MONOPHYLY AND PHYLOGENETIC RELATIONSHIPS OF THE PELECANIFORMES: A NUMERICAL CLADISTIC ANALYSIS

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ABSTRACT.—A phylogenetic analysis was undertaken to evaluate the monophyly of the Pelecaniformes and to determine interfamilial relationships within the order. A total of 52 characters was subjected to a numerical cladistic analysis. Pelecaniform monophyly was highly corroborated, with 12 postulated synapomorphies supporting that hypothesis. Within the pelecaniforms, the phaethontids are the sister-group of the remaining families, which are divided into two lineages, the fregatids on the one hand and the pelecanids, sulids, and phalacrocoracids (including anhingids) on the other. Within the latter clade, sulids and phalacrocoracids are each other's closest relatives. This pattern of interfamilial relationships was strongly corroborated by the data, and alternative hypotheses, especially those postulating a close relationship between phaethontids and fregatids, are much less parsimonious.

The study also presents corroborating evidence that pelecaniforms and procellariiforms are sister-taxa, although this hypothesis requires further analysis. Evidence supporting a relationship between pelecaniforms and ciconiiforms is evaluated and considered insufficient to warrant acceptance of that hypothesis at this time.

The hypothesis that the Whale-headed Stork (*Balaeniceps rex*) has a relationship to one or more pelecaniform taxa was investigated and rejected. The characters said to indicate a close relationship are interpreted here to be convergences that arose as mechanical responses to similarities in feeding behavior. *Received 10 January 1985, accepted 16 May 1985.*

THE phylogenetic relationships of the Pelecaniformes have interested systematic ornithologists for many decades [see the detailed review by Sibley and Ahlquist (1972: 65–70)]. The most influential paper in this century probably has been that of Lanham (1947), whose phylogenetic conclusions were based primarily on an analysis of skeletal similarities and differences. He supported the hypothesis of pelecaniform monophyly, with the frigatebirds (Fregatidae) and tropicbirds (Phaethontidae) being sister-groups and related to a lineage composed of all the remaining families. Relationships within the latter clade were postulated to be subdivided into the pelicans (Pelecanidae) on the one hand, and gannets and boobies (Sulidae), cormorants (Phalacrocoracidae), and anhingas (Anhingidae) on the other; the sulids were considered to be the sister-group of the cormorants and anhingas.

Although some systematists have raised doubts about the monophyly of the Pelecaniformes, the families usually have been placed together. This decision has been based almost entirely on a single shared character, namely the totipalmate foot. In assessing relationships within the order, the majority of previous workers have concluded that pelecanids, sulids, phalacrocoracids, and anhingids comprise a natural group. Opinion has been divided, however, regarding the phylogenetic placement of the fregatids and phaethontids, and although some workers have placed them together, most have relegated each to a separate suborder within the Pelecaniformes (e.g. Wetmore 1960, Storer 1971; see Sibley and Ahlquist 1972 for a summary).

With respect to interordinal affinities, most systematists have identified either the Procellariiformes or Ciconiiformes as possible close relatives of the pelecaniforms, but in no case has adequate documentation been provided. Some have noted a close anatomical resemblance between fregatids and diomedeids (Beddard 1898, Lanham 1947, Simonetta 1963), and virtually all who have studied the problem agree that phaethontids are the most aberrant family of the order.

I present evidence supporting the hypothesis that the Pelecaniformes constitute a monophyletic group. Most of the phylogenetic relationships postulated by Lanham (1947) are

confirmed, but the placement of fregatids with phaethontids is not supported by evidence based on an analysis of shared derived characters. Furthermore, using cladistic analysis, much stronger evidence can now be provided to corroborate not only the monophyly of the order but also the interrelationships of the included families. In addition, evidence is presented that suggests a sister-group relationship between the Pelecaniformes and Procellariiformes.

SYSTEMATIC METHODS AND MATERIALS

Using cladistic methodology, hypotheses of monophyly are tested by the parsimonious distribution of postulated shared derived characters, or synapomorphies (Hennig 1966, Eldredge and Cracraft 1980, Nelson and Platnick 1981, Wiley 1981). Hypotheses of synapomorphy usually are erected using the well-known comparative technique of outgroup analysis (Wiley 1975, 1981; Gaffney 1979; Eldredge and Cracraft 1980; Watrous and Wheeler 1981; Farris 1982; Maddison et al. 1984). The argumentation scheme of outgroup analysis takes the following form: If a character (or character state) is shared among two or more ingroup taxa and also is found within postulated closely related outgroups, the character is primitive within the ingroup; if the character is restricted to ingroup taxa, it can be considered to be derived within that ingroup. Various workers have drawn attention to some of the underlying (and often unstated) assumptions of this method, namely, that the ingroup is monophyletic and that the outgroups are actually closely related to the ingroup (see Maddison et al. 1984 for a detailed discussion, and Raikow 1982 for an example using birds). Thus, the question of ingroup monophyly may be an integral part of the study itself, and relationships among the outgroups and their affinities to the putative ingroup may be uncertain.

One approach to this problem is to begin with a higher-level phylogenetic hypothesis (containing both ingroup and outgroup taxa), whose monophyly is well established, and then document the monophyly of the ingroup by searching for characters unique to those taxa. Raikow (1982), for example, adopted the class Aves as his higher-level taxon, and then assessed the monophyly of the Passeriformes by searching for uniquely derived characters. Monophyly also can be corroborated if characters defining the group are derived but not unique, i.e. if they have been acquired independently in the ingroup and one or more outgroups. Such a conclusion, however, is predicated on acceptance of a phylogenetic hypothesis that is globally parsimonious over both the ingroup and the outgroups (Maddison et al. 1984).

A second approach avoids the problems of accepting prior (working) hypotheses about monophyly and character polarity (Farris 1982, Maddison et al. 1984, Swofford 1984): for a given character-taxon matrix, the most parsimonious network is computed over all taxa using unordered characters (that is, character-states are not polarized and evolutionary transitions are allowed to occur from any one state to any other). Once an undirected tree is generated, it can be rooted using one of several possible conventions, for example by specifying one or more outgroups or by designating a hypothetical ancestral taxon. If the ingroup taxon emerges as a discrete group within the undirected cladogram, its monophyly can be accepted and further tested by succeeding analyses that incorporate hypotheses of character polarity. Methodologically, the use of unordered characters is strictly cladistic because congruence in character-state transitions is being optimized on the tree.

In this analysis undirected trees or networks were computed using the Phylogenetic Analysis Using Parsimony (PAUP) program (version 2.2) of David L. Swofford (University of Illinois, Illinois Natural History Survey). As I will discuss below, the Pelecaniformes emerged as a natural group in the analysis of unordered characters. Accordingly, subsequent analyses on ordered (polarized) characters were undertaken using pelecaniforms as the ingroup. Relationships within the pelecaniforms were investigated by comparisons to outgroup taxa that are frequently considered to be closely related, including the Procellariiformes, Gaviiformes (including grebes, Podicipedidae), and Sphenisciformes (Sibley and Ahlquist 1972; Cracraft 1981, 1982). Ordered trees were rooted by two procedures: first, by specifying spheniscids and/or gaviids as the root, and second, by constructing a hypothetical common ancestor (Kluge and Farris 1969, Farris 1970, Lundberg 1972, Maddison et al. 1984) based on comparisons with these outgroups and with many nonpasserine birds as well.

Parsimony is the single most important philosophical principle underlying phylogenetic analysis (Farris 1982, 1983). According to this principle, ad hoc hypotheses of homoplasy (parallelism, reversal) are minimized, and congruence of character distributions is maximized. The principle does not assume, or assert, that the process of character transformation is itself "parsimonious" (whatever that term might mean in this context), only that our choice among competing scientific hypotheses must be based on an objective and rational criterion. Parsimony is that criterion. Thus, in the analyses discussed here, the number of character transformations is the entity being minimized, with optimization procedures assigning internode character states so as to minimize the f-values (Farris 1972). Naturally, if the data set were changed, either by adding, subtracting, or recoding characters or taxa, tree lengths could be altered. The consistency index for a tree (Kluge and Farris 1969) is a measure of the relative amount of

TABLE 1. Matrix for character states of all families included in this study.

Taxa	Characters and character states[a]																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Spheniscidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaviidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Podicipedidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Diomedeidae	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Procellariidae	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0
Hydrobatidae	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	2	0	0	0
Phaethontidae	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Fregatidae	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Pelecanidae	1	0	1	1	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Sulidae	1	1	1	1	1	1	1	2	1	1	1	0	1	1	0	0	0	0	0	1	0	1	0	1
Phalacrocoracinae	2	0	1	1	1	1	1	2	1	1	2	1	1	1	0	1	1	1	1	1	0	1	0	1
Anhinginae	2	0	1	1	0	1	1	2	1	1	2	1	1	1	0	1	1	1	1	1	0	1	0	0
Balaenicipitidae	0	0	1	1	1	1	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1

[a] Characters are numbered according to the sequence in the text. Character-state codes: 0 = primitive; 1, 2 = derived (see text for description of character states.)

homoplasy in the data for a given tree and is simply the total number of steps minus the number of homoplastic transformations divided by the total steps. Thus, an index of 1.00 would indicate the characters of a tree show no reversal or parallel changes.

The evidence presented in this paper consists of characters from skeletal anatomy, external morphology, and behavior. Extensive series of skeletons representing all genera of pelecaniforms and all relevant families of nonpasserines were examined or borrowed from the collections of the Field Museum of Natural History (FMNH), Chicago; the American Museum of Natural History (AMNH), New York; and the Louisiana State University Museum of Zoology (LSU), Baton Rouge. Behavioral characters were taken from the literature (see citations below), and their phylogenetic value was assessed using the above methods. Most of the osteological characters discussed here for the pelecaniforms and procellariiforms are illustrated in Shufeldt (1888, 1902) and Mivart (1878).

Character analysis.—Fifty-two skeletal and behavioral characters were coded (0, primitive; 1, 2, derived) for 13 higher taxa. The complete taxon-character matrix is presented in Table 1. Character polarity within the pelecaniforms was determined by the comparative methods discussed above. The numbers of the following characters are used to identify each character in Table 1, Figs. 6 and 7, and the text.

(1) Mediopalatine processes: 0, not enlarged; 1, enlarged toward the pterygo-palatine joint; 2, present only at the pterygo-palatine joint, lost anteriorly. An enlarged process is absent or nearly so in the Spheniisciformes and Gaviiformes (only slightly developed posteriorly). Most other groups of nonpasserines have processes; in general, however, they do not have processes developed posteriorly near the pterygo-palatine joint (Fig. 1A), and it is this condition that is postulated to be derived here.

(2) Upper tympanic recess: 0, small; 1, greatly enlarged. A relatively small, deep foramen exists in sphenisids, gaviiforms, and most other nonpasserines. A greatly enlarged recess that opens immediately anterior to the quadrate articulation (Saiff 1978; see Fig. 2) is postulated to be derived.

(3) Bony nostrils: 0, large; 1, greatly reduced (Shufeldt 1888: figs. 2, 3, 12, 13). The nostrils are large in gaviiforms, sphenisids, and many nonpasserines.

(4) Rostrum: 0, long nasal groove absent; 1, long groove present. Gaviiforms, sphenisids, and other nonpasserines lack a long groove.

(5) Bill shape: 0, terminal hook absent; 1, hook present (Shufeldt 1888: figs. 2, 13). Gaviiforms, sphenisids, and most other nonpasserines lack a hook.

(6) Supraorbital salt glands: 0, present; 1, absent (Shufeldt 1888: figs. 24, 39, 40, 43). Supraorbital depressions for salt glands are present in procellariiforms (Shufeldt 1888: figs. 2, 3, 12), gaviiforms, and sphenisids.

(7) Quadrate, medial condyle: 0, anterior lip present; 1, anterior lip absent or greatly reduced. A well-developed anterior lip is present in diomedeids, gaviiforms, and sphenisids.

(8) Palatines: 0, unfused (Fig. 1A); 1, fused posteriorly (Fig. 1B); 2, fused throughout length (Shufeldt 1888: fig. 26). The unfused condition is found in all the outgroups and virtually all nonpasserines.

(9) Vomer: 0, present; 1, absent. The vomer is present in some pelecaniforms (Fig. 1), all outgroups, and most nonpasserines.

(10) Maxillopalatines: 0, large; 1, greatly reduced. The maxillopalatines of some pelecaniforms (Fig. 1), all outgroups, and most nonpasserines are large.

(11) Braincase compression: 0, not compressed dorsoventrally; 1, moderately compressed dorsoventrally (Shufeldt 1888: fig. 25); 2, strongly compressed dorsoventrally. The braincase in some pelecaniforms,

TABLE 1. Extended.

													Characters and character states														
25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
1	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	0	1	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
1	0	0	0	1	0	0	1	1	1	1	2	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
1	1	0	0	0	1	0	1	0	2	1	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
1	1	0	1	1	1	0	1	1	2	1	2	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0
1	1	1	2	1	1	1	1	0	2	1	2	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0
1	1	1	2	1	1	1	1	1	2	1	2	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

procellariiforms, the outgroups, and most nonpasserines is not compressed dorsoventrally.

(12) Braincase expansion: 0, relatively foreshortened anteroposteriorly; 1, expanded anteroposteriorly. The braincase is not expanded in some pelecaniforms, the outgroups, or most nonpasserines. Braincase expansion seems to be independent of braincase compression (character 11) because the braincase of sulids is compressed but not expanded.

(13) Quadrate, orbital process: 0, large; 1, moderately to greatly reduced (Shufeldt 1888: figs. 25, 39). The process is large in many pelecaniforms, the outgroups, and most nonpasserines.

(14) Presphenoid sinus, lateral wall: 0, present and large; 1, reduced in size. The lateral wall is present in some pelecaniforms (Fig. 2), the outgroups, and many nonpasserines (see Saiff 1974: 218, fig. 1; 1978: 355).

(15) Presphenoid sinus, posterior end: 0, bony ring absent; 1, bony ring present. The posterolateral end of the lateral wall of the sinus can curve medially to form a bony ring. The ring is absent in diomedeids, gaviiforms, spheniscids, pelecaniforms, and apparently other nonpasserines.

(16) Postorbital processes: 0, present and well developed; 1, poorly developed or absent (Shufeldt 1888: fig. 39). Well-developed postorbital processes are present in virtually all birds, including diomedeids, spheniscids, gaviids, and most other nonpasserines.

(17) Opisthotic processes: 0, directed downward; 1, directed posteriorly. The processes are directed downward in all the outgroups and most nonpasserines.

(18) Occipital style: 0, absent; 1, present. An occipital style is unique to anhingids and phalacrocoracids (Owre 1967: 107–108, 127) and is lacking in all outgroups.

(19) Interorbital septum: 0, present (Shufeldt 1888: figs. 2, 13, 25, 40); 1, absent (Shufeldt 1888: fig. 39). A septum (partially or completely ossified) is present in all outgroups (except grebes) and in most nonpasserines.

(20) Nasal septum: 0, unossified; 1, ossified. The septum is unossified in all outgroups.

(21) External nares: 0, nostrils lateral and not tubular; 1, nostrils lateral and tubular; 2, nostrils located at midline and tubular. The nares are lateral and are not tubular in gaviiforms, spheniscids, pelecaniforms, and other nonpasserines.

(22) Sternum, keel: 0, long and extends nearly entire length of sternal body (Shufeldt 1888: figs. 8, 21); 1, short (posterior portion reduced) and straight, projects strongly anteriorly (Mivart 1878: plates LIX–LXI; Shufeldt 1888: figs. 29, 30). In spheniscids, gaviiforms, and most nonpasserines, the keel is long and does not project relatively far anteriorly.

(23) Sternoclavicular fusion: 0, unfused; 1, fused (Mivart 1878: plates LIX–LXI; Shufeldt 1902: figs. 42, 50, 51). The clavicles and keel of the sternum are unfused in all outgroups and virtually all nonpasserines.

(24) Pelvis, posterior iliac crest: 0, raised and well defined (Shufeldt 1888: figs. 10, 11); 1, not raised and poorly defined (Figs. 3 and 4; Mivart 1878: plates LIX–LXI; Shufeldt 1888: fig. 32). The crest is raised in spheniscids, gaviiforms, and many other nonpasserines.

(25) Pelvis, preacetabular ilium: 0, plane of ilium more or less vertical; 1, plane of ilium markedly more horizontal (Figs. 3 and 4; Mivart 1878: plates LIX–LXI). In all the outgroups, except spheniscids, and in most other nonpasserines, the ilium is more or less vertical.

(26) Pelvis, ilioischiatic fenestra: 0, small relative to postacetabular ilium (Fig. 4A, C); 1, relatively large (Fig. 4B; Mivart 1878: plates LIX–LXI; Shufeldt 1888: figs. 31, 32). The fenestra is relatively small in diomedeids, gaviiforms, spheniscids, and many nonpasserines.

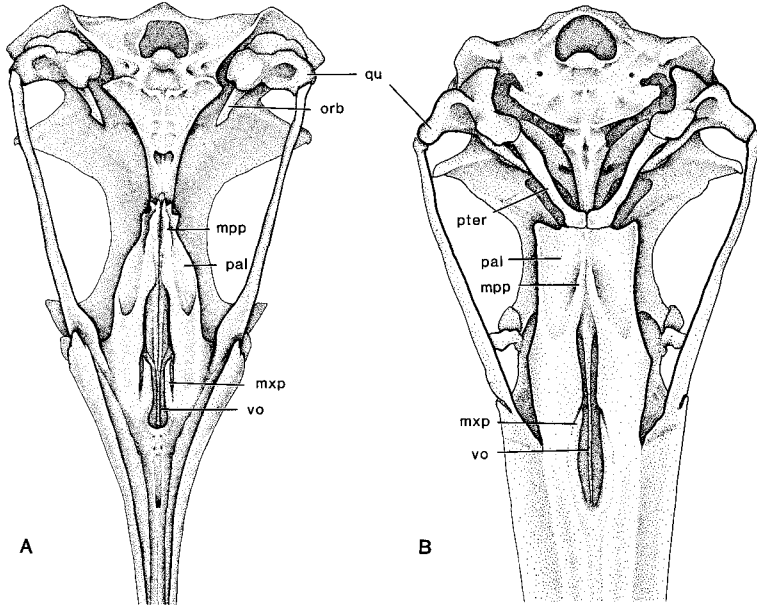(27) Pelvis: 0, broad; 1, narrow, compressed later-

Fig. 1. Ventral view of the skulls of (A) *Phaethon rubricauda* (LSU 81378) and (B) *Fregata minor* (FMNH 104717). Abbreviations: mpp, mediopalatine processes; mxp, maxillopalatines; orb, orbital process of quadrate; pal, palatines; pter, pterygoid; qu, quadrate; vo, vomer.

omedially (Mivart 1878: plate LXI). In some outgroups the pelvis is compressed. Diomedeids, however, and most nonpasserines have a relatively broad pelvis (Fig. 3), which is postulated to be primitive here.

(28) Pelvis, preacetabular ilium: 0, lateral margin not strongly curved; 1, margin strongly curved (Mivart 1878: plate LX); 2, margin very strongly curved (Mivart 1878: plate LXI). The margin is not strongly curved in some (primitive) pelecaniforms and the outgroups (Fig. 3).

(29) Humerus, ligamental furrow: 0, shallow and not extensive internally; 1, deep and extends internally to undercut the humeral head (Fig. 5B). The furrow is shallow and not extensive internally in diomedeids (Fig. 5A), gaviiforms, and many nonpasserines; it is a deep pit in spheniscids but not extensive internally.

(30) Humerus, deltoid crest: 0, well developed; 1, greatly reduced. The crest is well developed in fregatids, phaethontids, diomedeids, and most nonpasserines (Fig. 5), but is reduced in spheniscids and gaviiforms. A well-developed crest is postulated to be primitive within pelecaniforms.

(31) Humerus, entepicondyle: 0, low and blunt; 1, high and bladelike. The entepicondyle is low and blunt in some pelecaniforms, procellariiforms, gaviids, spheniscids, and most nonpasserines (Fig. 5).

(32) Tibiotarsus, internal condyle: 0, notched distally and more or less on same plane as external condyle; 1, greatly enlarged, rounded, and projects

strongly distally relative to external condyle. The internal condyle of the outgroups is notched distally (except in spheniscids) and is more or less on the same plane as the external condyle.

(33) Tarsometatarsus, shape: 0, long relative to hindlimb length; 1, greatly reduced in length relative to hindlimb length (Shufeldt 1902: fig. 4). The outgroups (except spheniscids) and most nonpasserines have relatively long tarsometatarsi (procellariiforms also exhibit some reduction).

(34) Tarsometatarsus, hypotarsus: 0, low and relatively elongate proximodistally, not foreshortened; 1, projects and foreshortened proximodistally; 2, projects strongly posteriorly. The ridge of the outgroups is low and relatively elongate proximodistally.

(35) Foot: 0, not totipalmate; 1, totipalmate. This is a unique condition within birds.

(36) Gular pouch: 0, absent; 1, present but not extensively naked; 2, present and naked. A pouch is absent in the outgroups. Phaethontids have a pouch, but it is covered with feathers and is said to be inconspicuous in life (Gross 1912: 67; Plath 1914), hence the explanation for the belief that it is lacking in this family.

(37) Feeding behavior of young: 0, not fed down gullet of adult (e.g. Bailey 1952: 41); 1, fed down gullet of adult (van Tets 1965: 52). The young of all the outgroups except spheniscids do not feed by sticking their heads down the gullets of the adults.

(38) Prelanding call: 0, absent; 1, present. Pelecan-

iforms have a prelanding call, apparently derived from a Food-begging call (van Tets 1965: 73). This stereotyped behavior is apparently absent in the outgroups.

(39) Nest relief: 0, nest material not exchanged; 1, material exchanged. This stereotyped behavior appears to be absent in phaethontids and the outgroups. Handling of nest materials is not unknown in diomedeids (Bailey 1952: 25), but it apparently involves tossing and not mutual exchange.

(40) Young: 0, hatched downy; 1, hatched naked. In phaethontids and all the outgroups, the young are downy.

(41) Incubation: 0, eggs incubated by body; 1, eggs incubated beneath feet. All outgroups incubate eggs under the body.

(42) Hop display: 0, absent; 1, present. This display is apparently an abbreviated flight movement (van Tets 1965: 25) and presumably is absent from all the outgroups.

(43) Sky-pointing display: 0, absent; 1 present. A sky-pointing display is present during pretakeoff (in *Sula bassanus*) or male advertising (other *Sula*, Phalacrocoracidae, Anhingidae) (van Tets 1965: 27–28). This display presumably is lacking in the outgroups.

(44) "Kink-throating" display: 0, absent; 1, present. This display, in which the throat region is expanded by depression of the hyoid (van Tets 1965: 58–59), is absent in the outgroups.

(45) Humerus, deltoid crest: 0, not strongly triangular in shape, rounded rather than narrowly pointed; 1, triangular in shape, projects to sharp point (Fig. 5). The crest of the outgroups is not triangular or produced to a sharp point.

(46) Quadrate, lateral excavation: 0, not excavated sharply; 1, excavated sharply, especially posterolaterally (Cracraft 1982: 38, fig. 2). Nonpasserine birds, in general, do not have a sharply excavated quadrate (see Cracraft 1982: 38).

(47) Temporal fossa: 0, does not extend to midline; 1, extends to (or nearly to) midline (Cracraft 1982: 38, fig. 2). Most nonpasserines do not have a well-defined temporal fossa that extends to the midline.

(48) Squamosal, quadrate articulation: 0, does not extend laterally as a horizontal platform; 1, extends laterally as horizontal platform with well-marked muscle scar on its lateral side (Cracraft 1982: 38, fig. 2). Nonpasserines generally lack this configuration (although *Pelecanoides* perhaps comes closest).

(49) Pelvis, sacral vertebrae: 0, with well-developed transverse processes; 1, transverse processes very reduced and virtually lacking (Cracraft 1982: 40, fig. 4). Nonpasserines have transverse processes even though they may be reduced somewhat in width in some taxa.

(50) Pelvis, shape: 0, pre- and postacetabular portions more or less same length; 1, preacetabular portion much shorter that postacetabular portion (Cracraft 1982: 40–41, figs. 4, 5). The two portions of the
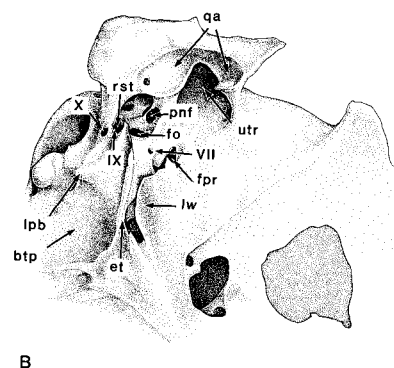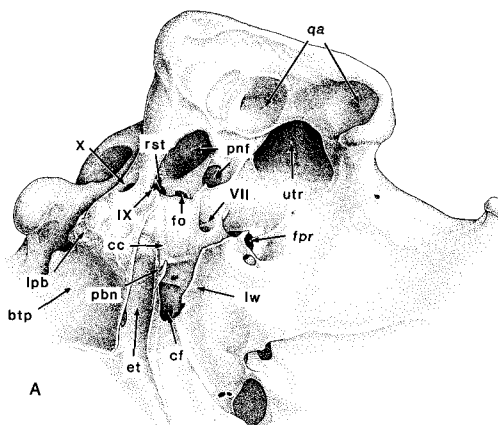

A

B

Fig. 2. Ventral view of the left otic and basitemporal region of (A) *Diomedea irrorata* (FMNH 105001) and (B) *Fregata minor* (FMNH 104717). Abbreviations: btp, basitemporal plate; cc, carotid canal; cf, foramen for carotid artery; et, eustachian tube; fo, fenestra ovalis; fpr, foramen prooticum; lpb, lateral process of basitemporal plate; lw, lateral wall of presphenoid sinus; pbn, parabasal notch for palatine nerve; pnf, pneumatic foramen; qa, quadrate articulations; rst, recessus scalae tympani; utr, upper tympanic recess; VII, facial nerve foramen; IX, notch (or foramen) for glossopharyngeal nerve; X, foramen for vagus nerve.

pelvis are approximately the same length in nonpasserines (Figs. 3 and 4).

(51) Femur, fibular condyle: 0, not enlarged relative to external condyle and not twisted laterally; 1, enlarged and twisted laterally (Cracraft 1982: 42, fig. 6). Other nonpasserines possess a relatively small condyle that is not twisted laterally.

(52) Tibiotarsus, inner cnemial crest: 0, does not extend far distally; 1, extends far distally down shaft. A relatively short inner cnemial crest is found in
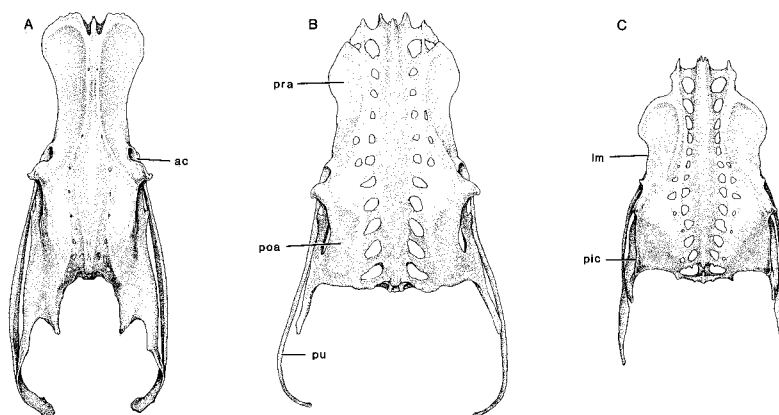
Fig. 3.   Dorsal view of pelves of (A) *Diomedea irrorata* (FMNH 105001), (B) *Phaethon rubricauda* (LSU 81378), and (C) *Fregata minor* (FMNH 104717). Abbreviations: ac, acetabulum; lm, lateral margin of preacetabular ilium; pic, posterior iliac crest; poa, postacetabular ilium; pra, preacetabular ilium; pu, pubis.

procellariiforms, pelecaniforms, and all other non-passerines.

RESULTS

ANALYSES USING UNORDERED CHARACTERS

Two analyses using unordered characters were undertaken to assess the unity of the Pelecaniformes. One analysis rooted the resulting tree by using a hypothetical ancestor having all characters scored as zero, the other by specifying spheniscids as the root (penguins generally are agreed to be phylogenetically distant from pelecaniform taxa). In both analyses, all of the families traditionally included in the Pelecaniformes were clustered together, thus providing corroboration of the hypothesis of pelecaniform monophyly (Fig. 6). The shortest tree using a hypothetical ancestral taxon for the root is that shown in Fig. 6A (88 steps), whereas an 87-step tree specifying spheniscids as the root is depicted in Fig. 6B. Both trees show some homoplasy (parallelism/convergence and reversal), with tree 6A having a consistency index of 0.670 and tree 6B an index of 0.678. Differences between the two trees derive only from the alternative ways in which they were rooted.

Because my goal was to assess pelecaniform interrelationships, emphasis was placed on those characters shared among pelecaniform taxa. Consequently, an exhaustive search for similarities among the outgroups was not undertaken, and thus relationships among these

latter taxa cannot be expected to be resolved fully (note, for example, the separation of the procellariiform taxa on the trees).

The topologies shown in Fig. 6 are the most parsimonious for the given data, with differences between 6A and 6B being the result of specifying different roots. It is important to note, however, that a unique solution for character-state transitions on these trees may not exist when characters exhibit homoplasy. Thus, for a multistate character having three states, six transitions are possible, and different sequences of these transitions might be arranged on a given tree without decreasing or increasing the number of steps.

In summary, when no prior assumptions are made regarding character polarity, cladistic analysis performed on the data set of Table 1 unites all pelecaniform taxa.

ANALYSES USING ORDERED CHARACTERS

The analyses using ordered characters produced tree topologies identical to those based on unordered characters, but the optimizations of the characters on these trees exhibit some significant differences (compare Fig. 6A with Fig. 7). The trees of ordered characters also were rooted using a hypothetical common ancestor with all characters coded zero and by specifying spheniscids as the root. Both procedures resulted in identical topologies and character-state transformations within the Pelecaniformes and their immediate outgroups (procel-
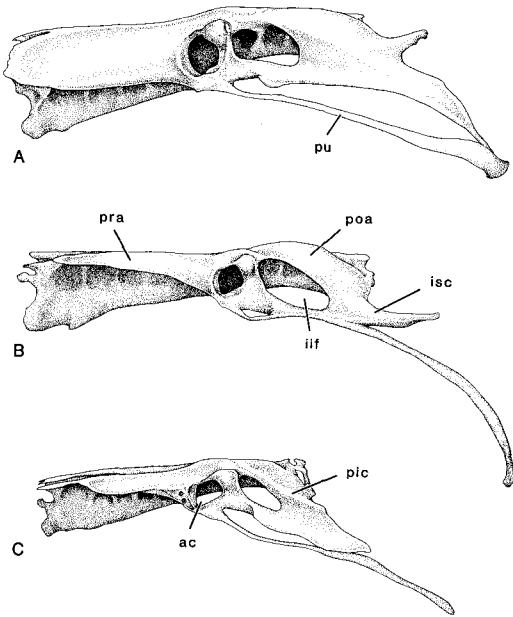
Fig. 4. Side view of pelves of (A) *Diomedea irrorata* (FMNH 105001), (B) *Phaethon rubricauda* (LSU 81378), and (C) *Fregata minor* (FMNH 104717). Abbreviations: ac, acetabulum; iif, ilioischiatic fenestra; isc, ischium; pic, posterior iliac crest; poa, postacetabular ilium; pra, preacetabular ilium; pu, pubis.
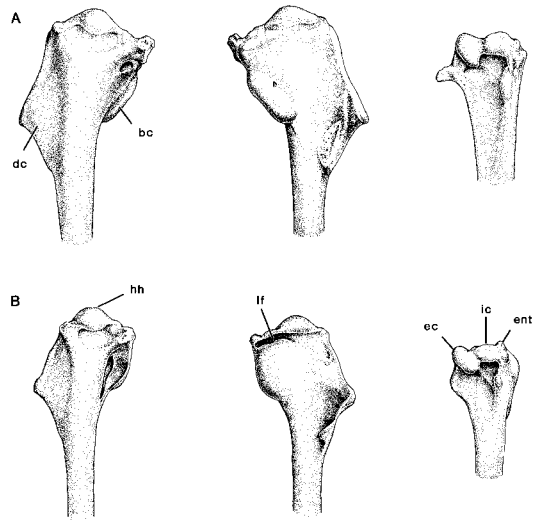

Fig. 5. Proximo-anconal (left), proximo-palmar (center), and disto-palmar (right) views of humeri of (A) *Diomedea irrorata* (FMNH 105001) and (B) *Fregata minor* (FMNH 104717). Abbreviations: bc, bicipital crest; dc, deltoid crest; ec, external condyle; ent, entepicondyle; hh, head of humerus; ic, internal condyle; lf, ligamental furrow.

lariiform taxa). Therefore, the only tree to be discussed here is the one using a hypothetical ancestor as the root (Fig. 7).

A single most parsimonious tree of 89 steps was found, having a consistency index of 0.663 (Fig. 7). Characters 1, 2, 4, 5, 10, 16, 19, 21–33, 37, 45, and 47 exhibited some parallelism or reversal. The pattern of phylogenetic relationships within the pelecaniforms is highly corroborated at each node of the tree (Fig. 7).

Monophyly of the Pelecaniformes (Fig. 7: node 7).—This study suggests that the hypothesis of pelecaniform monophyly can be highly corroborated. Of the 12 postulated synapomorphies, only 5 show some homoplasy. The non-homoplastic synapomorphies include (numbers refer to those of the character analysis): (6) loss of supraorbital depressions, (7) reduced or absent lip on medial condyle of quadrate, (26) relatively large ilioischiatic fenestra, (29) deep ligamental furrow of humerus, (35) totipalmate foot, (36) gular pouch, and (38) a prelanding call. In addition, 5 characters are consistent with the hypothesis of monophyly but show parallelism or reversal. Having nostrils that are non-

tubular and lateral (21) is interpreted as a reversal because the procellariiform taxa are not united into a single outgroup; inasmuch as no evidence exists that the procellariiforms are not monophyletic, the condition in pelecaniforms is undoubtedly primitive and therefore of no value in defining the group. Pelecaniforms possess a relatively horizontal preacetabular ilium (25), a character also developed in parallel in the spheniscids; this character is thus a good synapomorphy for the order. The internal condyle of the tibiotarsus (32) is greatly enlarged and also was developed in parallel in the spheniscids. A greatly foreshortened tarsometatarsus (33) is interpreted as a synapomorphy for the order, but a similar condition was developed in parallel in the spheniscids. Moreover, within the pelecaniforms this character shows a reversal to a primitively elongate condition in both pelicans and cormorants. A relatively small tarsometatarsus thus appears interpretable as a synapomorphy of the order. Finally, the young of pelecaniforms feed by sticking their heads down the gullets of the adults (37), a behavior that is also present in spheniscids. This parallelism is thus a good synapomorphy for the order.
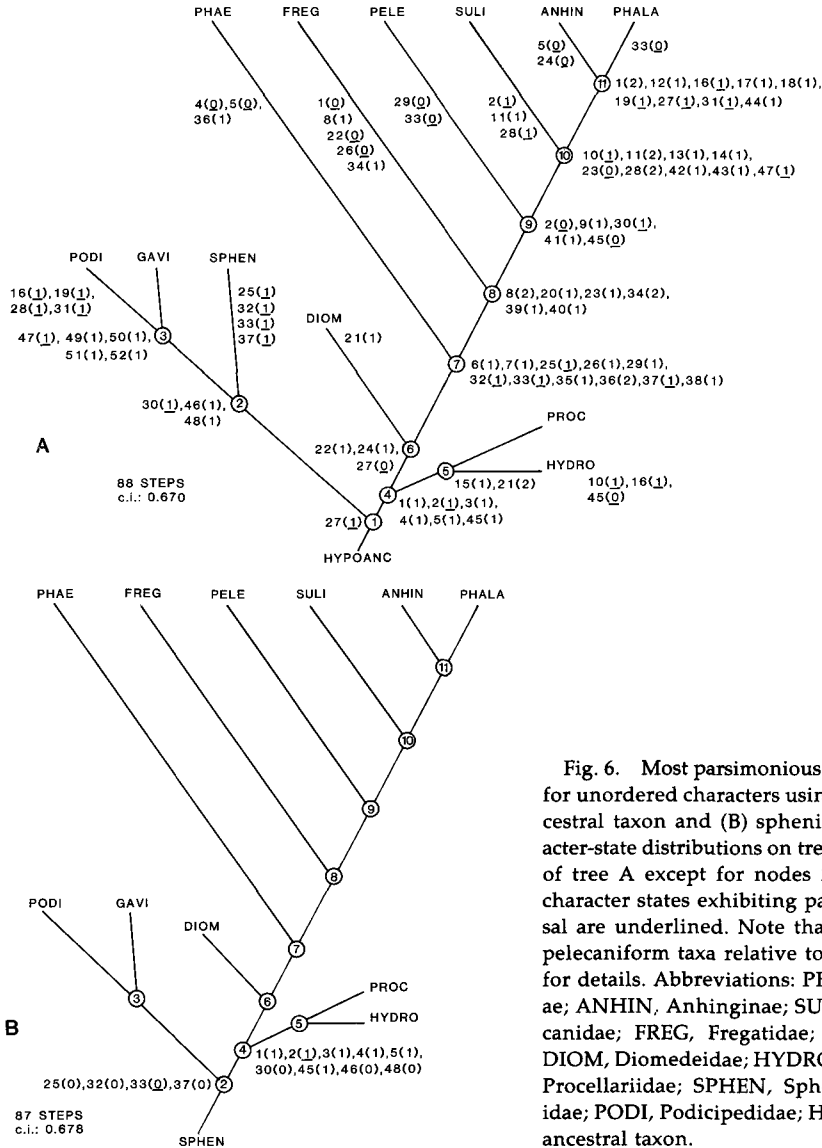
PHAE   FREG   PELE   SULI   ANHIN   PHALA

5(0)   33(0)
24(0)

4(0),5(0),   1(0)   29(0)   2(1)   ⑪ 1(2),12(1),16(1),17(1),18(1),
36(1)   8(1)   33(0)   11(1)   19(1),27(1),31(1),44(1)
              22(0)   28(1)
              26(0)
              34(1)   ⑩ 10(1),11(2),13(1),14(1),
                          23(0),28(2),42(1),43(1),47(1)

⑨ 2(0),9(1),30(1),
   41(1),45(0)

PODI   GAVI   SPHEN

16(1),19(1),   25(1)   ⑧ 8(2),20(1),23(1),34(2),
28(1),31(1)   32(1)   39(1),40(1)
                33(1)   DIOM
47(1),49(1),50(1),③ 37(1)   21(1)
51(1),52(1)

⑦ 6(1),7(1),25(1),26(1),29(1),
   32(1),33(1),35(1),36(2),37(1),38(1)

30(1),46(1),②
48(1)   PROC

A   HYDRO
                22(1),24(1),⑥   10(1),16(1),
88 STEPS   27(0) ⑤ 15(1),21(2)   45(0)
c.i.: 0.670   ④ 1(1),2(1),3(1),
                27(1)① 4(1),5(1),45(1)

HYPOANC

PHAE   FREG   PELE   SULI   ANHIN   PHALA

⑪

⑩

⑨

PODI   GAVI

③   DIOM   ⑧

②   ⑦
                ⑥   PROC
B   ⑤   HYDRO
25(0),32(0),33(0),37(0)② ④ 1(1),2(1),3(1),4(1),5(1),
87 STEPS   30(0),45(1),46(0),48(0)
c.i.: 0.678

SPHEN

Fig. 6. Most parsimonious (minimum length) trees for unordered characters using (A) a hypothetical ancestral taxon and (B) spheniscids as the root. Character-state distributions on tree B are identical to those of tree A except for nodes 2 and 4, as shown. All character states exhibiting parallelism and/or reversal are underlined. Note that both trees cluster the pelecaniform taxa relative to all outgroups. See text for details. Abbreviations: PHALA, Phalacrocoracinae; ANHIN, Anhinginae; SULI, Sulidae; PELE, Pelecanidae; FREG, Fregatidae; PHAE, Phaethontidae; DIOM, Diomedeidae; HYDRO, Hydrobatidae; PROC, Procellariidae; SPHEN, Spheniscidae; GAVI, Gaviidae; PODI, Podicipedidae; HYPOANC, hypothetical ancestral taxon.

Monophyly of the suborder Steganopodes (Fig. 7: node 8).—Within the pelecaniforms two basal lineages can be defined, one leading to the phaethontids and the other to the remaining four families. The latter lineage, termed here the Steganopodes, is postulated to be monophyletic on the basis of seven shared derived characters, none of which shows any homoplasy. These characters include: (8) fusion of the palatines posteriorly, (20) an ossified nasal septum, (23) fusion of the sternum and clavicle (this character is reversed in higher pelecani-

forms; see below), (34) a tarsometatarsus with hypotarsus that projects posteriorly and is foreshortened proximodistally, (36) completely naked gular pouch, (39) stereotypic nest-relief behavior, and (40) young hatched naked. These characters thus separate fregatids from phaethontids and unite the former with the other pelecaniforms.

Monophyly of the infraorder Pelecani (Fig. 7: node 9).—Within the Steganopodes the fregatids are the sister-group of all other families. This latter clade, the infraorder Pelecani, is hy-
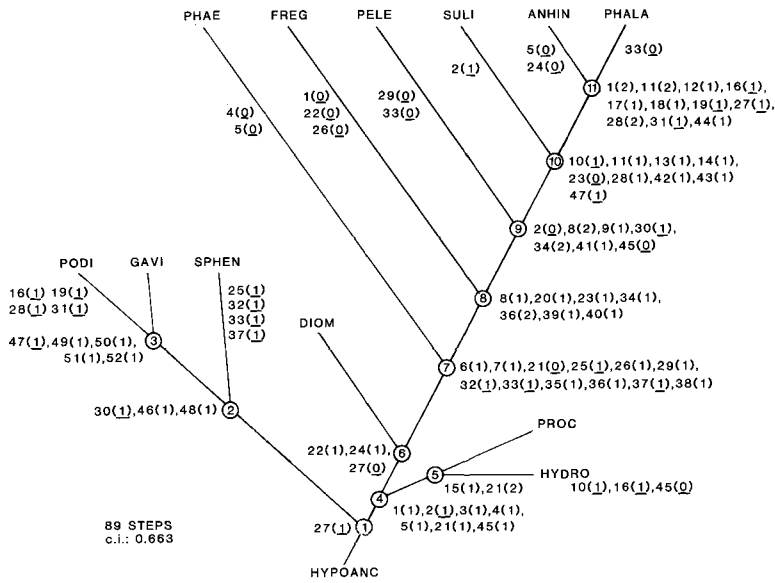
Fig. 7. Most parsimonious (minimum length) tree for ordered characters using a hypothetical ancestral taxon as the root. All character states exhibiting parallelism and/or reversal are underlined. Abbreviations are as in Fig. 6. See text for details.

pothesized to be monophyletic because it is defined by seven derived characters. Of these, four are nonhomoplastic, including: (8) palatines fused throughout their length, (9) loss of vomer, (34) hypotarsus projecting very strongly posteriorly, and (41) eggs incubated beneath the feet. In addition, three characters exhibit homoplasy and are consistent with the hypothesis of monophyly: (2) upper tympanic recess is reduced in size, which is interpretable as a reversal, (30) deltoid crest of the humerus is greatly reduced, which is a parallelism shared with the gaviids, podicipedids, and spheniscids, and (45) a rounded deltoid crest, which is a reversal to the primitive condition.

Monophyly of the superfamily Suloidea (Fig. 7: node 10).—The families Sulidae and Phalacrocoracidae (including the anhingas) are postulated to form a monophyletic assemblage within the Pelecani on the basis of sharing nine derived characters. Five of these are nonhomoplastic, including: (11) braincase moderately compressed dorsoventrally, (13) orbital process of quadrate reduced in size, (14) lateral wall of presphenoid sinus reduced in size, (42) presence of a hop display, and (43) presence of a sky-pointing display. Four homoplastic characters also corroborate this clade: (10) greatly reduced maxillopalatines, which is a parallel-

ism shared with hydrobatids, (23) loss of sternoclavicular fusion, which is a reversal to the primitive condition, (28) lateral margin of preacetabular ilium moderately curved, which is parallel with the condition in grebes, and (47) temporal fossa extending to midline, which is a parallelism shared with loons and grebes.

Monophyly of the Phalacrocoracidae (Fig. 7: node 11).—Eleven synapomorphies support the hypothesis of a sister-group relationship between cormorants and anhingas. Seven of these characters are nonhomoplastic, including: (1) mediopalatine processes present only at the ptergo-palatine joint, (11) braincase very strongly compressed dorsoventrally, (12) braincase expanded anteroposteriorly, (17) opisthotic processes directed posteriorly, (18) possession of an occipital style, (28) lateral margin of preacetabular ilium very strongly curved, and (44) presence of a "kink-throating" display. In addition, four characters are homoplastic, yet corroborate this clade: (16) poorly developed postorbital processes, which are parallel to the condition in podicipedids and hydrobatids, (19) loss of interorbital septum, which is again parallel to that of grebes, (27) compressed postacetabular pelvis, which is interpreted as a parallelism with the condition defining node 1 (Fig. 7), and (31) a high, bladelike entepicon-

dyle of the humerus, which is parallel to the condition seen in grebes.

Monophyly of pelecaniform families.—No effort was made in this study to enumerate the apomorphous characters defining each family as being monophyletic. Indeed, no one has seriously questioned their monophyly. The analysis presented in Fig. 7 lists characters for each family, but all are interpretable as reversals or parallelisms simply because defining characters of these families were not entered initially into the analysis.

DISCUSSION

Relationships between the Pelecaniformes and Procellariiformes.—Although the main purpose of this study was to clarify the monophyly and interrelationships of the pelecaniforms, some of the data also bear on our understanding of the interordinal affinities of the order. Given the taxa and characters included in this study, the analyses discussed above support the hypothesis of a sister-group relationship between the pelecaniforms and procellariiforms. Six shared derived characters corroborate that hypothesis (Fig. 7: node 4), including: (1) mediopalatine processes enlarged toward the pterygo-palatine joint, (2) upper tympanic recess greatly enlarged, (3) bony nostrils greatly reduced, (4) rostrum with long nasal groove, (5) bill with terminal hook, and (45) deltoid crest of humerus triangular in shape and projecting to a sharp point. One other character shown in Fig. 7—(21) lateral tubular nostrils—is also interpretable as a defining character but almost certainly is assigned to the wrong hierarchical level. This resulted because character states 22(1) and 24(1) united diomedeids with the pelecaniforms at node 6 (Fig. 7), thus dismembering the procellariiforms (both characters are lacking in procellariids and hydrobatids). Tubular nostrils generally are acknowledged to be a synapomorphy of the procellariiforms, and presumably that interpretation will be verified once additional procellariiform characters are added to the analysis.

Each of the six defining characters of pelecaniforms plus procellariiforms exhibits reversal at higher hierarchical levels, but this does not lessen their systematic value in corroborating the monophyly of these two orders. Yet, because a limited number of higher taxa were included in the study, that hypothesis of mon-

ophyly will require additional analysis in the future. At present, however, little evidence exists for supporting a sister-group relationship between either order and some other taxon. Some of the possible alternative hypotheses warrant additional discussion here.

Relationships of the Pelecaniformes: alternative hypotheses.—Opinions about the monophyly of the pelecaniforms and their relationships to other orders abound in the literature, yet few studies actually present explicit phylogenetic hypotheses along with supporting data. Virtually all students of pelecaniform anatomy have noted that phaethontids and fregatids are "different" from the other pelecaniforms, yet most of these workers have continued to accept the monophyly of the order. Moreover, anatomical similarities between fregatids and procellariiforms (particularly diomedeids) have been noted frequently (Shufeldt 1888, 1902; Wetmore 1960), but this has not led to serious consideration of a relationship between the two orders. Instead, pelecaniforms have been linked most often with the ciconiiforms (Garrod 1874; Stejneger 1885; Fürbringer 1888; Seebohm 1889, 1890; Gadow 1892, 1893), despite the fact that strong evidence for this hypothesis has not been presented. Gadow (1893: 131–132), for example, listed nine characters "defining" his "Ciconiiformes" (ciconiiforms + pelecaniforms), yet each one is distributed widely in other groups (see Gadow's own summary table, 1893: 76–85). That Gadow's paper is perhaps the best documented of all those supporting a relationship between pelecaniforms and ciconiiforms emphasizes the weakness of this hypothesis.

Saiff (1978) undertook an extensive analysis of the middle-ear region in pelecaniform and ciconiiform birds but also made comparisons with his earlier results on procellariiforms (Saiff 1974). These studies were predominately descriptive, but Saiff drew some systematic interpretations. With respect to the interordinal relationships of pelecaniforms, Saiff (1978: 368) concluded:

"*Phaethon* shows a number of resemblances to Procellariiformes (but is quite distinct from them). The other Pelecaniformes are very distinct from Procellariiformes and the middle ear does not even offer firm support to the generally accepted idea that Procellariiformes and Pelecaniformes are closely related. On the other hand, close relationship between Pelecaniformes (aside from *Phaethon*)

and Ciconiiformes is strongly supported by the middle ear morphology."

A critical assessment of Saiff's study is outside the scope of this paper inasmuch as it would involve extensive descriptions of middle-ear regions for numerous taxa. Nevertheless, data collected during the course of this study contradict some of his observations and conclusions.

As Saiff noted, the middle-ear region of *Phaethon* resembles that of procellariiforms (particularly *Diomedea*), yet is very distinct because the basicranial region is so highly modified. The major similarity—the very large upper tympanic recess (character 2)—is postulated in this paper to be a synapomorphy of the procellariiforms and pelecaniforms. Saiff (1978) did not attempt to assess whether similarities were primitive or derived. Furthermore, his observation (1978: 368) that other pelecaniforms are very distinct from procellariiforms is open to question. In Fig. 2, for example, the middle-ear regions of *Diomedea* and *Fregata* are seen to be exceedingly similar, particularly in the relative positions of the articular surfaces, cranial nerve foramina, and the various pneumatic foramina (although they do exhibit differences; Saiff 1978). These patterns of middle-ear anatomy, shared between postulated basal members of these two orders, are consistent with a hypothesis of close relationship.

Saiff's (1978) second conclusion, that a close relationship between ciconiiforms and pelecaniforms is "strongly supported" by middle-ear anatomy, is perplexing because he presented little evidence. Other than an inconclusive statement (1978: 368) that the middle-ear patterns of the two orders show "a similarity of foramina," no specific support for this hypothesis is presented. In contrast, I have been unable to identify characters of the basicranial region that could be used to unite ciconiiforms and pelecaniforms.

In summary, present morphological evidence supports a sister-group relationship between pelecaniforms and procellariiforms. Other hypotheses, including that of a pelecaniform relationship with ciconiiforms, are not supported by any substantial evidence at this time, particularly by characters evaluated within the context of a cladistic analysis. The basicranial regions of these taxa are a rich source of anatomical variation, but additional inves-

tigations are needed to elucidate the taxonomic significance of that variation.

Relationships within the Pelecaniformes: alternative hypotheses. —The interfamilial relationships of the pelecaniforms have inspired minimal controversy. Virtually all workers have agreed that cormorants and anhingas are sister-taxa and that sulids are their sister-group. And, the large majority has accepted the hypothesis that pelecanids are "more distant" from cormorants and anhingas than are the sulids. Without question, most of the controversy over pelecaniform interrelationships has centered on phaethontids and fregatids, and many contemporary systematists have postulated (or accepted without much discussion) their close relationship (e.g. Lanham 1947, Mayr and Amadon 1951, Sibley and Ahlquist 1972; see also Mivart 1878).

The primary rationale for acceptance of a relationship between phaethontids and fregatids has been the work of Lanham (1947). As he noted (1947: 65), however, the similarities used to unite these two families also are shared with the procellariiforms, and indeed characters such as the presence of a vomer or maxillopalatines are primitive and cannot be used to test hypotheses of relationship within the pelecaniforms.

I examined Lanham's hypothesis by optimizing the character-state data of Table 1 on a tree of the same topology as that of Fig. 7, except that phaethontids and fregatids were considered to be sister-taxa. The resulting tree had a length of 95 steps (consistency index = 0.621), 6 steps more than the phylogenetic arrangement shown in Fig. 7. The data also reveal that no synapomorphies support the monophyly of phaethontids and fregatids. Moreover, compared with the character-state distributions shown in Fig. 7, six homoplastic characters have been added to the phaethontid lineage and one to that of the fregatids. Thus, the phylogenetic hypothesis uniting phaethontids and fregatids is much less parsimonious, when evaluated over the entire structure of the tree, than the arrangement of Fig. 7. Just as importantly, analysis of the data in Table 1 provides no positive evidence for a sister-group relationship of these two families.

Is Balaeniceps a pelecaniform?—Systematic ornithologists have noted anatomical similarities between the Whale-headed Stork (*Balaeniceps rex*) and various pelecaniforms, particularly

pelecanids, but it was not until Cottam's (1957) study that the possibility of a close relationship was taken seriously. Although acknowledging this latter study, most authorities have continued to maintain *Balaeniceps* within the Ciconiiformes. In arguing for the polyphyletic nature of the ciconiiforms, however, Olson (1979) accepted Cottam's "convincing, or at least provocative argument," mainly for the reason that "the grooved rostrum with strongly hooked tip, the prominent coracoidal facets of the furcula, and the fusion of the furcula with the apex of the sternal carina are distinctly pelecaniform features."

Cottam's methods of comparison and data analysis conformed to a tradition that was established in the late 19th century by the great German systematists such as Gadow and Fürbringer. Thus, systematic relationships were postulated after an assessment of the degree of overall similarity and difference among the various taxa. This type of analysis generally does not determine whether the observed similarities are primitive or derived at a specific hierarchical level, nor does it interpret the characters within the framework of alternative phylogenetic hypotheses. These methodological inadequacies do not lead necessarily to incorrect assessments of relationship: conclusions can be correct for the wrong reasons. Such inadequacies imply, however, that the conclusions do not have the force of strong argument behind them.

In the case of Cottam's analysis, several objections can be raised. First, no specific hypothesis of pelecaniform relationships was proposed; therefore, in assessing the affinities of *Balaeniceps* to that group, no specific phylogenetic hypothesis was corroborated or refuted. Second, Cottam did not evaluate the hypothesis that *Balaeniceps* shares suites of derived characters with ciconiiform taxa and therefore should be placed within that group. Given these shortcomings, a more detailed and analytical assessment of the relationships between *Balaeniceps* and pelecaniforms was deemed necessary. I coded the character states for *Balaeniceps* and subjected them to analyses identical to those already discussed. The results show that when character-state data for *Balaeniceps* are interpreted within the framework of the systematic relationships of Fig. 7, numerous character conflicts arise. I will outline the nature of those conflicts here, but a more detailed consider-

ation of the relationships of *Balaeniceps* to the Ciconiiformes will be considered in a separate paper on the systematics of that order. Finally, I will suggest a possible reason for the existence of some of the striking structural similarities between *Balaeniceps* and various pelecaniform taxa.

When *Balaeniceps* was incorporated into an analysis using ordered character transformations and a hypothetical ancestral taxon as the root, two equally parsimonious trees (length = 97 steps, consistency index = 0.608) were produced (Fig. 8). In both, *Balaeniceps* appears as the sister-group of the procellariiforms + pelecaniforms. The only difference between the two trees lies in the alternative arrangements of the procellariiform taxa. Thus, given a simple, parsimonious analysis of the data, the relationships of *Balaeniceps* lie well outside the Pelecaniformes.

The character-state distributions on both trees are very similar. For tree 8A, *Balaeniceps* is united to the procellariiforms and pelecaniforms (node 4) on the basis of six postulated synapomorphies: 3(1) reduced bony nostrils, 4(1) presence of long rostral groove, 5(1) terminal hook on bill, 6(1) supraorbital salt glands absent, 7(1) anterior lip of medial condyle of quadrate absent or greatly reduced, and 24(1) posterior iliac crest poorly defined. All of the characters, except the reduced bony nostrils, are reversed at higher hierarchical levels.

In the phylogenetic arrangement of 8A, *Balaeniceps* itself has the following defining characters: 8(2) palatines fused throughout length, 10(1) maxillopalatines greatly reduced, 20(1) ossified nasal septum, and 23(1) fused sternoclavicular joint. All of these character states are interpretable as parallelisms, with similar characters developed at higher hierarchical levels.

The character-state distributions of tree 8B are not very different from those of tree 8A, but dismembering the procellariiforms results in several alterations. For example, the absence of supraorbital salt glands [6(1)] and reduced lip on the medial condyle of the quadrate [7(1)] no longer define node 4 but now are interpretable as defining characters of *Balaeniceps*.

These results contradict the assumption of previous workers (Cottam 1957, Olson 1979) that some characters of *Balaeniceps*, such as the rostral groove, hooked bill, fused palate, and fused sternoclavicular joint, are evidence for affinities with the pelecaniforms. Unless such
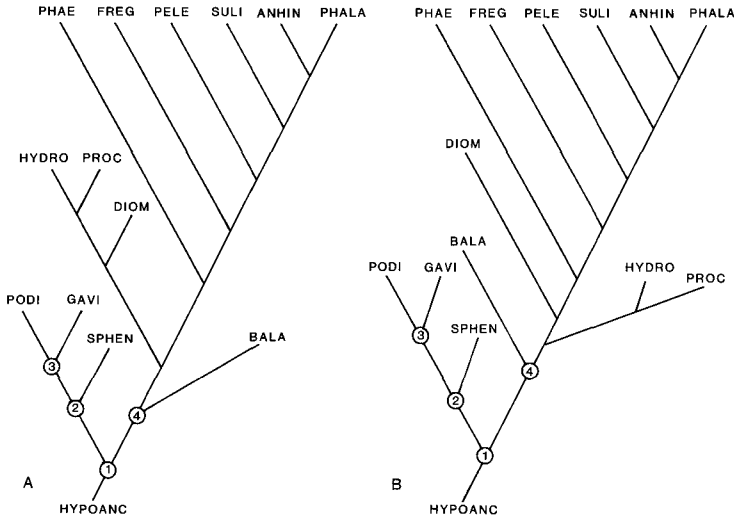
Fig. 8. Two equally most parsimonious trees (97 steps; consistency index = 0.608) for all the taxa of Fig. 7 and *Balaeniceps* (BALA). Character-state transitions are ordered, and a hypothetical common ancestor is used to root the tree. Abbreviations are as in Fig. 6. Note that the only difference between the trees lies in the placement of procellariiform taxa. See text for details.

assumptions are tested by evaluating the hierarchical arrangement of these characters with respect to a parsimonious phylogenetic hypothesis, one often may be led to incorrect systematic interpretations. Such, apparently, has been the case with *Balaeniceps*.

That one cannot easily interpret *Balaeniceps* as a pelecaniform is emphasized further when hypotheses about their possible interrelationship are explored in more detail. Figure 9 shows three possible placements of *Balaeniceps* that might be inferred from the discussions of previous workers, although such hypotheses were rarely, if ever, stated explicitly. Ordered character-state distributions were optimized for each of the three trees. Tree 9A, in which *Balaeniceps* is the sister-group of the Pelecaniformes, had a length of 98 steps (consistency index = 0.602); tree 9B, in which *Balaeniceps* is the sister-group of the infraorder Pelecani, had a length of 104 steps (consistency index = 0.567); and, finally, tree 9C, in which *Balaeniceps* is the sister-group of the pelecanids, had a length of 108 steps (consistency index = 0.546).

It is readily apparent that as *Balaeniceps* is postulated to have a relationship at increasingly higher levels of the hierarchy, that relationship becomes less and less parsimonious and the hypotheses display an increasing amount of homoplastic character distributions. Unless

one is willing to abandon parsimony as a working principle of science, the data analyzed in this study do not support a relationship between *Balaeniceps* and any pelecaniform taxa.

Saiff (1978) examined the middle-ear region of *Balaeniceps* and concluded that the genus probably is related to pelecaniforms (1978: 366–367):

"The fenestra ovalis, recessus scalae tympani, and the pneumatic foramen posterior to these in *Balaeniceps* are much as in the Pelecanidae. Also similar in both the Balaenicipitidae and the Pelecanidae is the position of the lateral wall of the presphenoid sinus with respect to the medial side of the quadrate shaft. The highly pneumatic floor of the presphenoid sinus of *Balaeniceps* closely resembles the arrangement in most of the pelicans which lack a floor to the presphenoid sinus entirely. It would appear there is [sic] more data to ally *Balaeniceps* with the Pelecaniformes than with the Ciconiiformes."

Unfortunately, this comparison did not emphasize the identification of shared characters and in the process obscured not only differences between *Balaeniceps* and pelecanids but also similarities between *Balaeniceps* and other ciconiiforms. Thus, Saiff's comments about the fenestra ovalis, recessus scalae tympani, and their associated pneumatic foramen are not suf-
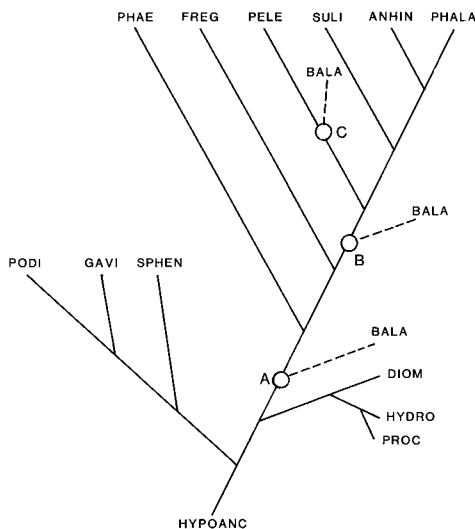
Fig. 9.   Three alternative hypotheses for the relationships of *Balaeniceps* (BALA) to pelecaniform taxa. Character states of Table 1 are optimized on each tree using ordered character-state transitions and a hypothetical common ancestor as the root. Tree A was 98 steps (consistency index = 0.602), tree B was 104 steps (c.i. = 0.567), and tree C was 108 steps (c.i. = 0.546). Abbreviations are as in Fig. 6. See text for details.

ficiently specific to differentiate *Balaeniceps* and pelecanids from other taxa.

My observations on the lateral wall of the presphenoid sinus imply different conclusions from those of Saiff. The sinus itself is a bulbous chamber that extends medially and slightly anteriorly beneath the foramen prooticum in ciconiiforms, including *Balaeniceps*. In pelecaniforms, in contrast, the chamber is narrow and is directed more anteriorly, and not as medially, beneath the foramen prooticum (*Phaethon* approaches the ciconiiform condition more than other pelecaniforms). Part of the reason for the bulbous condition of the sinus in ciconiiforms is that the posterolateral portion of the wall bulges outward; in pelecaniforms, including *Phaethon*, the wall is flattened. The sinus of *Balaeniceps* resembles other ciconiiforms, but its lateral wall does not bulge prominently; this condition is more similar to that of ardeids than to phoenicopterids or ciconiids. Finally, the posterolateral wall of the presphenoid sinus abuts the medial side of the quadrate in ciconiiforms (including *Balaeniceps*). The two structures are separated in pelecaniforms and pro-

cellariiforms. These observations lead me to conclude that the middle-ear region does not offer direct evidence to link *Balaeniceps* with pelecanids or other pelecaniforms. The evidence, on the other hand, is consistent with the hypothesis that *Balaeniceps* is allied with ciconiiforms, but more detailed comparative studies of the middle-ear region are necessary before this can be confirmed.

The most parsimonious conclusion is that *Balaeniceps* is not a pelecaniform. I suggest, as have most previous workers, that the genus probably is related to the ciconiiforms. Behavioral data (Buxton et al. 1978) seem to support this conclusion, although their phylogenetic significance needs to be analyzed more rigorously. One can construct a plausible, but speculative, explanation for some of the similarities between *Balaeniceps* and pelecaniforms. Hence, I suggest that the hooked bill, the fused palatines, the straight nasal-frontal hinge including fusion of the nasals and premaxilla, the fused furculum and keel, and perhaps the short, broad, arched sternum are all mechanical designs to accommodate similar modes of feeding. The foraging behavior of the pelecaniforms, in which they dive into the water for fish, is well known. The foraging behavior of *Balaeniceps* is less well known but resembles that of most pelecaniforms in the way in which mechanical forces would be distributed to the head and body (Guillet 1979, Möller 1982). *Balaeniceps* typically forages from thick platforms of floating vegetation, moving slowly and apparently making visual contact with prey (often lungfish and large teleosts). Prey capture involves "collapsing," in which wings and legs are extended, and the bird collapses forward and downward onto the vegetation and prey (Guillet 1979, Möller 1982). The force of impact with the prey is made by the upper mandible, and the upper part of the thorax is subject to hard contact with the dense vegetational substrate. In righting itself the bird uses its wings, but to some extent it also pushes against the substrate with its bill.

This foraging behavior calls for anatomical designs that resist substantial impact forces. Thus, fusion of cranial elements and fusion of the furculum with the sternum perhaps represent "convergent" mechanical responses to similar internal stresses (primarily compressional forces) in both *Balaeniceps* and pelecaniforms. In *Balaeniceps*, the forces are generated

by impact with dense mats of vegetation, with water, and with large prey items; in pelecaniforms, the forces arise primarily from impact with water. This behavioral-functional similarity seemingly explains the occurrence of similar morphologies in unrelated groups, and therefore represents one of the more striking examples of convergence within the class Aves.

Comments on classification.—The data of this paper support the sequence of phylogenetic relationships outlined in Fig. 7. These relationships can be expressed precisely in the following classification:

Order Pelecaniformes
  Suborder Phaethontes
      Family Phaethontidae
  Suborder Steganopodes
    Infraorder Fregatae
      Family Fregatidae
    Infraorder Pelecani
      Superfamily Pelecanoidea
        Family Pelecanidae
      Superfamily Suloidea
        Family Sulidae
        Family Phalacrocoracidae
          Subfamily Phalacrocoracinae
          Subfamily Anhinginae

Systematic methods and the study of avian phylogeny.—In recent years, the ornithological community has witnessed a mild renaissance within systematic ornithology. An increasing number of papers are being published using comparative methodologies and techniques that, just 10 or 15 years ago, either were not available or had just become so. Yet, accompanying this resurgence of activity has been a heightened level of controversy, not so much over the empirical results of these studies, but rather over the methods used to obtain those results. To the nonsystematist, much of this debate must seem polemical at times, but deeper issues are involved, and nonsystematists have a vested interest in understanding them. After all, systematics is the branch of evolutionary biology that is responsible for reconstructing historical pattern; without that knowledge, many of the findings of comparative ecology, behavior, and physiology would lose much of their interpretive foundation.

This paper touches on a number of issues pertaining to the principles and methods of phylogenetic analysis that have been the focus of recent debate within systematic ornithology. It therefore seems appropriate to search for some general conclusions that may be drawn from studies of this type, primarily those concerned with how the methods adopted in this paper stand in relation to those recommended by other avian systematists. The aim of this brief discussion is to help clarify for nonsystematists certain conflicts that have surfaced in the literature and to draw attention to some limitations of these different methods.

The different schools of systematics have been characterized repeatedly in the literature. Recent controversy within systematic ornithology revolves around cladistics and its critics on the one hand, and proponents of molecular distance analysis and their critics on the other. Cladistic analysis is based on a simple principle: hierarchies (three or more taxa) are constructed by maximizing congruence of postulated shared derived characters (synapomorphies), with the implication that postulated homoplastic character-state distributions are also minimized. Analyses presented in this paper illustrate the point that whether a particular character state is considered a synapomorphy or not depends on the particular topology of the tree upon which that character-state transition is optimized. This paper also emphasizes that homoplasies are themselves synapomorphies; they are simply independently evolved shared derived characters capable of defining taxa. In contrast to some other methods often used in ornithology, cladistics rejects shared primitive characters (symplesiomorphies) as evidence of monophyly.

Most cladistic analyses in the ornithological literature have used nonnumerical methods. If data sets are large and include significant parallelism and reversal, however, then discovering the best-fit tree can be extremely difficult. Three numerical cladistic programs apply what can be called "true parsimony" methods. The best known is the Wagner 78 program of James S. Farris (Farris 1970, 1972; see Wiley 1981: 178–192). This program is widely available but has been modified so often that care must be taken in using it. Moreover, when data sets contain relatively high amounts of homoplasy, considerable effort must be made to ensure obtaining the most parsimonious tree (the program is not designed to yield numerous equally parsimonious trees). By far the best programs are PHYSYS (written by J. S. Farris) and PAUP (written

by D. L. Swofford). Both can find the minimum-length tree by searching for all possible combinations of taxa (at least for relatively restricted numbers of taxa), and both find equally parsimonious trees.

These are true-parsimony cladistic methods in that they search for the most parsimonious trees over the entire data set. Character compatibility (clique) methods also claim to be cladistic (Estabrook et al. 1975, 1976), but they use "parsimony" on "sanitized" (Sober 1983) data for which incongruent characters often are excluded from the final tree. This method has been strongly criticized by Farris and Kluge (1979), Mickevich and Parenti (1980), Farris (1983), and Churchill et al. (1984). Clique analysis has been applied only sporadically within ornithological systematics (Payne and Risley 1976; Strauch 1978, 1984).

The application of numerical cladistic techniques has several distinct advantages over conventional "hand-calculated" methods. First, a complete data matrix is required, something that usually has been lacking in earlier studies, cladistic and noncladistic. Second, finding minimum-length trees is much faster and more accurate, particularly when parallelisms and reversals are frequent. Third, equally parsimonious trees also emerge from the analysis when they might once have been overlooked (again, when parallelisms and reversals are common). And finally, character-state data can be optimized on any given tree, thus making quantitative comparisons among alternative hypotheses easy to perform. All of these advantages are illustrated in the present paper.

Critics of cladistics have charged that cladists in fact do not practice the principles they advocate (e.g. Olson 1982, 1983). The claim is made, for example, that cladists often do not cluster by synapomorphy, do not specify primitive-derived sequences, use differences between taxa as evidence of nonrelationship, and use "arguments of convergence" to refute hypotheses of relationship (Olson 1982). Such claims might be dismissed as mere hand waving were it not possible that nonsystematists might take them seriously. Furthermore, such claims obscure the important issues dividing avian systematists and disguise the need for defenders of traditional systematic techniques to explicate their own methods and principles of comparison (Raikow and Cracraft 1983, Cracraft 1983).

Although the method of presentation is new, the principles upon which the present study is based are no different from those underlying previous cladistic analyses within the ornithological literature. Indeed, misunderstandings over those principles are a prime reason for the contemporary debates, and the results of this paper provide a basis for discussing how some of those misunderstandings might have arisen. To claim that cladists do not cluster by synapomorphy, for example, is simply to ignore, rather than understand, their work. If this criticism instead means that taxa sometimes are not corroborated by well-defined derived characters, then one has identified a limitation of a particular set of data, not of the methods used to analyze those data. Cladists, likewise, do not postulate monophyly on the basis of shared primitive characters, although (1) it is always possible that mistakes will be made, especially when character polarity is uncertain, or (2) particular character states may be reversals to primitive conditions, in which case they are still synapomorphous character-state transitions. The analyses of unordered character-state transitions included in this paper illustrate the point that knowledge of character polarity is not an absolute requirement of cladistic analysis. One can optimize postulated synapomorphous conditions on a tree using unordered as well as ordered (polarized) characters. Most cladists would agree that polarizing characters adds information to the analysis, but this is not at all a methodological requirement of cladistic analysis, a point not always appreciated even by cladists. Finally, do cladists use differences among taxa as *evidence* of nonrelationship? The answer is no (Raikow and Cracraft 1983). On the other hand, might not cladists sometimes suspect that observed differences suggest the possibility that two taxa are not sister-groups? Yes, they might, but one would not expect such a suggestion to be confused with the notion of necessary and sufficient evidence. Some workers have argued, for example, that *Balaeniceps* is not a ciconiiform because it is so different from other taxa in that order. The results of this analysis, in contrast, postulate that *Balaeniceps* is not a pelecaniform (*sensu stricto*), not because of its differences but because a cladistic analysis of character distributions is unable to support any hypothesis of relationship. Given the limited taxonomic sample, one cannot claim that *Balaeniceps* is a ciconiiform, but one can claim

that analysis of a specified data set suggests its relationships lie outside the pelecaniforms.

Critics of cladistics generally advocate, directly or indirectly, the methods of phenetics, whereby taxa are clustered using overall similarity (that is, symplesiomorphy as well as synapomorphy). Numerical phenetic techniques have been used widely within ornithology, primarily on distance matrices of electrophoretic data (see Matson 1984 and Buth 1984 for reviews) but also on morphological data (Schnell 1970; Payne and Risley 1976; Wood 1979, 1983). Brush and Witt (1983) undertook a phenetic analysis of pelecaniforms using electrophoretic data derived from feather proteins, but came to no definite conclusion about the pattern of their interrelationships. Distance matrices also can be analyzed cladistically, notably by distance-Wagner procedures (Farris 1972).

Of more immediate concern here is the use of molecular distance data in resolving higher-level relationships of birds. These data have been derived from electrophoretic studies, immunological distances, and more recently, from DNA-DNA hybridization. Farris (1981) and Swofford (1981) have discussed problems inherent in distance analysis. J. S. Farris and A. G. Kluge have recently argued that immunological distance data are simply unreliable as indicators of relationship (Farris 1985; A. G. Kluge pers. comm., paper presented at 1984 meetings of Amer. Soc. Ichthyol. Herpetol., Stillwater, Oklahoma): many trees of very different topologies can be fit to the original distance matrix almost as well as the best-fit tree can be fit. Whether this also will be true of DNA-DNA distances is unknown because the relevant data with which to examine this question are rarely published. Thus, one-way hybridization data—from a single, or select few, radioactively labeled taxa hybridized to many unlabeled taxa—are uninterpretable with respect to their *precise* phylogenetic information content; no objective and quantitative method of analysis for these types of data has yet been published within the ornithological literature. Conclusions based on incomplete data matrices are equivocal at best. Even when such matrices are published, however, much more discussion will be needed regarding their analysis. Not only must care be taken to determine the best-fit tree for the data—and some trees already published do not fulfill this criterion of parsimony—more discussion (and empirical justification) is needed about whether an underlying assumption of rate constancy is appropriate or even necessary (see Farris 1981, 1983, 1985).

Nonsystematists are faced with many difficulties in interpreting the results of systematists. One basis of interpretation—whether the results are congruent with one's own prior belief—should be avoided. Systematists sometimes argue from belief, of course, but "belief" lies outside the evidentiary criterion of science. Interpretive difficulties are particularly acute when conflicting hypotheses result from different methods and techniques. Systematists themselves have not paid sufficient attention to this problem. But resolution of conflict can never occur when one *believes* that the results of others are inherently incorrect because of the method of analysis or the technique utilized. It is as illogical and unproductive for a molecular systematist to claim that all conflicting morphological data are "convergence" as it would be for a morphological systematist to claim that molecular data are inherently incapable of resolving relationships because molecular data are also subject to convergence. Avian systematics needs a diversity of data, but it needs just as much for all systematists to provide a rationale for the methods used to interpret those data.

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