus pterygoideus: (a) reduced or present as indistinct impression on ventromedial surface of prearticular; (b) impression is deeply excavated; (c) impression deeply excavated and bilobed. (Dullemeijer 1951a: fig. 9b) CI = 1.0.

44. Attachment of M. adductus mandibulae internus pterygoideus: (a) posterodorsal edge with normal margins; (b) posterodorsal edge produced into strong ridge. CI = 1.0.

45. Attachment of M. adductus mandibulae internus pterygoideus: (a) anteriormost insertion is planar; (b) anteriormost insertion is into distinct fossa, bounded by strong dorsal ridge. CI = 0.5.

46. Fossa aditus: (a) greatly reduced in size, smaller than oval crista of coronoid process, restricted to upper third of prearticular; (b) larger than oval crista, occurs in lower half of prearticular. (Dullemeijer 1951a: fig. 9a) CI = 1.0.

47. Internal attachment of M. adductus mandibulae pseudotemporalis in fossa aditus: (a) indistinct or absent; (b) present as distinct line. CI = 1.0.

48. Attachment of M. adductus mandibulae internus pseudotemporalis: (a) present as indistinct impression; (b) strongly produced. CI = 1.0.

49. Attachment of M. adductus mandibulae internus pseudotemporalis: (a) rugose ridge; (b) robust ledge. (Dullemeijer 1951a: fig. 9b) CI = 0.33 (variable in *Anhinga*).

50. Attachment of M. adductus mandibulae internus pseudotemporalis: (a) very small; (b) subequal to length of ventral external opening of fossa aditus; (c) greater in length than external opening of fossa aditus. (Owre 1967: fig. 54b) CI = 0.67 (variable in *Anhinga*).

51. Attachment of M. adductus mandibulae internus pseudotemporalis: (a) distinct from external opening of fossa aditus; (b) connects to external opening. (Dullemeijer 1951a: fig. 9b) CI = 1.0.

52. Insertion of M. depressus mandibulus: (a) lateral insertion slightly excavated, dorsal insertion indistinct; (b) lateral insertion convex, dorsal insertion robust. CI = 0.5.

53. Dorsal mandibular groove: (a) arises posteriad to medial mandibular groove; (b) arises subequally with medial mandibular groove. CI = 1.0.

54. Symphysis: (a) accessory bone strongly produced into commissure; (b) accessory bone does not reach into commissure. (Ono 1980: fig. 2) CI = 0.5.

CORACOID

55. Anterior intramuscular line: (a) changes direction below level parallel with superior edge of sternocoracoidal process; (b) changes direction in line with the sternocoracoidal process; (c) changes direction above sternocoracoidal process. (Ono 1980: fig. 4) CI = 1.0.

56. Anterior intramuscular line: (a) intersects sternal facet nearest internal distal angle; (b) intersects sternal facet nearest sternocoracoidal process. (Lambrecht 1933: fig. 104) CI = 0.5.

57. Subfurcular angle: (a) narrow, less than 90°; (b) broad, greater than 90°. CI = 0.5.

58. Subfurcular fossa: (a) reduced or absent; (b) deeply excavated. CI = 1.0.

59. Attachment of M. supracoracoideus: (a) planar; (b) excavated into distinct fossa, immediately adjacent to acrocoracoid surface; (c) excavation broad. (Owre 1967: fig. 12) CI = 1.0 (variable in *Anhinga*).

60. Brachial tuberosity: (a) interior margin simple; (b) interior margin produced into ridge superior to attachment of M. supracoracoideus; (c) interior margin rugose. CI = 1.0 (variable in *Anhinga*). U

61. Brachial tuberosity: (a) normally produced; (b) very deep scar between it and glenoid facet. CI = 1.0.

62. Accessory fossa: (a) absent, reduced, or indistinct; (b) deep, subcircular pit just superior to attachment of M. supracoracoideus; (c) excavation ovoidal and shallow. (Baumel et al. 1979: fig. 6b) CI = 1.0. U

63. Procoracoid: (a) entire; (b) bisected by irregular canal; (c) cleaved into two separate prominences. CI = 1.0.

HUMERUS

64. Ligamental furrow: (a) does not reach head; (b) distinctly notches head. CI = 0.5.

65. Ligamental furrow: (a) entire length of equal depth; (b) lateralmost part excavated into pit. CI = 1.0.

66. Ligamental furrow: (a) mesial margins simple; (b)

mesial margin marked by strongly produced crest. (Ono 1980: fig. 7) CI = 1.0.

67. Deltoid shaft: (a) medioproximal surface concave; (b) medioproximal surface strongly convex. CI = 1.0.

68. Deltoid shaft: (a) lateroproximal surface concave; (b) lateroproximal surface more or less convex. CI = 0.33.

69. Deltoid shaft: (a) laterodistal surface concave; (b) laterodistal surface strongly convex. CI = 1.0.

70. Median crest: (a) linearly joins deltoid shaft; (b) strongly indented at junction with deltoid shaft. (Ono 1980: fig. 7) CI = 0.5.

71. Bicipital crest: (a) distal aspect is smoothly curved; (b) distal aspect sharply indented. CI = 1.0.

72. Bicipital furrow: (a) surface planar; (b) with strong lateral ridge. CI = 1.0.

73. Bicipital furrow: (a) normally indented; (b) extremely excised. CI = 1.0.

74. Capital groove: (a) entire length of equal depth; (b) transverse ridge forms deep pit proximalmost to head. (Ono 1980: fig. 7) CI = 1.0.

75. Capital groove: (a) excised, open at distal and proximal ends; (b) excavated, closed by distal and proximal ridges. CI = 1.0 (variable in *Anhinga*).

76. Pneumatic fossa: (a) internal surface apneumatic; (b) distinctly pneumatic. CI = 1.0.

77. Pectoral attachment: (a) angle between it and deltoid crest greater than 45°; (b) less than 45°. CI = 1.0. (variable in *atriceps*)

78. External tuberosity: (a) distal surface planar; (b) distal surface deeply incised into groove. CI = 1.0.

79. Ectepicondyle: (a) ligamental furrow very small; (b) thin and shallow; (c) wide and deep. CI = 0.29. (variable in *Anhinga*)

80. Attachment of M. coracobrachialis posterior: (a) reduced or indistinct; (b) marked by deep pit. (Owre 1967: fig. 13) CI = 1.0 (variable in *Anhinga*).

81. Attachment of M. proscapulohumerus: (a) reduced or indistinct; (b) produced into prominent tuberosity. (Owre 1967: fig. 13) CI = 1.0.

82. Brachialis impression: (a) reduced or indistinct; (b) deeply excised. (Owre 1967: fig. 13) CI = 0.5.

83. Brachialis impression: (a) strong ventral ridge near impression of supracoracoideus; (b) ventral ridge absent. (Owre 1967: fig. 14) CI = 0.5.

ULNA

84. External condyle: (a) simple; (b) with strong proximally produced ridge. (Ono 1980: fig. 8) CI = 1.0.

85. Attachment of M. bicipitus: (a) separate; (b) connects brachialis impression by strong ridge. CI = 1.0.

86. Humero-ulnar depression: (a) small, shallow; (b) broad and deeply excised; (c) narrow and deeply excised. (Ono 1980: fig. 8) CI = 1.0.

87. Attachment of M. scapulatricipitis: (a) shallow or indistinct; (b) deeply excavated. (Owre 1967: fig. 15b, "triceps, scapular head") CI = 1.0.

88. Attachment of anterior articular ligament: (a) subquadrate; (b) foreshortened proximally and

distally into distinct triangular shape. (Baumel et al. 1979: fig. 9a) CI = 1.0.

CARPOMETACARPUS

89. Metacarpus II: (a) distal tuberosity absent, reduced, or obsolete; (b) tuberosity strongly produced. (Ono 1980: fig. 10) CI = 1.0 (variable in *Anhinga*).

90. Metacarpus III: (a) anterior carpal fossa absent, reduced, or indistinct; (b) fossa deeply excavated. CI = 0.5 (variable in *Anhinga*).

91. Metacarpus III: (a) proximal width less than half the width of metacarpus II; (b) proximal width greater than half the width of metacarpus II. CI = 1.0 (variable in *nigrogularis*).

92. Internal ligamental fossa: (a) nearly emarginate; (b) proximalmost margins deeply excised. CI = 1.0.

93. Internal ligamental fossa: (a) surface just proximal is planar; (b) surface just proximal marked by deep fossa. CI = 1.0.

94. Pisiform process: (a) separate; (b) connected to pollical facet by strong proximal crest at midline. (Ono 1980: fig. 10) CI = 1.0.

STERNUM

95. Sternal plates: (a) angle with carina greater than 90°; (b) at most 90°. CI = 0.50.

96. Ventral manubrial spine: (a) small or absent; (b) strongly produced. CI = 0.33.

97. Ventral manubrial spine: (a) internal surface planar; (b) concave; (c) convex. (Shufeldt 1902: pl. VI, fig. 30) CI = 1.0 (variable in *Anhinga*). U

FURCULA

98. Attachment of M. rhomboideus superficialis: (a) crest is absent, reduced, or indistinct; (b) crest is strongly produced. (Owre 1967: fig. 11d) CI = 0.5.

99. Attachment of M. rhomboideus superficialis: (a) crest extends from anterior surface to furcular angle; (b) crest does not reach furcular angle; (c) crest indistinct or obsolete. (Ono 1980: fig. 3) CI = 0.67.

100. Medial surface of furcular shaft proximal to coracoidal facet: (a) surface of shaft convex; (b) surface concave or excavated. (Baumel et al. 1979: fig. 6a) CI = 0.25 (variable in *Anhinga*).

101. Hypocleidus: (a) strong dorsomedial ridge; (b) ridge absent. CI = 0.5.

102. Symphysis: (a) internal aspect concave; (b) internal aspect expanded mesially into hollow cup. CI = 0.33.

103. Furcular process: (a) normally produced; (b) expanded mesially into shelf. CI = 1.0.

SCAPULA

104. Acromion: (a) inferolateral surface planar; (b) inferolateral surface strongly produced into hook. CI = 1.0.

105. Attachment of M. tensor patagialis brevis: (a) reduced, absent, or indistinct; (b) strongly produced into robust tuberosity. (Ono 1980: fig. 5) CI = 0.5.

PELVIS

106. Postacetabular elements: (a) 8; (b) 9. (Shufeldt 1902: pl. V, fig. 22) CI = 1.0.

107. Posterolateral impression of M. externus iliofibularis: (a) lateral scar reduced, less than one intervertebral foramen in length; (b) lateral scar robust, at least one intervertebral foramen in length; (c) lateral scar robust, at least one intervertebral foramen in length. (Stejneger and Lucas 1889: pl. III, fig. 2) CI = 0.67.

108. Posterolateral impression of M. externus iliofibularis: (a) lateral scar separate; (b) lateral scar connected to strong posterior scar. (Stejneger and Lucas 1889: pl. III, fig. 2) CI = 1.0.

109. Posterolateral impression of M. externus iliofibularis: (a) mesial scar absent or reduced; (b) mesial scar connects anterior scar. CI = 1.0.

110. Intramuscular line of M. iliacus preacetabulae: (a) arises on posterior edge of preacetabulum; (b) arises on lateral edge of preacetabulum. (Stejneger and Lucas 1889: pl. III, fig. 2) CI = 0.25.

111. Antitrochanteric ilium: (a) planar; (b) ventrally produced. CI = 1.0.

FEMUR

112. Attachment of M. ischiofemoralis: (a) lateral impression is reduced; (b) impression strongly produced giving sharp angularity to posterolateral femoral surface. (Owre 1967: fig. 40a bottom) CI = 0.33.

113. Attachment of M. iliotrochanter: (a) impression is reduced or indistinct; (b) impression deeply excavated. (Owre 1967: fig. 40a bottom) CI = 1.0.

114. Attachment of M. iliotrochanter: (a) impression is broad and subcircular; (b) impression is very narrow. (Ono 1980: fig. 12) CI = 1.0.

115. Attachment of M. iliotrochanter: (a) impression is oriented transversely on femoral surface; (b) impression runs in superior–inferior orientation. CI = 1.0.

116. Attachment of M. flexis perforatus digitalis III: (a) planar above internal condyle; (b) deeply excavated above internal condyle. (Owre 1967: fig. 40b bottom) CI = 0.33.

117. Attachment of M. flexis perforatus digitalis III: (a) superior impression is reduced or planar; (b) superior impression is deeply excavated along shaft. CI = 1.0.

118. Attachment of M. femoritibialis internus: (a) anterior intramuscular impression reduced or planar; (b) intramuscular impression is deeply excavated. (Owre 1967: fig. 40d bottom) CI = 1.0.

119. Attachment of M. iliacus iliotrochanteris medialis: (a) impression is reduced or planar; (b) impression is produced into robust tuberosity. (Owre 1967: fig. 40a bottom) CI = 1.0.

120. Intramuscular line between M. flexis perforatus digitalis III and IV: (a) reduced or indistinct; (b) produced into rugose crest. (Owre 1967: fig. 40b bottom) CI = 1.0.

121. Internal condyle: (a) superiomedial fossa shallow, emarginate; (b) fossa deeply excavated, bounded by sharp crests. CI = 1.0.

122. Flexor attachment on external condyle: (a) produced medially; (b) produced laterally. CI = 1.0.

123. External condyle: (a) medial prominence broad and rounded; (b) medial prominence produced into thin blade. CI = 1.0.

124. External condyle: (a) medial and lateral prominences separate; (b) prominences connected by transverse ridge causing a deep pit. CI = 0.5.

125. External condyle: (a) rotular groove shallow; (b) rotular groove wide and deep; (c) rotular groove narrow and deep. (Ono 1980: fig. 12) CI = 1.0.

126. External condyle: (a) internal surface broad and rounded; (b) internal surface distinctly narrowed. CI = 1.0.

127. External condyle: (a) superior surface shallow or planar; (b) superior surface excavated into fossa. CI = 1.0.

128. Trochanter: (a) anterior angle distinct; (b) anterior angle indistinct, curvilinear. (Ono 1980: fig. 12) CI = 1.0.

TIBIOTARSUS

129. Attachment of M. flexis cruris lateralis + medialis: (a) mesial impression reduced or planar; (b) mesial impression strongly produced. (Owre 1967: fig. 41) CI = 1.0.

130. Internal articular notch (incisura tibialis): (a) angle is broad, greater than 90°; (b) angle is deep, subequal to 90°. (Baumel et al. 1979: fig. 13b) CI = 0.25.

131. Plantaris fossa: (a) shallow; (b) excavated. (Ono 1980: fig. 13) CI = 0.25.

132. Supratendinal bridge: (a) inferior and superior margins subparallel; (b) margins medially constricted into hourglass shape. CI = 1.0.

133. Outer cnemial crest: (a) distolateral process weakly produced into a ridge; (b) strongly produced distally into robust hook. CI = 1.0.

TARSOMETATARSUS

134. Trochlea metatarsus II: (a) plantar curve simple; (b) strong medioplantar process extends distally. (Ono 1980: fig. 14-3b) CI = 1.0.

135. Trochlea metatarsus III: (a) dorsal curve simple; (b) strongly produced dorsally. (Ono 1980: fig. 14-1c) CI = 1.0.

136. Distal accessory foramen: (a) with external opening; (b) with internal opening into distal foramen. CI = 0.5.

RHAMPHOTHECA

137. Terminal end: (a) linear, pointed; (b) uncinate, sharply hooked. CI = 1.0.

APPENDIX 2. Data matrix of character state codings of 35 taxa of Phalacrocoracidae, *Anhinga* spp., and hypothetical ancestor (hypanc). Character state numbers and codings refer to characters and states described in Appendix 1; codings are as follows: 0 = a, 1 = b, 2 = c, 9 = missing, p = polymorphic.

| Taxon | Character number | | | | | | |
|---|---|---|---|---|---|---|---|
| | 10 | 20 | 30 | 40 | 50 | 60 | 70 |
| 1. **hypanc** | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 |
| 2. *Anhinga* **spp.** | 1000000000 | 0000000000 | 000000pp00 | 0000000000 | 0000000pp | 0000000000 | 0000000000 |
| 3. *africanus* | 0001000100 | 1000000000 | 1000001100 | 0000000000 | 1000010001 | 0001201100 | 0001010000 |
| 4. *coronatus* | 0001000100 | 1000000000 | 1000001100 | 0000000000 | 1000010001 | 0001211100 | 0001010000 |
| 5. *pygmaeus* | 0001000100 | 1000001000 | 1000001100 | 0000000000 | 1000010001 | 0001211100 | 0001000000 |
| 6. *niger* | 0001000100 | 1000001000 | 1000001100 | 0000000000 | 1000010001 | 0001211100 | 0001000000 |
| 7. *melanoleucos* | 0001000100 | 1000001000 | 1000001100 | 0000000000 | 1000010001 | 0001211100 | 0001000000 |
| 8. *perspicillatus* | 0011020000 | 1100000000 | 0000001100 | 0000000000 | 1000010001 | 0000100000 | 1000000100 |
| 9. *penicillatus* | 0011020000 | 1100000000 | 0000100000 | 0000000000 | 1000000001 | 0000100000 | 0000000100 |
| 10. *harrisi* | 0011020000 | 1100110000 | 0000100000 | 0000000000 | 1000001011 | 0000100000 | 0000000100 |
| 11. *fuscescens* | 0011020000 | 1101110000 | 0000100000 | 0000000000 | 1000000011 | 0000100000 | 0100000000 |
| 12. *neglectus* | 0011020010 | 1101110000 | 0000110000 | 0000000000 | 1000000011 | 0000100000 | 0000000000 |
| 13. *olivaceus* | 0011001000 | 1100000000 | 0000000010 | 0000000000 | 1000000010 | 1000101000 | 0000000000 |
| 14. *auritus* | 0011001000 | 1100000000 | 0000000000 | 0000000000 | 1000000010 | 1000101000 | 0000000000 |
| 15. *varius* | 0011001000 | 1100000000 | 0000010000 | 0000000000 | 1000000010 | 1000101000 | 0000000000 |
| 16. *sulcirostris* | 0011001000 | 1100000100 | 0000100000 | 0000000000 | 1000000010 | 1000101000 | 0000001000 |
| 17. *capillatus* | 0011001000 | 1100000000 | 1000000001 | 0101000100 | 1000000011 | 0001101000 | 0000001000 |
| 18. *carbo* | 0011001000 | 1200000000 | 1000000001 | 0101000100 | 1000000011 | 0011101000 | 0000001000 |
| 19. *nigrogularis* | 0010010010 | 0011010000 | 0000001100 | 1000000100 | 0000000012 | 0010010010 | 0010000100 |
| 20. *capensis* | 0010010210 | 0011010000 | 0000001100 | 1010000100 | 0000000012 | 0100010010 | 0010000100 |
| 21. *bougainvillii* | 0010010010 | 0011010000 | 0000001100 | 1000000100 | 0000000012 | 0100010010 | 0010000100 |
| 22. *atriceps* | 0010010010 | 0011010012 | 0000001100 | 1000000100 | 0010000012 | 0000010020 | 0010000100 |
| 23. *bransfieldensis* | 0010010010 | 0011010011 | 0000001100 | 0000000100 | 0010000012 | 0000010021 | 0010000100 |
| 24. *georgianus* | 0010010010 | 0011010011 | 0000001100 | 1000000100 | 0010000012 | 0000010021 | 0010000100 |
| 25. *verrucosus* | 0011020000 | 1100010010 | 0000001100 | 1000000100 | 0010000012 | 0000010020 | 0010000100 |
| 26. *campbelli* | 0010110010 | 0010010000 | 0000001100 | 1000100100 | 0010100012 | 0000010020 | 0010000101 |
| 27. *chalconotus* | 0011010010 | 0011010000 | 0000001100 | 1000100101 | 0010100012 | 0110010022 | 0211100100 |
| 28. *onslowi* | 0011010010 | 0011010000 | 0001001100 | 1000100101 | 0010100012 | 0010010020 | 0011000100 |
| 29. *ranfurlyi* | 9999999999 | 9999999999 | 9999999999 | 9999999999 | 9999999999 | 9999010020 | 0011000101 |
| 30. *colensoi* | 0011110010 | 0010010000 | 0001001100 | 1000100101 | 0010100012 | 0010010020 | 0011000101 |
| 31. *magellanicus* | 0190000011 | 0010010000 | 0000001100 | 0000111101 | 0021000012 | 0010010020 | 0010000100 |
| 32. *pelagicus* | 0190000011 | 0110010000 | 0000001100 | 0000011101 | 0110000012 | 0010010020 | 0010000100 |
| 33. *urile* | 0190000011 | 0110010000 | 0000001100 | 0000011101 | 0010000012 | 0010010020 | 0010000110 |
| 34. *aristotelis* | 0010000011 | 0110010000 | 0100001100 | 0000011101 | 0010000012 | 0010010020 | 0020000100 |
| 35. *gaimardi* | 0010000011 | 0110010000 | 0010001100 | 0000001110 | 0010000112 | 0010010020 | 0020000100 |
| 36. *punctatus* | 1010000011 | 0110010000 | 0000001100 | 0000001110 | 0010000012 | 0010010020 | 0020000100 |
| 37. *featherstoni* | 1010000011 | 0110010000 | 0000001100 | 0000001110 | 0010000012 | 0010010020 | 0020000100 |

APPENDIX 2.  Continued.

|  | Character number | | | | | | |
|---|---|---|---|---|---|---|---|
| Taxon | 80 | 90 | 100 | 110 | 120 | 130 | 137 |
| 1. **hypanc** | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000 |
| 2. **Anhinga spp.** | 00000000pp | 0110000000 | 000000p00p | 0000000991 | 0000000000 | 0000000000 | 0000000 |
| 3. *africanus* | 0000000000 | 0000010000 | 0100011100 | 1010010010 | 0100000100 | 0000000000 | 0000011 |
| 4. *coronatus* | 0000000000 | 0000010000 | 0100011100 | 1010010010 | 0100000100 | 0000000000 | 0000011 |
| 5. *pygmaeus* | 1000000000 | 0100010000 | 0100111100 | 1010010010 | 0000000000 | 0000000001 | 0000011 |
| 6. *niger* | 1100000000 | 0000010000 | 0100111000 | 1010010010 | 0000000000 | 0000000000 | 0000011 |
| 7. *melanoleucos* | 1101000000 | 0000010000 | 0100111100 | 1010010010 | 0000000000 | 0000000000 | 0000011 |
| 8. *perspicillatus* | 0000000011 | 0000020001 | 0100091001 | 0000010001 | 0000000000 | 0000000000 | 0000001 |
| 9. *penicillatus* | 0000000021 | 0000020001 | 0100011001 | 0000010001 | 0000000000 | 0000000000 | 0000001 |
| 10. *harrisi* | 0000000021 | 0000020001 | 0100011001 | 0000010001 | 0000000000 | 0000000001 | 0000001 |
| 11. *fuscescens* | 0010000021 | 0000020001 | 0100011011 | 0000010001 | 0000000000 | 0000000001 | 0000001 |
| 12. *neglectus* | 0000000021 | 0001020001 | 0100011011 | 0000010001 | 0000000000 | 0000000001 | 0000001 |
| 13. *olivaceus* | 0000000011 | 0100010001 | 0110011000 | 0000010001 | 0000000000 | 0000000000 | 0000001 |
| 14. *auritus* | 0001000011 | 0101110001 | 1110011000 | 0000010001 | 0000000000 | 0000000000 | 0000001 |
| 15. *varius* | 0000000011 | 0101110001 | 1110011000 | 0000010001 | 0000000000 | 0000001000 | 0000001 |
| 16. *sulcirostris* | 0000000011 | 0100111001 | 1110011000 | 0000010001 | 0000000000 | 0000000000 | 0000001 |
| 17. *capillatus* | 0000000011 | 0000010001 | 0110011000 | 1000010001 | 0000000000 | 0000010000 | 0000001 |
| 18. *carbo* | 0000000011 | 0000010001 | 0110011000 | 1000010001 | 0000001000 | 0000000000 | 0000001 |
| 19. *nigrogularis* | 0000000010 | 0000000000 | 0000000011 | 0000101001 | 0000000000 | 0000200011 | 0000011 |
| 20. *capensis* | 0000000010 | 0000000000 | 0000000010 | 0000101001 | 0001000000 | 0000200011 | 0000011 |
| 21. *bougainvillii* | 0000000010 | 0000000000 | 0000010020 | 0000101001 | 0000000000 | 0000200011 | 0100011 |
| 22. *atriceps* | 0000001010 | 0000000010 | 0000000010 | 0000101000 | 0000010000 | 0000100011 | 0000011 |
| 23. *bransfieldensis* | 0000001020 | 0000000010 | 0000000010 | 0000101000 | 0000010000 | 0000100011 | 0000011 |
| 24. *georgianus* | 0000001020 | 0000000010 | 0000000010 | 0000101000 | 0000010000 | 0000100011 | 0010011 |
| 25. *verrucosus* | 0000001020 | 0000000010 | 0000000010 | 0010002000 | 0000010000 | 0010100011 | 0010011 |
| 26. *campbelli* | 0000011010 | 0000000010 | 0000100010 | 0100002000 | 0010010000 | 0000100011 | 0000011 |
| 27. *chalconotus* | 0000001000 | 0010000090 | 0000100011 | 0100002000 | 0010010000 | 1000100010 | 0000111 |
| 28. *onslowi* | 0000001000 | 0010000010 | 0000100011 | 0100002000 | 0010010010 | 0000100010 | 0000111 |
| 29. *ranfurlyi* | 0000001090 | 0090000090 | 9000100011 | 0100002000 | 0010010000 | 0100100019 | 0000911 |
| 30. *colensoi* | 0000001000 | 0010000010 | 0000100011 | 0100002000 | 0010010000 | 0000100110 | 0000111 |
| 31. *magellanicus* | 0000001010 | 0010000010 | 0000112011 | 0100002100 | 0010000000 | 0001100010 | 0000111 |
| 32. *pelagicus* | 0000001010 | 0010000010 | 0000112011 | 0000002100 | 0010000000 | 0001100010 | 0011111 |
| 33. *urile* | 0000001010 | 0010000010 | 0000112011 | 0000002100 | 0010000001 | 0001100010 | 1001111 |
| 34. *aristotelis* | 0000001020 | 0010000010 | 0000112010 | 0100002101 | 0010000000 | 0001100010 | 0000111 |
| 35. *gaimardi* | 0000001000 | 0010000010 | 0001112011 | 0100002101 | 1111010000 | 0000100010 | 0000111 |
| 36. *punctatus* | 0000001100 | 0010000110 | 0001112011 | 0000002101 | 1110010000 | 0000100010 | 0000111 |
| 37. *featherstoni* | 0000001100 | 1010000010 | 0001112011 | 0000002101 | 1110010000 | 0000100010 | 0000111 |