PHYLOGENETIC REANALYSIS OF STRAUCH'S OSTEOLOGICAL DATA SET FOR THE CHARADRIIFORMES[1]

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Abstract. Strauch's (1978) compatibility analysis of relationships among the shorebirds (Charadriiformes) was the first study to examine the full range of charadriiform taxa in a reproducible way. Subsequently Mickevich and Parenti (1980) leveled serious charges against Strauch's characters, method of phylogenetic inference, and results. To account for these charges, Strauch's characters were re-examined and recoded, and parsimony analyses were performed on the revised matrix. A parsimony analysis on 74 taxa from the revised matrix yielded 855 shortest trees, each length = 286 and consistency index = 0.385. In each shortest tree there were two major lineages, a lineage of sandpiper-like birds and a lineage of plover-like birds; the two formed a monophyletic group, with the auks (Alcidae) being that group's sister taxon. The shortest trees were then compared with other estimates of shorebird relationships, comparison suggesting that the charges against Strauch's results may have resulted from the Mickevich and Parenti decisions to exclude much of Strauch's character evidence.

Key words: Charadriiformes; phylogeny; compatibility analysis; parsimony analysis; taxonomic congruence.

INTRODUCTION

The investigation of evolutionary relationships among shorebirds (Aves: Charadriiformes) has a long history (reviewed in Sibley and Ahlquist 1990). Almost all studies used morphology to make inferences about shared ancestry; inferences were made using an intuitive method.

Much of the literature of systematics deals with the identification of characters which are good estimators of phylogenetic history. Early systematists had little more than their own insights to help them choose the characters which best indicate relationships. The stability of much of zoological classification is testimony to their good judgment in their choices. Their methods, however, have made it difficult or impossible for others to follow or repeat the steps from observations of specimens to the statements of relationship among taxa (Strauch 1978:269).

Appropriately, Strauch's own (1978; Fig. 1) investigation of charadriiform relationships was explicit in both its assumptions and method of clustering taxa, and is therefore repeatable. Indeed, among morphological studies examining the full range of charadriiform taxa, only that of Strauch meets the criterion of repeatability; a second such study is currently under way (McKitrick, unpubl. manuscript).

Strauch scored 227 charadriiform taxa for 70 characters. Sixty-three of the characters were taken from either the skull or postcranial skeleton; the remaining seven involved the respective origins of three neck muscles, as published in Burton (1971, 1972, 1974) and Zusi (1962). These data were analyzed using the method of character compatibility (Estabrook 1972; Estabrook et al. 1975, 1976a, 1976b; McMorris 1975; Estabrook et al. 1977).

In compatibility analysis, characters are treated as partially-ordered sets; that is, each character is viewed as a set of states, with the states being ordered by some hypothesis of character evolution (Fig. 2). Strauch generated hypotheses of character evolution using a common = primitive criterion. The most common state was determined with reference to the Charadriiformes alone. For many characters, the most common state in two outgroups—the cranes and their relatives (Gruiformes) and the pigeons (Columbiformes)—was identified as well, but if the most common outgroup state differed from the most common charadriiform state, then the latter was coded as primitive (e.g., characters 38, 45, and 56).

Many of Strauch's characters had more than two states. For each of these an ordered transformation series was constructed, though Strauch said (1978: 277) that his hypotheses of order were sometimes only a guess.
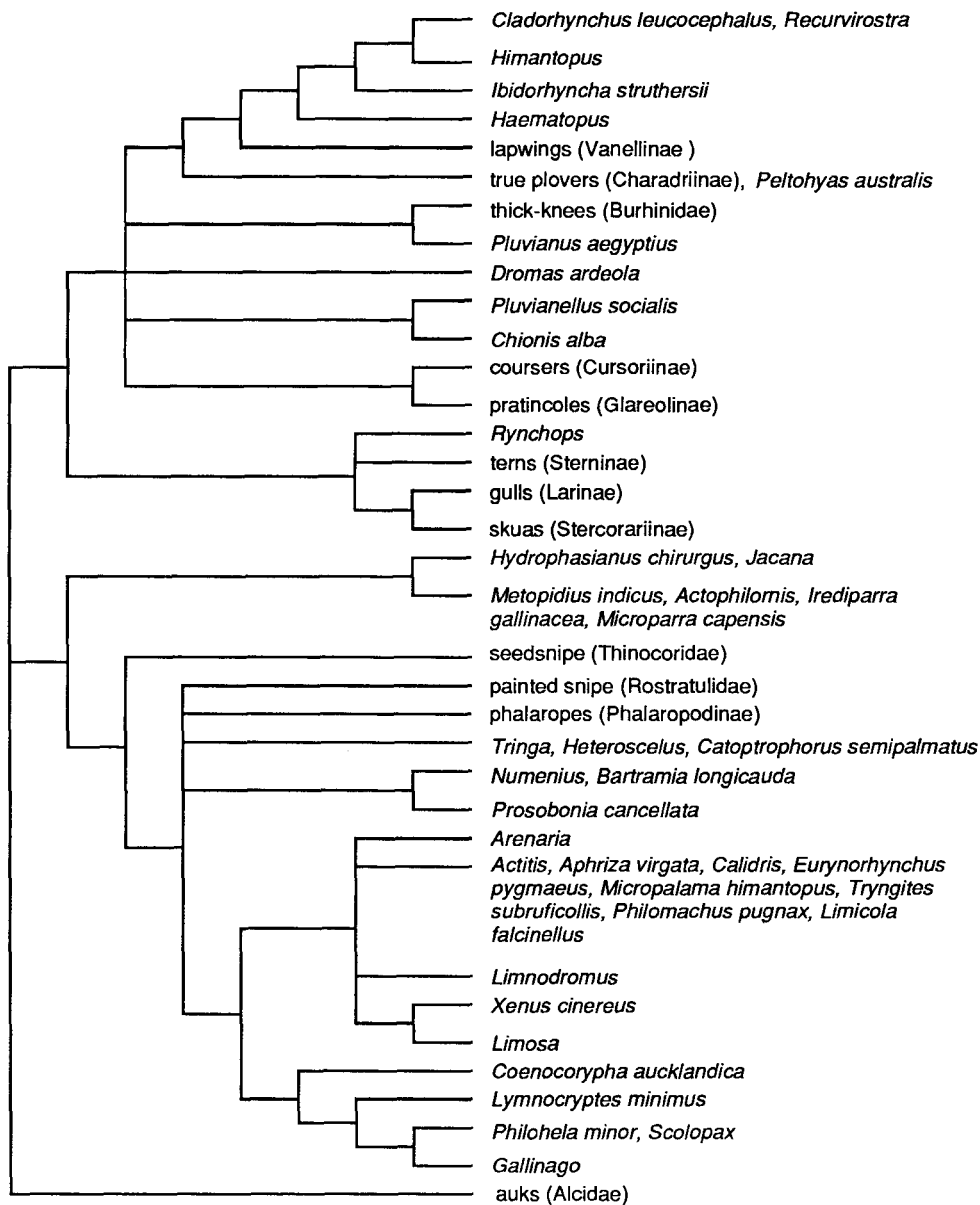
[174]

FIGURE 1. Strauch's hypothesis of shorebird relationships. The tree is modified from his (1978) fig. 36; modifications were made as specified in his fig. 2.

As its name suggests, the character-compatibility method requires that the compatibility of characters be assessed. To determine whether or not two characters are compatible, their cartesian product is calculated. The result is a new set that can be visualized as a lattice; the lattice has a vertex for every possible combination of states from both characters (Fig. 3). If vertices representing character-state combinations not in the study collection are discarded and the result is a non-reticulate tree—any non-reticulate tree—then the characters are compatible. Character compatibility thus refers to the condition in which the sequence of character-state transformations hypothesized for two or more characters can be accommodated by a single phylogenetic tree.
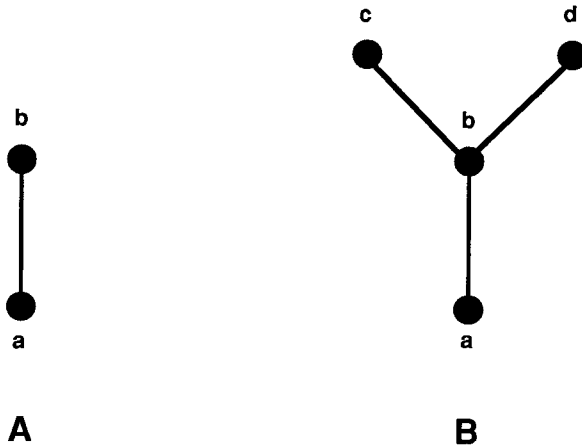
FIGURE 2. Characters as partially ordered sets. In the ball-and-stick diagrams shown here, each ball is a character state; the balls are connected so as to depict hypotheses of character-state polarity and order. In diagram A, state a is primitive and state b is derived. In diagram B, a is primitive; b is derived from a; and both c and d are derived independently from b.

The likelihood of finding a large set of mutually compatible characters is taken to be small unless compatibility results from shared evolutionary history. Thus, large sets of compatible characters provide better evidence of shared history than do small sets, and permit greater confidence that the tree capable of accommodating their respective transformation series is the true genealogy.

Initially, the largest set of mutually compatible characters is determined. This initial analysis typically resolves the deepest part of the tree, but fails to resolve relationships at less general hierarchical levels.

Within each group identified by the initial analysis, the resolution of relationships is accomplished by determining which characters vary in that group and then identifying from those variable characters a largest clique. The process may be repeated in smaller and smaller groups until the tree is suitably resolved.

Mickevich and Parenti (1980) leveled serious charges against the Strauch study. One charge addressed Strauch's use of the compatibility method. Mickevich and Parenti argued that compatibility analysis, by using only mutually compatible characters to determine tree topology, selectively ignores characters that are incompatible; they wrote, "We see no philosophical distinction between the practice of disregarding data because of individual preference and discarding data because of some formal mathematical criterion for which, as far as can

be determined, there is no underlying biological validity" (1980:109). A second charge addressed the particulars of Strauch's character-state coding, ordering, and polarization; a third addressed Strauch's results, which were claimed to be "radically different from all previous published hypotheses" (1980:109).

Mickevich and Parenti, disagreeing with some of Strauch's coding procedures, rejected 35 of his 70 characters, then analyzed the remaining 35 using the computer program WAGNER 78 (Farris 1978). Two shortest Wagner networks were found; these were rooted with a hypothetical ancestor constructed from characters for which Strauch described an outgroup state (Lundberg 1972). The consensus tree calculated from these two shortest networks is shown in Figure 4.

Unfortunately, the Mickevich and Parenti reanalysis is itself not entirely satisfactory. As indicated by the character descriptions below, the Mickevich and Parenti rationale for rejecting characters is heavy-handed, unevenly applied, and occasionally erroneous. For example, nine characters (11, 14–17, 33, 36, 39, and 59) were rejected because taxa with multiple states were given single state assignments. In most instances, however, the number of multistate taxa was small—only one out of 227 taxa for character 33—and in one case (character 17) there were no variable taxa. In another example, two characters (8 and 46) were rejected because some of their states were defined solely on the basis of con-
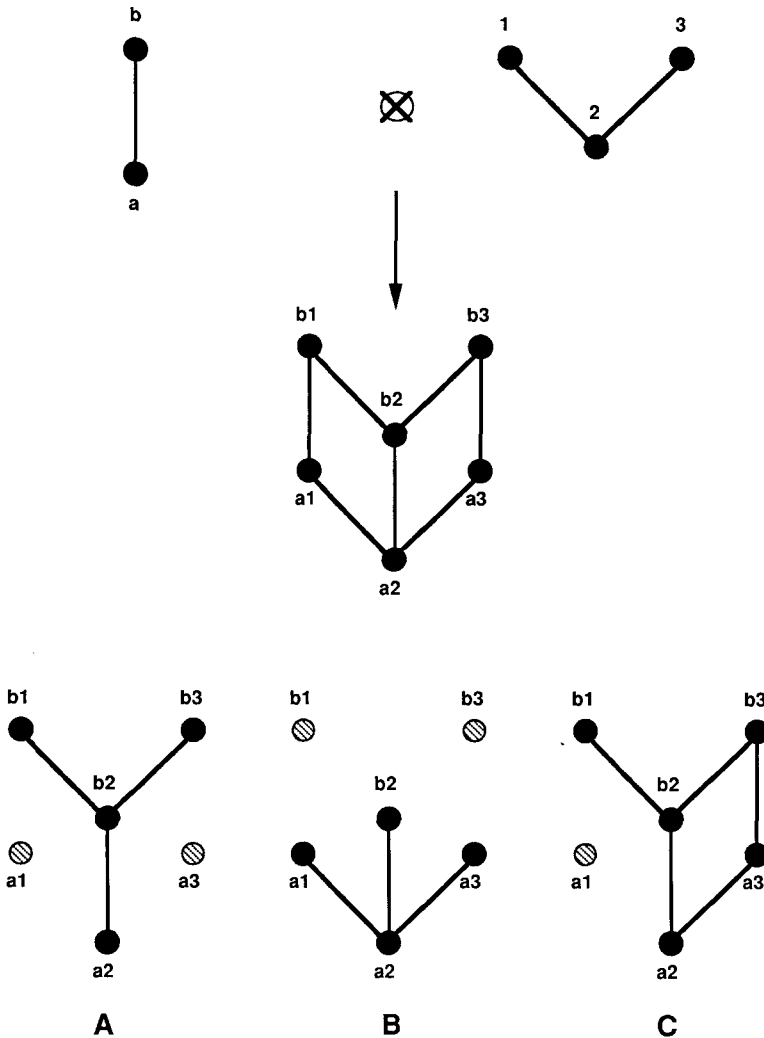
FIGURE 3. Character compatibility (modified from Strauch's [1978] fig. 4). The cartesian product of two characters (top row) is calculated; that product can be visualized as a lattice (middle row), with vertices in the lattice (e.g., a1, a2, b1, and etc.) representing every possible combination of character states. Combinations of states not observed in any of the taxa analyzed (shown in the bottom row as hatched circles) are then deleted from the lattice. If this procedure results in a non-reticulate tree, the characters are compatible (3A and B); if it does not (3C), the characters are incompatible.

gruence with other character evidence; the same was true for an additional five characters (4, 31, 33, 39, and 66), but Mickevich and Parenti did not note it.

Moreover, at least one example was found in which the Mickevich and Parenti results are not consistent with their revision of the Strauch (1978) data matrix. The Strauch matrix contains, among other things, four skuas (Stercorariinae). The Mickevich and Parenti consensus tree groups those skuas into two lineages; yet all four are invariant for the 35 characters that Mickevich and Parenti analyzed. Four taxa cannot be grouped into two lineages when those taxa are scored as being identical.

In sum, although Mickevich and Parenti pointed out flaws in the Strauch study, their critique and subsequent reanalysis are flawed as well. Consequently, in the present study I recode all of Strauch's characters and analyze the revised
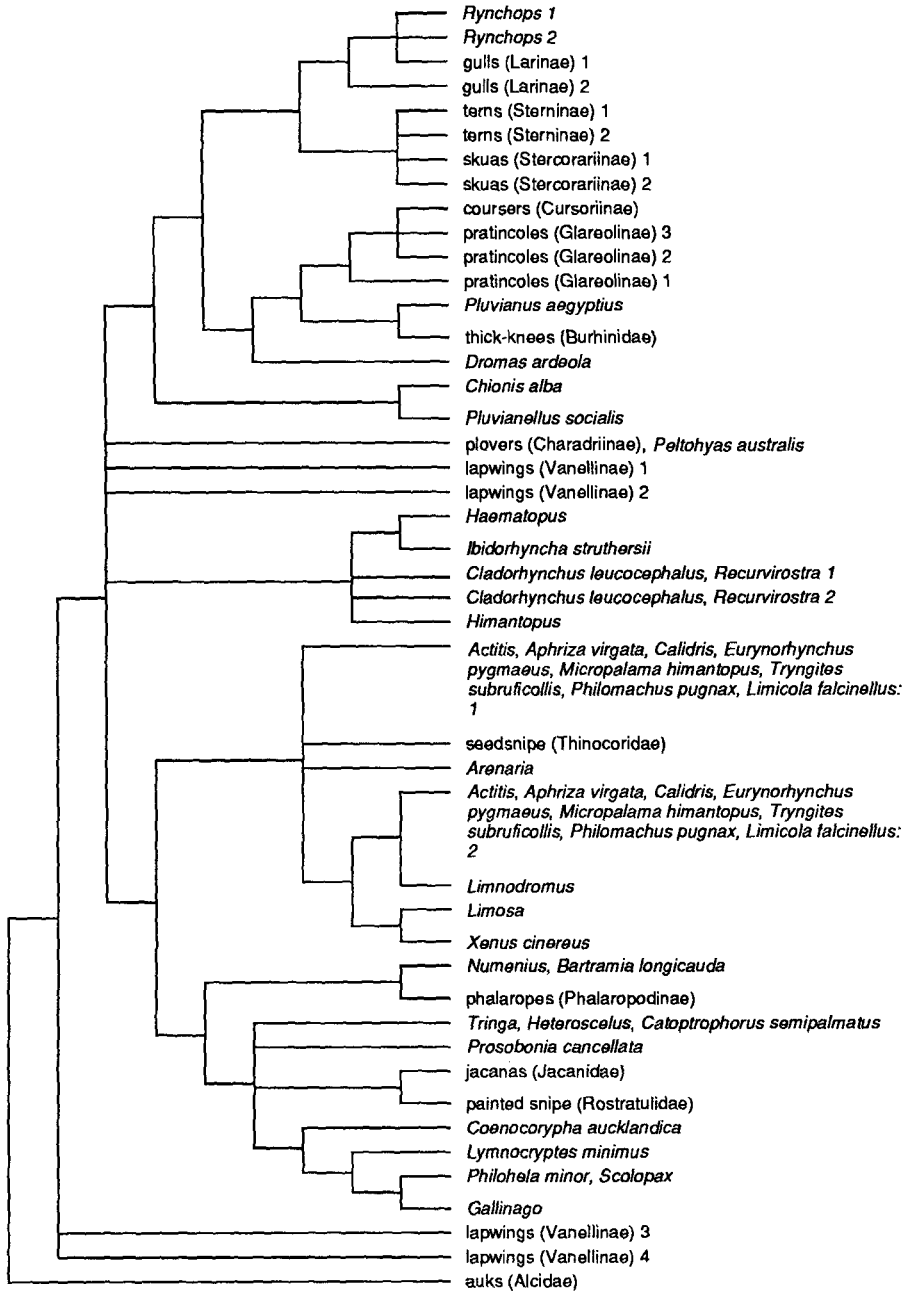
FIGURE 4. The Mickevich and Parenti estimate of shorebird relationships. The topology shown is an Adams consensus tree, calculated from the two minimum-length resolutions that Mickevich and Parenti found.

matrix generated by the recoding process. My objective is to produce a hypothesis of charadriiform phylogeny that accounts for the Mickevich and Parenti critique, but without discarding as many potentially informative data as they did. Such a hypothesis can then be used as a framework for examining character evolution within the Charadriiformes (e.g., Chu 1994).

REVISION OF STRAUCH'S DATA MATRIX

CHARACTERS REJECTED BY MICKEVICH AND PARENTI

The 35 characters rejected by Mickevich and Parenti are discussed in turn below. For each character the Mickevich and Parenti rationale for rejection is examined and either supported, modified, or not supported.

Character 8: form of the bill tip

Mickevich and Parenti argued that the derived states for character 8 were defined on the basis of presumed convergence, i.e., that a single shared state was recoded as two or more states when preliminary analysis suggested that the shared state was homoplasious. This is incorrect: Strauch did change the coding for this character during the course of his investigation, but only because his initial coding scheme proved inadequate to describe the diversity in shorebird bill tip morphology, not because of any initial analysis suggesting homoplasy.

Coding: in Strauch, six states, A through F; unchanged here.

Character 9: shape of the cross-section of the dorsal bar of the upper jaw

Character 9 was rejected by Mickevich and Parenti because its derived states are autapomorphic. However, of the three derived states identified by Strauch, only one (state B) is an autapomorphy. Rejecting the character seems excessive, because it has two derived states that are shared in addition to the one that is not shared.

Coding: in Strauch, four states, A through D; unchanged here. Additionally, I assigned multiple states to one taxon, *Xenus cinereus*; Strauch assigned only one state to *Xenus,* despite his indication that the species is variable.

Character 11: medial condyle of quadrate

Strauch recognized three states for character 11: A, in which the anterolateral face of the medial condyle bears a distinct groove; B, in which there is no groove; and C, in which the groove is reduced or absent, but the condyle itself is raised and twisted. State A was hypothesized to be primitive.

Mickevich and Parenti rejected character 11 because variable taxa were assigned not multiple states but A, the presumed primitive state. Strauch recognized only the Glareolidae (coursers and pratincoles) as being variable, the vari-

ation referring to presence or absence of the anterolateral condylar groove. However, Strauch did not assign the primitive state to any glareolid taxon. Instead, he assigned all glareolids derived state C, a legitimate state assignment since state C was defined not by the variable grooving, but by a unique, invariant orientation of the condyle itself.

Coding: in Strauch, a single character with three states, A, B, and C. I recoded this character as two new characters. The first character, describing the anterolateral groove of the medial condyle, had two states corresponding to Strauch's states A and B (i.e., to presence and absence of the anterolateral groove, respectively). All taxa to which Strauch assigned state C were question-marked, since Strauch does not make clear which of those taxa are variable with respect to the groove. The second character, describing orientation of the medial condyle, had two states, one corresponding to Strauch's states A and B (lowered and untwisted), the other to his state C (raised and twisted).

Character 14: maxillopalatine strut A

Mickevich and Parenti pointed out, correctly, that variable taxa were assigned the state thought to be primitive. However, only 19 of the 140 taxa assigned the primitive state were variable; the variable taxa were *Charadrius cucullatus* and all members of the genera *Haematopus, Ibidorhyncha, Himantopus, Cladorhynchus* and *Recurvirostra.* Instead of rejecting the character outright, I elected to give each variable taxon a multiple state assignment, thereby indicating that some individuals had one state and some, the other.

Coding: in Strauch, two states, A and B; unchanged here.

Character 15: maxillopalatine strut B
Character 16: maxillopalatine strut C

As Mickevich and Parenti again correctly pointed out, variable taxa were assigned the hypothesized primitive state for both characters 15 and 16. For each character the number of variable taxa is no higher than nine (out of 227 taxa in Strauch's analysis); thus I did not reject either.

All of the variable taxa are in the genus *Tringa.* Unfortunately, however, Strauch says only that "some specimens" of *Tringa* are variable (1978: 299), raising the question, "Some specimens of which *Tringa?*" Since Strauch provides no an-

swer, I was forced to question-mark all members of that genus for both characters.

Coding: in Strauch, each character has two states, A and B; neither is changed here.

Character 17: maxillopalatine strut D

Character 17 was rejected by Mickevich and Parenti because variable taxa were assigned the presumed primitive state. However, Strauch did not indicate that any taxa were variable for this character.

Coding: in Strauch, two states, A and B; unchanged here.

Character 18: supraoccipital foramina

The supraoccipital foramina are the fonticuli occipitalis of Baumel (1979), a pair of openings located on either side of the cerebellar prominence. Mickevich and Parenti rejected the foramina as a potential source of historical information on the grounds that their "positional homology is unresolved" (1980:112). However, neither Strauch's character description nor my own examination of charadriiform skulls has suggested that the foramina differ sufficiently in position or configuration to warrant rejection of the character on positional grounds.

Coding: in Strauch, two states, A and B; unchanged here.

Character 21: prearticular process of the mandible

Mickevich and Parenti rejected this character because its presumed derived states are autapomorphic. However, the character has five states, only one of which (state D) is limited to a single taxon. Because each of the remaining four states is shared, rejecting the character outright eliminates a considerable amount of information potentially useful for grouping.

Coding: in Strauch, five states, A through E; unchanged here.

Characters 24–30: head and neck muscle characters

These characters describe the origins of three neck muscles, as published in Burton (1971, 1972, 1974) and Zusi (1962). However, neither Burton nor Zusi examined many of the taxa included in Strauch's study, so Strauch used Burton's and Zusi's data to assign each unexamined taxon the state shown by a presumed close relative that had been examined.

Mickevich and Parenti recognized the impropriety of assigning character states to unobserved

taxa, and rejected characters 24–30 because of it. I retained the characters, but assigned character states only to those taxa scored by either Burton or Zusi. All remaining taxa (Appendix 1) were scored as having missing data.

Coding: in Strauch, characters 24–29 had two states each, A and B; character 30 had three states, A through C. In no case was the coding changed.

Character 31: number of caudal vertebrae, omitting the pygostyle

This character was rejected by Mickevich and Parenti because of unresolved positional homology. Rejection of this and similar characters identified by Strauch suggests a philosophical disagreement with the use of meristic characters in phylogenetic analyses. I see no *a priori* reason to reject such characters, so long as the set of things to be counted can be clearly delimited, and so long as the sets themselves meet certain requirements for structural and positional similarity.

Coding: in Strauch, six states, A, B, C, D, E, and G. There is no state F listed. Both states D and G code for six caudal vertebrae, with state G representing six vertebrae in the jacanas (Jacanidae) and state D, six vertebrae in any other shorebird. Strauch defended this coding scheme by arguing, "All Jacanidae have five vertebrae except *Hydrophasianus chirurgus,* which has six. The sixth caudal vertebrae in *chirurgus* is assumed to be derived, along with the greatly elongated tail of the species, from the normal five of the Jacanidae" (1978:305).

The recoding of one character state as two is inappropriate if the two differ only by the groupings in which they are observed. Thus I treated the two six-vertebrae states, D and G, as a single state, reducing the number of states to five: A, B, C, D/G, and E.

Character 32: number of neck vertebrae, omitting those with unfused cervical ribs
Character 35: number of sternal costal processes

Again, Mickevich and Parenti rejected meristic characters because of unresolved positional homology.

Coding: in Strauch, three states for character 32 (A through C) and four for character 35 (A through D); unchanged here.

Character 33: cervical vertebral strut

Character 33 was rejected by Mickevich and Parenti because a single species (out of 227!) was

variable and was assigned the character state hypothesized to be primitive. To correct this, I assigned the one species, *Pluvianus aegyptius,* multiple states.

Coding: in Strauch, three states, A through C. Both states B and C indicate the presence of a cervical vertebral strut, state B in the lapwings (Vanellinae) and state C in the thick-knees (Burhinidae). Strauch justified this redundancy by stating, "I originally coded the presence of a strut as the same state for the lapwings and the thick-knees, but after an initial analysis of the cladistic relationships within the Charadrii indicated that there is no close relationship between these groups I recoded the strut as two different states" (1978: 306).

Mickevich and Parenti pointed out (though not with respect to the cervical vertebral strut) that a character cannot be recoded just because the analysis of other characters suggests that recoding is warranted. To correct for such inappropriate coding decisions, I listed only two states for character 33, one (state A) for the absence of a cervical vertebral strut and the other (state B/C) for its presence.

Character 36: medial sternal notch

According to Strauch, some sandpipers (Scolopacidae) were variable for this character. Moreover, some were intermediate, with a medial foramen instead of a medial notch. Strauch's response was to code any variable or intermediate species as if it had the notch. I do not know which sandpipers were variable or intermediate, and so was forced to question-mark all of them, as if they were missing data.

Coding: in Strauch, two states, A and B; unchanged here.

Character 39: coracoidal foramen

Mickevich and Parenti rejected character 39 because Strauch made a single state assignment to three variable taxa (*Charadrius melanops, Rhinoptilus chalcopterus,* and *R. africanus*). Rather than reject the character because of how three out of 227 taxa were scored, I retained the character and rescored the three variable taxa as having multiple states.

Coding: in Strauch, three states, A through C. Both states B and C referred to the absence of a coracoidal foramen, C in the Glareolidae and B in all other shorebirds; Strauch says, "After preliminary analyses indicated that [*Glareola, Cursorius,* and *Rhinoptilus*] form a monophyletic group, the absence of a foramen in [that group]

was coded as a uniquely derived state" (1978: 309). Because it is inappropriate to use character-state distribution among hypothesized groups as a basis for recoding characters, I reduced the number of states to two, one (A) for the presence of the foramen and the other (B/C) for its absence.

Character 45: ectepicondylar prominence of the humerus

Mickevich and Parenti rejected this character because they claimed the coding description contains a typographical error; however, I found no erroneous state assignments.

Coding: in Strauch, two states, A and B; unchanged here.

Character 46: extensor process of the metacarpus

The inappropriate coding procedure noted by Mickevich and Parenti, and discussed below, caused them to reject character 46. I chose not to reject the character, though I did change the way it was coded.

Coding: in Strauch, nine states, A through I. States B and I describe wing knobs, with state B referring to wing knobs in *Pluvianus aegyptius* and state I, to knobs in *Chionis alba* and *Pluvianellus socialis.* Similarly, states C and F describe wing spurs in the lapwings, with state F referring to wing spurs in *Vanellus cayanus* and state C, to spurs in all other lapwing taxa. In defense of these coding decisions, Strauch wrote,

The wing knobs in *Pluvianellus, Chionis* and *Pluvianus* were originally coded as the same state. Later it became clear that evidence from other characters indicates that the knob in *Pluvianus* has been independently derived, and the character coding was changed accordingly. In addition, other evidence indicates that *Hoploxypterus* [= *Vanellus*] *cayanus* is not a member of the Vanellinae and that its wing spur has been derived independently of that found in the lapwings (1978:313).

In response, Mickevich and Parenti wrote, "The preliminary recoding of a character believed to be different because other characters support this difference is unjustified" (1980:111). I agree, and so reduced the number of character states from nine to seven: A, B/I, C/F, D, E, G, and H. State B/I refers to the presence of wing knobs; state C/F, to the presence of claw-like wing spurs.

Character 50: synsacral strut

A synsacral strut is the transverse brace that extends from the crista iliaca intermedia (Boas 1933), at the caudal margin of the acetabular

foramen, to one of the fused vertebrae associated with the synsacrum. The strut comprises the enlarged costal processes of a synsacral vertebra (Baumel 1979). Three of the four states for character 50 identify a different vertebra bearing the synsacral strut, whereas the fourth state indicates that the strut was absent altogether.

Mickevich and Parenti cited unresolved positional homology in rejecting character 50, perhaps because the character's states refer to different vertebrae. However, the issue of positional homology can be resolved by defining the character in a more inclusive way (as, e.g., enlargement of the costal processes in a particular block of three synsacral vertebrae).

Coding: in Strauch, four states, A through D; unchanged here.

Character 51: second synsacral strut

Mickevich and Parenti rejected character 51 because of unresolved positional homology. I rejected it as well, but for a different reason: Strauch indicated that several taxa are variable with respect to the second strut, but never identified the variable taxa. Because variable taxa are not identified I had no choice but to omit the character altogether.

Character 55: foramina on ventral surface of ilium

Character 55 describes the presence or absence of foramina on the lateral part of the caudal iliac crest (the anterior margin of Holman's [1961] renal bar). Mickevich and Parenti rejected this character because of unresolved positional homology, presumably a reference to the absence of more specific positional criteria for any one foramen. However, an examination of the two taxa for which Strauch found foramina, *Stercorarius pomarinus* and *S. parasiticus,* suggested that the foramina are consequent from pneumatization of the crista iliaca caudalis. Thus character 55 might be more precisely described in terms of the presence or absence of pneumatization. Under these conditions, positional similarity need only be demonstrated for the crista iliaca caudalis, which may or may not be pneumatized; it does not need to be demonstrated for any individual foramen.

Coding: in Strauch, two states, A and B. The same two states are used here as well, but they refer to the presence/absence of pneumatization, not the presence/absence of foramina.

Character 56: intrapophyseal foramina of synsacrum

Character 56 refers to the degree of ossification between the transverse processes of adjacent synsacral vertebrae. Mickevich and Parenti rejected it, as they did the previous character, on the grounds of unresolved positional homology. However, what may be important here is not the exact location of each interapophyseal foramen, but whether or not synsacral ossification is sufficiently extensive to reduce the number of foramina present. If degree of ossification is the meaningful variable, then the locations of particular foramina are unimportant, and objectives about positional equivalence are obviated.

Coding: in Strauch, two states, A and B; unchanged here.

Character 59: fusion of the ischium and the pubis

Mickevich and Parenti rejected character 59 because variable taxa were assigned the presumed plesiomorphous condition; I rejected it as well, but for a different reason. Strauch wrote, "Both [of the two states described for character 59] can be found in specimens of some species," yet he does not specify which species. Thus the greater problem is not that variable taxa were assigned one state or the other but that variable taxa were not identified at all.

Character 65–70: tendinal canals in the hypotarsus

All of these characters were rejected by Mickevich and Parenti because of unresolved positional homology. However, Strauch's hypotheses of homology are outlined reasonably clearly; he provides a diagram of the hypothetical charadriiform hypotarsus, as well as several labelled examples that permit the reader to see how the hypothetical hypotarsus was used to identify tendinal canals in actual specimens.

Coding: in Strauch, for characters 65 and 67, three states each, A through C; for characters 68, 69, and 70, two states each, A and B. None of the above were changed here.

Strauch assigned character 66, tendinal canal no. 3, a total of four states (A through D). State C described the condition in which no canal was visible, and state A, the condition in which the canal was an open groove. States B and D described the condition in which the canal was completely enclosed by bone, with state D representing an enclosed canal in the auks (Alcidae)

and state B, an enclosed canal in any other taxon. I cannot justify dividing the enclosed-canal condition into two states just because it occurs in two or more different groups; therefore, I reduced the number of states to three, A, B/D, and C.

CHARACTERS ACCEPTED BY MICKEVICH AND PARENTI

Mickevich and Parenti accepted 35 of Strauch's characters. Two of these had to be recoded; in each case, the rationale for recoding is discussed below. In addition, six contained erroneous state assignments. Erroneous state assignments were identified from handwritten corrections on a copy of Strauch (1978) housed in the University of Michigan Museum of Zoology Bird Division Library. All errors were corrected and the corrections verified by comparing Strauch's (1978) table I with his (1976) Appendix III.

Character 4: angle between jugal bar and lateral nasal bar

Strauch recognized three states for character 4. State A described the condition in which the angle between the jugal and lateral nasal bars is less than or equal to about 60°; states B and C described the condition in which the jugal bar-lateral nasal bar angle is about 70° or more.

Regarding state C, Strauch wrote, "like [state] (B), found in Thinocoridae [seedsnipe], assumed to be a result of the short, finch-like bill and possibly of independent origin" (1978:291). However, assumptions of independent origin are not sufficient grounds for erecting an additional character state. As a result, I combined states B and C into a single state, B/C, reducing the number of states for character 4 to two: A and B/C.

Character 25: origin of M. complexus on vertebra 4

Strauch assigned *Vanellus tricolor* state C, but character 25 has only two states, A and B. Consequently I question-marked *tricolor,* as if it was missing data.

Character 43: shape of the deltoid crest of the humerus

Character 43 contains an erroneous state assignment: *Calidris canutus* should be assigned state A rather than state B.

Character 48: distal metacarpal symphysis of carpometacarpus

For character 48, *Gygis alba* should be assigned state A rather than state B.

Character 49: proximal phalanx, digit III

Character 49 has two states, describing perforate and imperforate proximal phalanges for digit III. Strauch indicated that some specimens of the Phalaropodinae (phalaropes) and Glareolidae exhibited the perforate state. However, he assigned all of them the imperforate state, arguing that, "in all cases the perforation is a hole in a thin sheet of bone and appears to represent incomplete ossification or a damaged specimen" (1978:314).

Calling a perforate phalanx imperforate is acceptable if the apparent perforation results from damage, but not if it is thought to result from incomplete ossification: most, if not all, perforations in the phalanx are probably the result of ontogenetic truncation of the ossification process. Consequently, I treated the phalaropes and glareolids as if some species had both the perforate and imperforate states, and since Strauch never identified which phalaropes and glareolids were variable I was forced to code all of them as if they were missing data for this character.

In addition to requiring recoding, character 49 contains an incorrect state assignment: *Gygis alba* should be assigned state B rather than state A.

Character 53: number of lumbar vertebral parapophyses

For character 53, *Rostratula benghalensis* should be assigned state A, not state C.

Character 54: condition of posterior end of the renal depression

Rostratula benghalensis should be assigned state C, not state A.

MATERIALS AND METHODS

Before revision, the Strauch data matrix contained 70 characters. During revision, I omitted two of Strauch's original characters (51 and 59), split a third (character 11) into two, and changed the coding for an additional six (4, 31, 33, 39, 46, and 66). The net result was a reduction in the total number of characters, from 70 to 69.

Recoding also rendered identical the character-state descriptions for some of the 227 taxa in the original Strauch matrix. Taxa with identical state assignments were combined under single taxon labels, reducing the number of taxa in the revised matrix to 185; I then added a hypothetical ancestor to the matrix, bringing the number of taxa to 186.

States were assigned to the ancestor based on Strauch's information about two outgroups, the Gruiformes and Columbiformes. However, state assignments were made for only those characters in which all gruiform and columbiform taxa surveyed had the same character state; ten characters (4, 6, 9, 17, 33, 34, 42, 43, 45, and 46) met this requirement.

The revised matrix (186 taxa and 69 characters) is not printed here. Interested readers can reproduce it from Strauch's matrix following the procedures described in Appendix 2.

I analyzed the revised matrix cladistically using the computer program PAUP 3.0s (Phylogenetic Analysis Using Parsimony; Swofford 1991). All characters in the matrix were weighted equally; multistate characters were treated as unordered, and each multiple-state assignment, as if it represented a polymorphism. In addition, outgroup rooting was specified, with the hypothetical ancestor being designated as the outgroup.

The use of unordered characters is a significant departure from Strauch's (1978) procedure (Mickevich and Parenti [1980] do not indicate whether they used Strauch's hypotheses of character-state order or not). I employed unordered characters following Hauser and Presch (1991), who argue that hypotheses of order should be determined from a cladogram, much as one uses a cladogram to identify instances of homoplasy.

In the initial PAUP analysis, shortest trees were sought using a heuristic algorithm that employed a random addition sequence and tree bisection-reconnection branch-swapping; the addition/branch-swapping procedure was repeated ten times to compensate for the limitations that each addition sequence imposed. I also used the MULPARS option, which saves all of the equally-parsimonious trees that are found and inputs them one by one into the branch-swapping procedure.

Because of the large number of taxa and comparatively small number of characters, I suspected that many equally short trees would be found. As a result, I arbitrarily limited the number of shortest trees retained to 100 per replication. Thus after ten replications as many as 1,000 trees could have been saved. The actual number saved was 100, a consequence of only one replication finding trees of minimal length.

To search for additional minimum-length trees I ran a second PAUP analysis. Parameters em-

ployed in the second analysis were unchanged from those used in the first, with three exceptions.

(1) To get a starting tree for branch-swapping, I did not use stepwise addition; instead, I used Tree 1 of the 100 shortest trees found during the initial analysis.
(2) Using a predetermined starting tree made multiple replications irrelevant. The multiple-replication procedure is designed to compensate for addition-sequence limitations, and no such limitations exist when starting trees are obtained by a means other than stepwise addition. As a consequence, I used one replication rather than many.
(3) I set the maximum number of shortest trees saved to 2,500.

After 2,500 trees had been saved I allowed branch-swapping to proceed for 141 hr, during which time branch-swapping was completed on 892 of the trees. The second analysis was then terminated.

In the first two analyses I placed arbitrary ceilings on the number of shortest trees that PAUP could find, and in both cases the ceilings were reached. These results suggested that the population of shortest trees was very large, and raised concerns that even the 2,500-tree sample obtained in the second analysis was not representative of the population as a whole.

One way to reduce the population of shortest trees is to delete taxa. Accordingly, I ran a third, reduced-matrix PAUP analysis from which 112 of the 186 taxa had been deleted. Taxa were likely to be deleted if they participated in consensus polytomies; for example, in the case of a completely unresolved polytomy with six terminals, four of the six might be removed. Removal of such terminals was a reasonable strategy because it deleted taxa from clades that could not be resolved in an unambiguous way by the available evidence. However, deletion was selective with respect to shorebird taxonomy, insuring that all suprageneric taxa recognized by Peters (1934), Jehl (1975), and Sibley et al. (1988) were represented by at least one species in the analysis.

Parameters used in the third PAUP analysis were identical to those used in the initial analysis, except that I limited the number of shortest trees retained to 1,000 per replication. After ten replications up to 10,000 trees could have been re-

tained; however, 855 were found during replication 1 and none thereafter, suggesting that all shortest trees had been found.

RESULTS

The second of the first two analyses yielded a sample of 2,500 shortest trees. Each required 401 steps and had a consistency index (Kluge and Farris 1969) of 0.307. A strict consensus (Nelson 1979) of the 2,500 trees is shown in Figure 5 because of its previous use as a phylogenetic hypothesis for the Charadriiformes (Chu 1994).

The third analysis (i.e., the reduced-matrix analysis) yielded 855 shortest trees, each 286 steps long and with a consistency index of 0.385; from these, strict (Fig. 6) and 50% majority-rule consensus trees (Margush and McMorris 1981; Fig. 7) were calculated. Given the large number of taxa analyzed (74), the low consistency index calculated for each shortest tree is expected; for a 60-taxon analysis, Sanderson and Donoghue (1989) predict a consistency index of 0.349.

The topological differences between the results of a full-matrix analysis (Fig. 5) and a reduced-matrix analysis (Fig. 6) highlight the difficulties associated with data that are incapable of resolving relationships among the taxa of interest. If existing data cannot resolve relationships, a very large number of equally simple resolutions are possible, only some of which will be found and subjected to branch-swapping; others will neither be found nor swapped on. Conversely, if the existing data are capable of resolving relationships, a small number of shortest trees are possible, and the chances are reasonable that all will be found, even with a heuristic search. For this reason I will limit further discussion to the reduced-matrix analysis.

The reduced-matrix analysis (Fig. 6) indicated two major clades of charadriiform taxa:

(1) a lineage of sandpiper-like birds, including the sandpipers, painted snipe (Rostratulidae), jacanas, and seedsnipe; and

(2) a lineage of plover-like birds, including the true plovers (Charadriinae), lapwings, oystercatchers (Haematopodidae), the Ibisbill (*Ibidorhyncha struthersii*), stilts and avocets (Recurvirostridae), sheathbills (Chionididae), the Magellanic Plover (*Pluvianellus socialis*), coursers and pratincoles, thick-knees, the Crab Plover (*Dromas ardeola*), and gulls and their allies (Laridae).

The two major lineages were clustered into a monophyletic group, and the auks were hypothesized to be that group's sister taxon.

Within the lineage of sandpiper-like birds, the jacanas, painted snipe, and sandpipers formed a clade, with their sister taxon being the seedsnipe (Fig. 6). However, the jacanas and painted snipe were found to be derived sandpipers, not proximal outgroups to a monophyletic sandpiper group; thus the sandpipers as usually conceived (e.g., the Scolopacidae of both Peters 1934 and Sibley et al. 1988) are hypothesized to be paraphyletic.

Relationships within the lineage of plover-like birds were less clear. Strauch's data supported the existence of five plover-like clades, but did not resolve the relationships between them (Fig. 6). These clades are the larids and the Crab Plover (*Dromas ardeola*); the coursers and pratincoles; the thick-knees and Egyptian Plover (*Pluvianus aegyptius*); the sheathbills and Magellanic Plover (*Pluvianellus socialis*); and the stilts, avocets, Ibisbill (*Ibidorhyncha struthersii*), oystercatchers, lapwings, and true plovers.

Resolution of relationships was particularly poor within the last of these clades. The lack of resolution was a direct consequence of my decision to include the Ibisbill in the reduced-matrix analysis; deleting it reduced the number of shortest trees from 855 to 60 (Fig. 8).

Whether the Ibisbill was included or excluded, the majority of shortest trees did not support the existence of a monophyletic group comprised by the lapwings and true plovers (i.e., the Charadriidae sensu Peters 1934 or American Ornithologists' Union 1983). Additionally, no shortest tree supported the existence of a monophyletic lapwing group: in the reduced-matrix analysis the closest relative of *Vanellus cayanus* was *Phegornis mitchellii*, not *Vanellus vanellus* or *V. chilensis*. Strauch's (1978) compatibility analysis yielded a similar result in that it did not cluster *cayanus* with the other lapwings.

DISCUSSION

The present analysis did not support sandpiper monophyly, but it did recognize five sandpiper lineages (Fig. 6): the snipes, tringine sandpipers, calidrine sandpipers, phalaropes, and curlews. These lineages are similar to the scolopacid subfamilies recognized in Lowe's (1931) seminal investigation of shorebird morphology, but differ
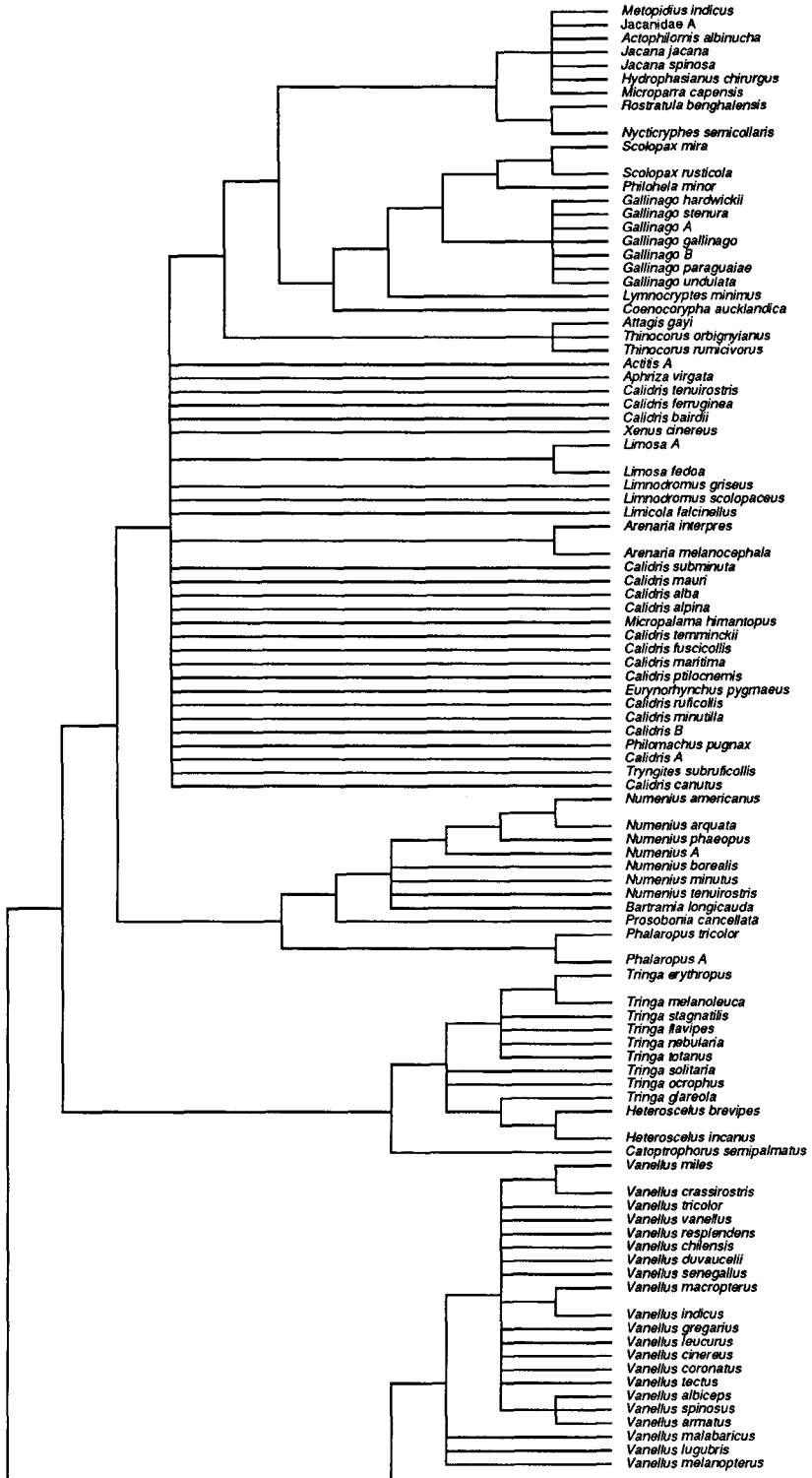
FIGURE 5.   Strict consensus of a sample of 2,500 shortest trees found during analysis of the revised Strauch matrix.
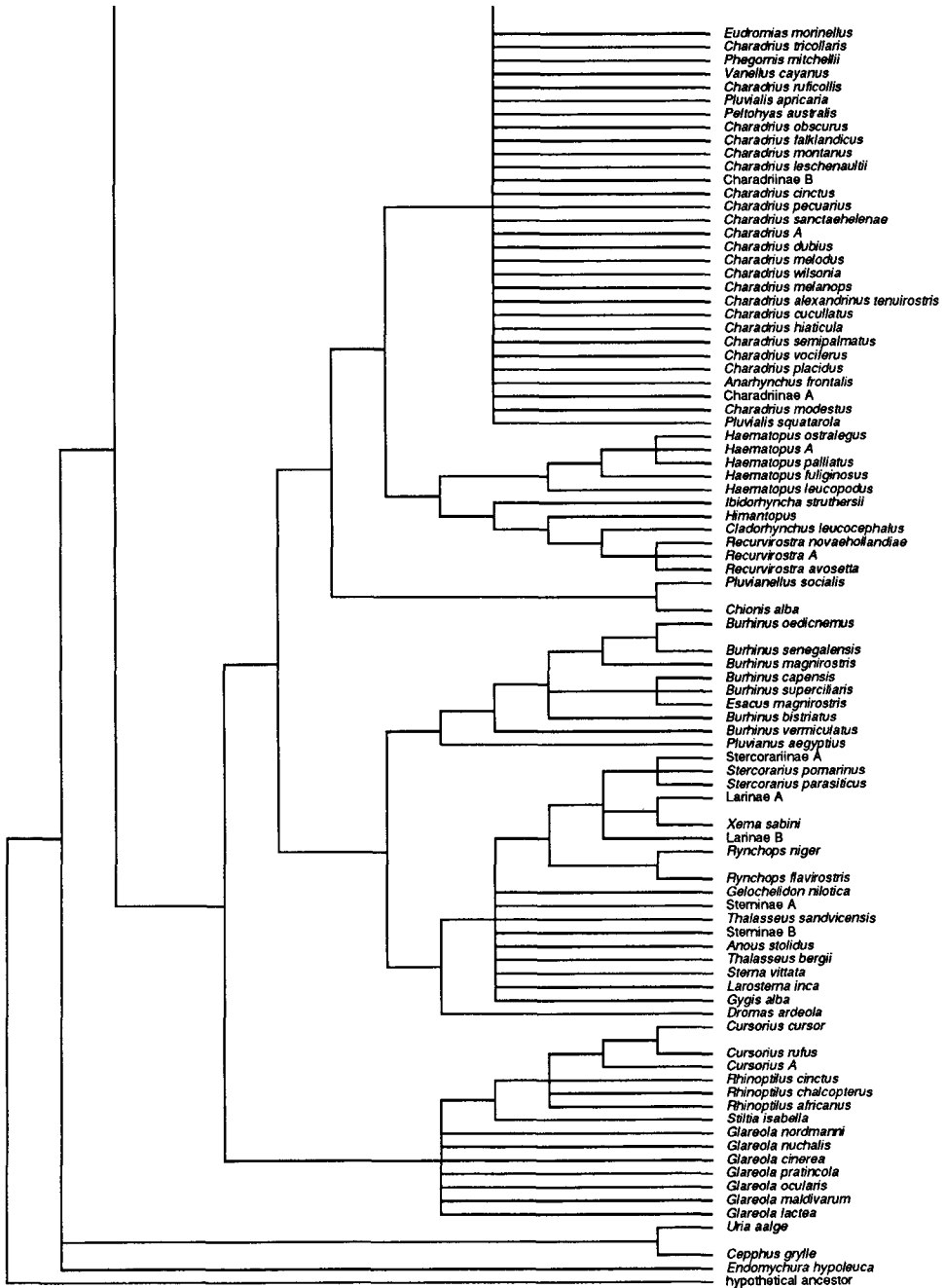
FIGURE 5. Continued.

in two important respects. First, dowitchers (*Limnodromus*) emerge with the calidrine sandpipers instead of the snipes, and godwits (*Limosa*) emerge with the dowitchers instead of the curlews. This hypothesis of relationships, in which dowitchers and godwits are viewed as closely related calidrine sandpipers, was originally proposed by Timmermann (1957a, 1957b) as a result of his comparative examination of shorebird ectoparasites. And second, a sister-group rela-

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                                        ┌──── Hydrophasianus
                                    ┌───┤──── Jacana jacana
                                ┌───┤   ┌──── Rostratula
                                │   └───┤──── Nyctryphes
                                │       ┌──── Coenocorypha
                            ┌───┤   ┌───┤──── Lymnocryptes
                            │   │   │   ┌──── Gallinago gallinago
                            │   └───┤───┤──── Gallinago paraguaiae
                            │       │   ┌──── Philohela
                            │       └───┤──── Scolopax rusticola
                            │           └──── Scolopax mira
                        ┌───┤           ┌──── Tringa glareola
                        │   │       ┌───┤──── Heteroscelus brevipes
                        │   │   ┌───┤   └──── Heteroscelus incanus
                        │   │   │   │   ┌──── Tringa erythropus
                        │   └───┤   └───┤──── Tringa melanoleuca
                        │       │       └──── Tringa flavipes
                        │       │       ┌──── Aphriza
                        │       │   ┌───┤──── Calidris tenuirostris
                    ┌───┤       │   │   └──── Calidris alpina
                    │   │       └───┤   ┌──── Arenaria interpres
                    │   │           │───┤──── Arenaria melanocephala
                    │   │           └───┤──── Limnodromus griseus
                    │   │               ┌──── Limosa A
                    │   │               └──── Limosa fedoa
                    │   └────────────────┌──── Phalaropus tricolor
                    │                    └──── Phalaropus A
                    │                    ┌──── Bartramia
                ┌───┤               ┌───┤──── Numenius A
                │   │           ┌───┤   └──── Numenius phaeopus
                │   │           │   │   ┌──── Numenius arquata
                │   └───────────┤   └───┤──── Numenius americanus
                │               │       ┌──── Thinocorus rumicivorus
                │               └────────└──── Attagis
                │                        ┌──── Stercorarius pomarinus
                │                    ┌───┤──── Stercorarius parasiticus
            ┌───┤                ┌───┤   └──── Larinae A
            │   │            ┌───┤   ┌──── Gelochelidon
            │   │            │   └───┤──── Rynchops nigra
            │   │            │       └──── Dromas
        ┌───┤   │        ┌───┤       ┌──── Glareola pratincola
        │   │   │        │   │    ┌───┤──── Rhinoptilus cinctus
        │   │   │        │   └────┤   └──── Cursorius A
        │   │   │        │        │   ┌──── Cursorius cursor
        │   │   │    ┌───┤        └───┤──── Cursorius rufus
        │   │   │    │   │            ┌──── Burhinus oedicnemus
        │   │   │    │   │        ┌───┤──── Burhinus senegalensis
        │   │   └────┤   │    ┌───┤   └──── Burhinus magnirostris
        │   │        │   │    │   │   ┌──── Burhinus capensis
        │   │        │   └────┤   └───┤──── Esacus magnirostris
        │   │        │        │       └──── Burhinus vermiculatus
        │   │        │        └──── Pluvianus
        │   │        │        ┌──── Pluvianellus
        │   │        └────────┤──── Chionis alba
    ┌───┤   │                 │   ┌──── Peltohyas
    │   │   │                 │   │──── Phegornis
    │   │   │             ┌───┤   └──── Vanellus cayanus
    │   │   │             │   │   ┌──── Charadrius melanops
    │   │   │             │   └───┤──── Charadrius alexandrinus tenuirostris
    │   │   │         ┌───┤       └──── Charadrius dubius
    │   │   │         │   │       ┌──── Vanellus vanellus
    │   │   └─────────┤   └───────┤──── Vanellus chilensis
    │   │             │           ┌──── Haematopus ostralegus
    │   │             │       ┌───┤──── Haematopus palliatus
    │   │             │   ┌───┤   └──── Haematopus fuliginosus
    │   │             │   │   └──── Haematopus leucopodus
    │   │             └───┤   ┌──── Ibidorhyncha
    │   │                 │   │──── Himantopus
    │   │                 └───┤──── Cladorhynchus
    │   │                     │   ┌──── Recurvirostra novaehollandiae
    │   │                     └───┤──── Recurvirostra avosetta
    │   │                         └──── Uria aalge
    │   └──────────────────────────┌──── Cepphus grylle
    └─────────────────────────────────── Hypothetical ancestor
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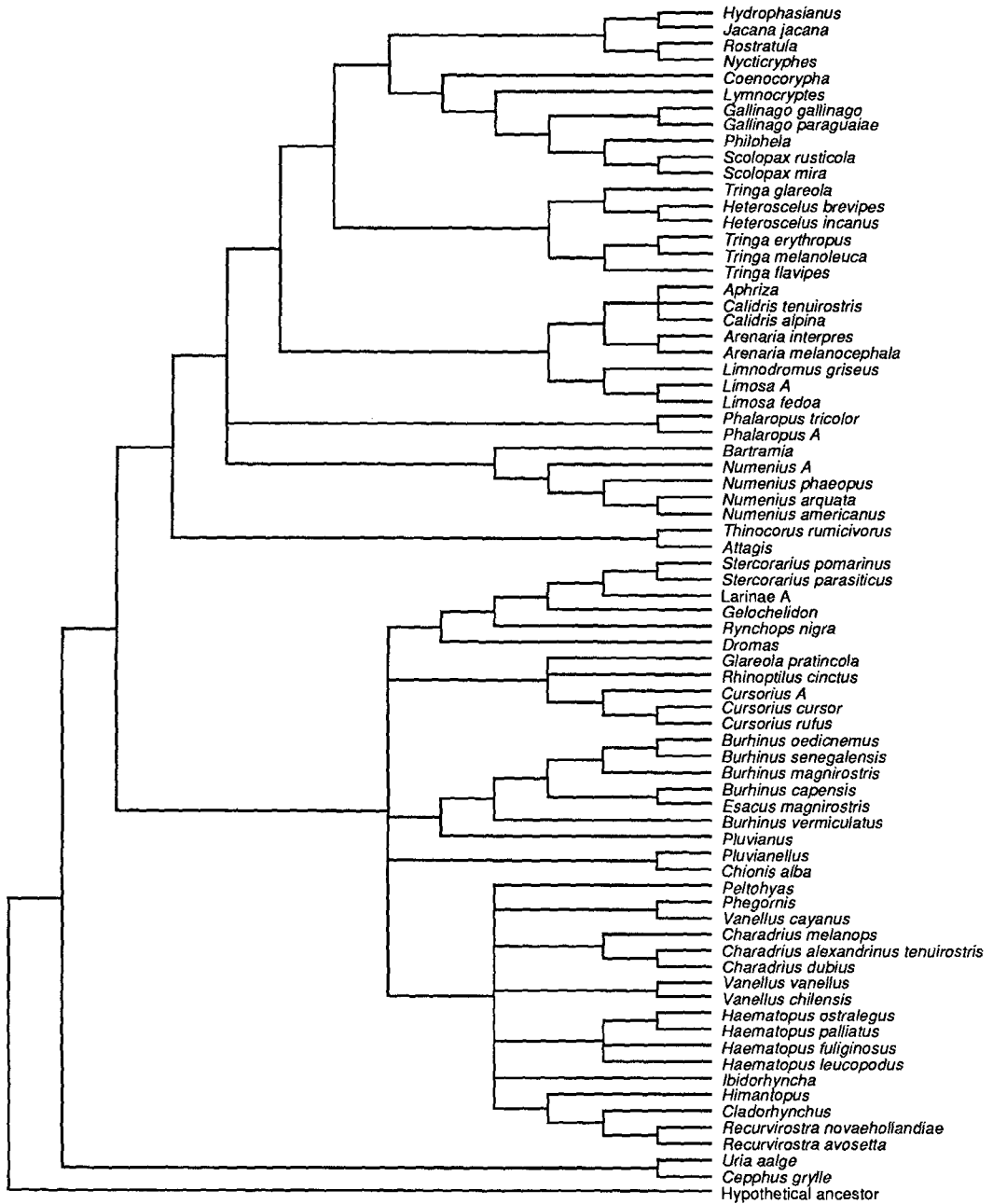FIGURE 6. Strict consensus of the 855 shortest trees found during a reduced-matrix analysis of the revised Strauch matrix. Each shortest tree had a length of 286 steps and a consistency index of 0.385.

tionship between the turnstones (*Arenaria*) and Surfbird (*Aphriza virgata*) was not supported, though both clustered with the calidrine sandpipers. The relationships of *Aphriza* as hypothesized here are similar to those hypothesized by Jehl (1968).

The enigmatic Crab Plover clustered with the gulls and gull-like birds. This grouping was initially hypothesized by Yudin (1965), though Lowe (1916) had noted similarities between the Crab Plover and gulls half a century earlier.

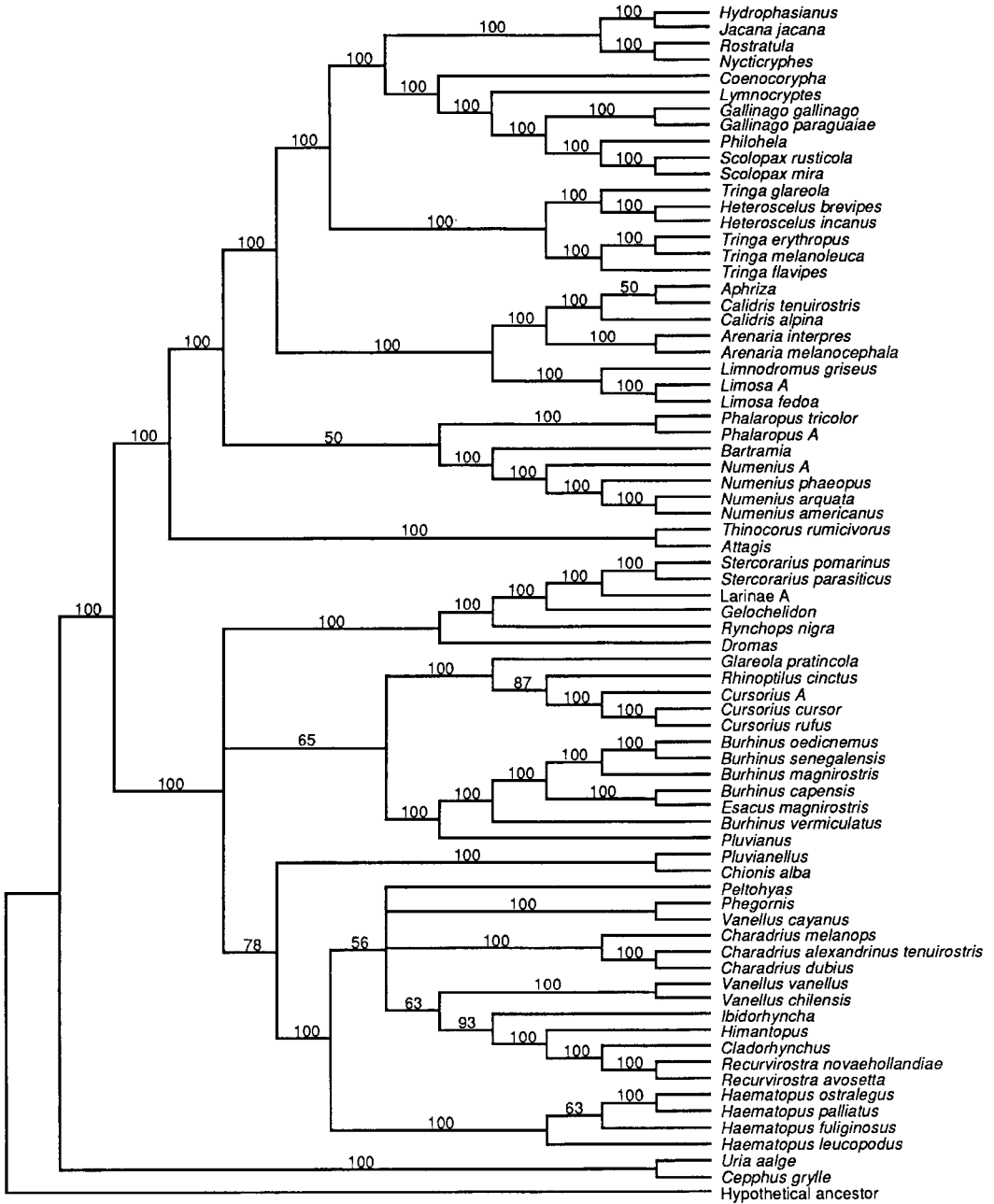Another enigmatic taxon, the Egyptian Plover,

FIGURE 7.   Fifty percent majority-rule consensus of the 855 shortest trees found during a reduced-matrix analysis of the revised Strauch matrix. Numbers adjacent to each node are the percentage of shortest trees having the resolution shown.

was grouped with the thick-knees. Strauch (1978) was the first to propose this relationship, but both his results and mine were presaged by Yudin's (1965:224) observation that the Egyptian Plover is "sharply differentiated from other Charadriiformes by precisely the same structural features as *Burhinus*."

Finally, two additional taxa of puzzling affin-
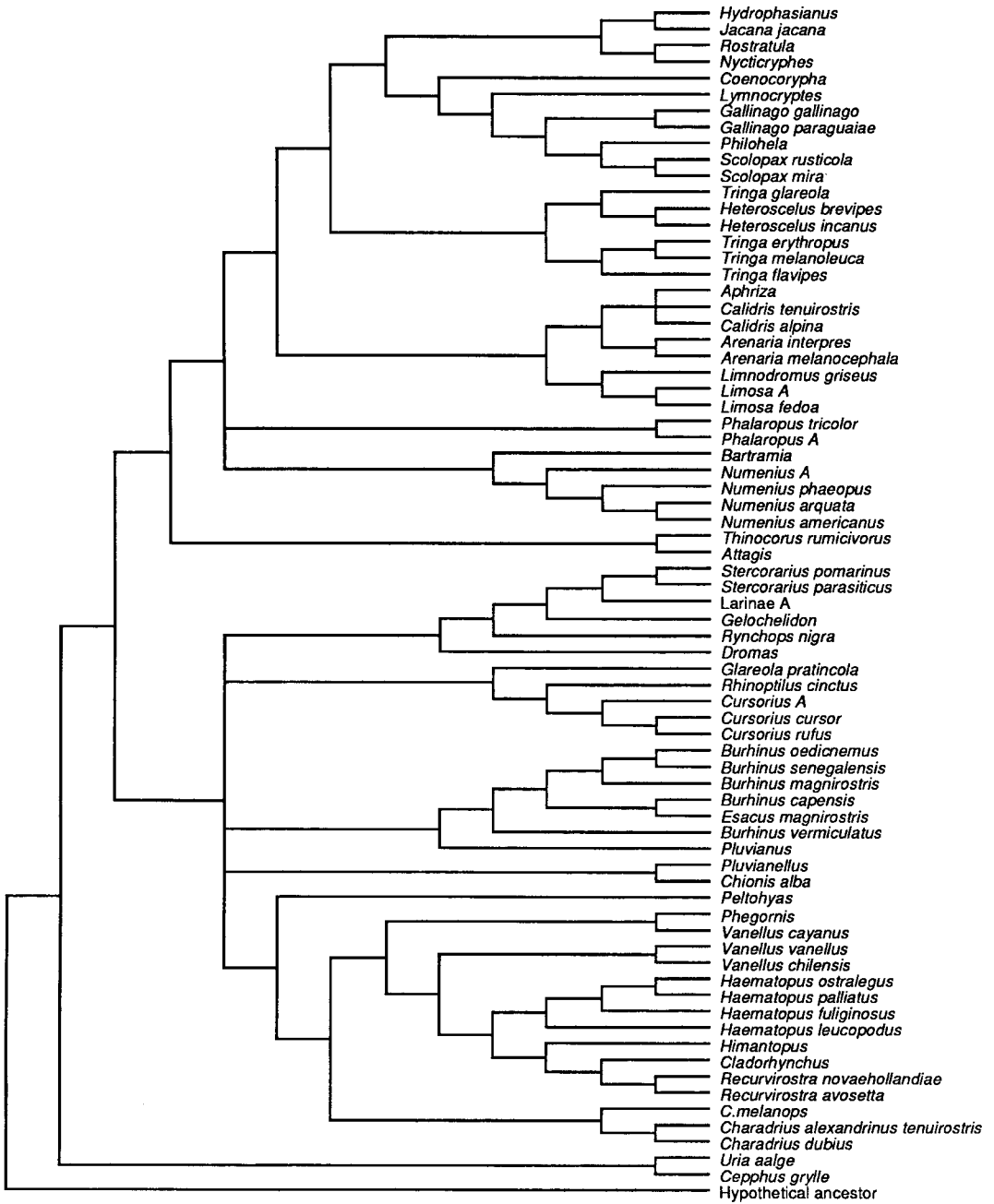
FIGURE 8.   Strict consensus of the 60 shortest trees found when the Ibisbill *(Ibidorhyncha struthersii)* was deleted from the reduced-matrix analysis. Each shortest tree was of length 278 and had a consistency index of 0.392.

ities, the sheathbills and the Magellanic Plover, were grouped with one another, as suggested by Jehl (1975) and later by Strauch (1978).

COMPARISON OF TREES GENERATED IN THE STRAUCH, MICKEVICH AND PARENTI, AND PRESENT STUDIES

Strauch (1978; Fig. 1), Mickevich and Parenti (1980; Fig. 4), and the present analysis placed the auks at the basal node in the charadriiform tree. The latter two found auks to be the sister taxon of all other charadriiform birds; the former was unable to resolve the position of the auk lineage, and so depicted it as part of a basal trichotomy.

More-inclusive groupings among the non-auk shorebirds were similar in the present study and that of Strauch, less so in that of Mickevich and Parenti. Both Strauch and the present study clustered the non-auk shorebirds into two groups, one of sandpiper-like birds and the other of plover-like birds (Figs. 1, 6). In contrast, Mickevich and Parenti found a lineage of lapwings to be the sister taxon to all other non-auk shorebirds (Fig. 4), with there being less resolution among the latter than in either the Strauch analysis or my reanalysis (monophyly of the sandpiper-like birds was supported unambiguously, but the position of several lineages of plover-like birds was not resolved).

Additional comparisons between trees generated in the present study, the Strauch tree, and the Mickevich and Parenti trees are provided below.

(1) My reanalysis of Strauch's data indicated that sandpipers are paraphyletic, with the jacanas and painted snipe being derived members of the group of sandpiper-like birds (Fig. 6). The Mickevich and Parenti analysis yielded similar result (Fig. 4). Conversely, Strauch found jacanas and seedsnipe to be the proximal outgroups for a monophyletic sandpiper lineage (Fig. 1).

(2) Shortest trees found in the present study failed to provide unambiguous support for the existence of a monophyletic group made up of the lapwings and true plovers. Both Strauch (Fig. 1) and Mickevich and Parenti (Fig. 4) argued against the monophyly of such a group.

(3) In both this study (Fig. 6) and that of Strauch (Fig. 1) the lapwings, true plovers, oyster-catchers, stilts, avocets, and the Ibisbill were found to comprise a natural group. On the Mickevich and Parenti topologies such a group would be an artificial assemblage (Fig. 4).

COMPARISON WITH THE SIBLEY AND AHLQUIST ESTIMATE OF SHOREBIRD RELATIONSHIPS

Sibley and Ahlquist (1990) used the method of DNA-DNA hybridization (Schildkraut et al. 1961; Britten and Kohne 1966; Shields and Straus 1975; Sibley and Ahlquist 1981) to estimate relationships of the birds of the world, including 69 species of shorebirds. In general, they sampled the different shorebird lineages less completely than did Strauch (1978). They did, however, include both a greater variety of auks and the Plains-wanderer (*Pedionomus torquatus*); the latter's similarities to charadriiform taxa were noted only recently (Olson and Steadman 1981).

The utility of comparisons with the Sibley and Ahlquist estimate may be questioned, because both Sibley and Ahlquist's methods and their results have received much criticism (e.g., Brownell 1983; Cracraft 1987; Houde 1987; Sheldon 1987; Sarich et al. 1989; Springer and Krajewski 1989; Lanyon 1992; Mindell 1992). However, the Sibley and Ahlquist estimate is the only other comprehensive hypothesis of shorebird relationships. As such, it is an estimate with which any charadriiform phylogeny should be compared.

Sibley and Ahlquist's evidence indicated that the Charadriiformes are made up of two groups, one of sandpiper-like birds and the other of plover-like birds (Fig. 9). Allowing for differences in the taxa examined, membership in each group was the same as in both Strauch's study and the present analysis, with one exception: Sibley and Ahlquist placed the auks within the group of plover-like birds, with the auks being most similar to larids.

In the Sibley and Ahlquist study the plover-like birds were themselves divided into two groups. One comprised the plovers, lapwings, stilts and avocets, oystercatchers, thick-knees, and sheathbills. The other comprised the coursers and pratincoles, the Crab Plover, auks, and larids. The latter is identical in membership to a clade supported by the Mickevich and Parenti analysis, except that Mickevich and Parenti placed thick-knees in that clade as well (Fig. 4).
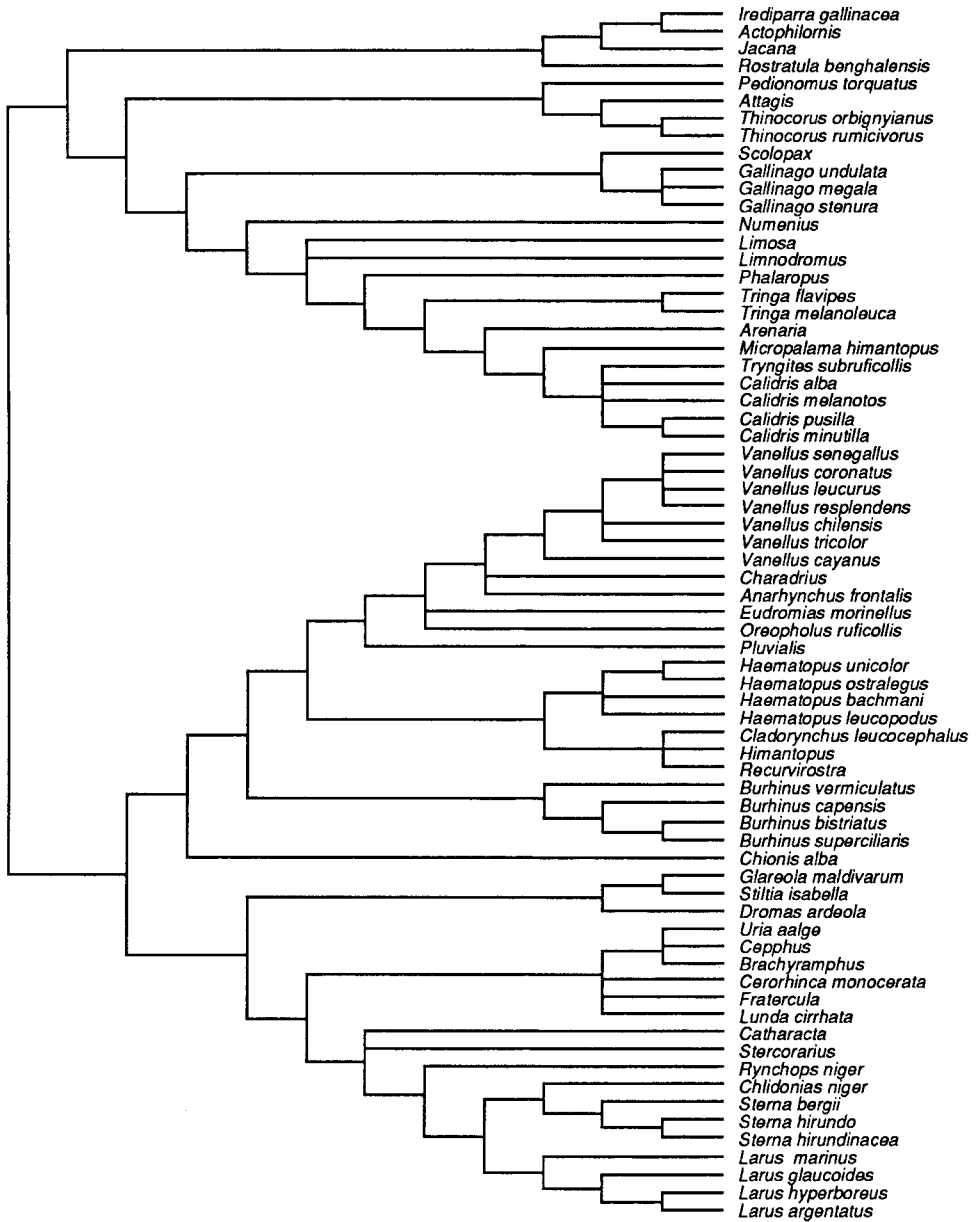
FIGURE 9. The Sibley and Ahlquist estimate of shorebird relationships. Topology was determined by UPGMA grouping of $\Delta T_{50}H$ values. See Sibley and Ahlquist (1990) for discussion regarding their choice of a distance metric and clustering method.

Sibley and Ahlquist found that the lapwings (including *Vanellus cayanus*) are more similar to one another than any is to other charadriiform birds. In addition, they found the true plovers to be the shorebirds most similar to lapwings. Neither of these results were supported by Strauch, Mickevich and Parenti, or the present study.

Finally, relationships within the Sibley and Ahlquist group of sandpiper-like birds were most like those hypothesized by Strauch. The sandpipers themselves emerged in a single cluster,

whereas the jacanas, painted snipe, and seed-snipe emerged outside of that cluster.

CONCLUSIONS

A single set of data was subjected to phylogenetic analysis three times: once by Strauch (1978), who collected the data; once by Mickevich and Parenti, as part of their review of Strauch's manuscript; and once here. The present study has several advantages over its predecessors. First, it is a parsimony analysis (like that of Mickevich and Parenti) rather than a compatibility analysis (like that of Strauch); the compatibility method has been strongly criticized for its exclusion of incompatible characters (Farris and Kluge 1979; Mickevich and Parenti 1980; Sober 1988). Second, the present study re-examines (and, where appropriate, modifies) Strauch's coding decisions in light of the Mickevich and Parenti review; at the same time, however, it discards fewer potentially informative data than Mickevich and Parenti did. And third, it provides a number of hypotheses about relationships at the species level that cannot easily be recovered from the Mickevich and Parenti paper. Such information is not available in Strauch's (1978) paper, either, but can be found in an earlier work of his (Strauch 1976).

Mickevich and Parenti (1980:108) assert that "[Strauch's] interpretation of charadriiform phylogeny is radically different from all previous published hypotheses, and may indicate peculiarities of the [compatibility] method, rather than a close approximation of actual interrelationships." In so doing, they assert that similarity of groupings (taxonomic congruence: Mickevich 1978) can be used to argue the relative merits of compatibility and parsimony methods, much as it was once used to argue the relative merits of phenetics and cladistics (e.g., Sneath and Sokal 1973; Mickevich 1978).

Sober (1988:142) argues persuasively that taxonomic congruence "bears on the standing of *hypotheses,* not on the *methods* used to select them." He continues (1988:142–143):

Let us suppose, just for the sake of argument, that cladistic parsimony is the best method for assessing the evidential meaning of character distributions. Let an initial set of fifty characters be such that (AB)C is the best hypothesis, when parsimony is used to analyze the data. A new data set is in-

troduced, also involving fifty characters, and A(BC) is the most parsimonious hypothesis for this second set. The data sets disagree. If parsimony is the correct way to discern evidential meaning, this result does not in the slightest impugn that method's credentials. When different pieces of data point in different directions, it is essential to consider what *all* the data say. A natural "principle of total evidence" enjoins us to find the most parsimonious tree, relative to all one hundred characters.

Sober addresses the situation in which different suites of characters yield different topologies, and concludes that incongruence among topologies is a commentary not on the method of phylogenetic inference but on the character evidence employed. However, his argument can be extended to a second situation: caution must be exercised when assailing a method for yielding topologies different from those generated with other methods, because the topological differences may stem from nothing more than an investigator's choice of characters.

If taxonomic congruence lends support to hypotheses, then groupings present in several of the hypotheses examined here are better supported than groupings present in only one of them. Two groups in particular are better supported in this manner: the sandpiper-like birds (a group comprised by the sandpipers, jacanas, painted snipe, and seedsnipe) and the plover-like birds (a group comprised by the lapwings, true plovers, oystercatchers, stilts and avocets, the Ibisbill, thick-knees, coursers and pratincoles, the Crab Plover, gulls and their allies, sheathbills, and the Magellanic Plover). The sandpiper-like group is hypothesized in Sibley and Ahlquist's analysis of DNA-DNA hybridization data, in Strauch's analysis of morphological characters, and in both my reanalysis of Strauch's data and the Mickevich and Parenti reanalysis. The plover-like group is hypothesized in all analyses except that of Mickevich and Parenti, and might have been hypothesized there as well, had Mickevich and Parenti not elected to exclude so much evidence from their study.

Of course, as a source of support for hypothesized groupings, congruence with additional hypotheses is a poor substitute for congruence with additional characters. It is the addition of new characters, and not a comparison of trees, that will prove the final arbiter in any discussion over which estimates of relationships are most strongly supported.

ACKNOWLEDGMENTS

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APPENDIX 1:

TAXA NOT EXAMINED BY BURTON OR ZUSI

The following taxa were not examined by either Burton (1971, 1972, 1974) or Zusi (1962) for features of the head and neck musculature: *Metopidius indicus*; *Microparra capensis*; *Actophilornis albinucha*; *Jacana jacana*; *Attagis gayi*; *Nycticryphes semicollaris*; all *Numenius* except *phaeopus* and *arquata*; *Calidris mauri* and *ptilocnemis*; *Arenaria melanocephala*; *Limnodromus scolopaceus*; *Limosa fedoa*; *Coenocorypha aucklandica*; all *Gallinago* except *stenura*, *gallinago*, and *paraguiae*; *Scolopax mira*; *Catharacta skua*; all *Stercorarius*; all gulls (*Gabianus scoresbii*, *Pagophila alba*, all *Larus*, *Rhodostethia rosea*, *Rissa tridactyla*, *Creagrus furcatus*, and *Xema sabini*); all terns except *Gelochelidon nilotica* (i.e., *Chlidonias niger*, *Phaetusa simplex*, *Hydroprogne caspia*, all *Sterna*, both *Thalasseus*, *Larosterna inca*, *Gygis alba*, and both *Anous*); *Rynchops flavirostris*; all *Glareola* except *pratincola* and *nuchalis*; *Cursorius rufus*; all *Burhinus* except *oedicnemus*, *capensis*, and *magnirostris*; *Esacus magnirostris*; *Phegornis mitchellii*; *Thinornis novaeseelandiae*; *Charadrius obscurus*, *montanus*, *collaris*, *venustus*, *ruficapillus*, *alticola*, *veredus*, *morinellus*, *sanctaehelenae*, *marginatus*, *cucullatus*, *semipalmatus*, *melodus*, and *placidus*; *Vanellus melanopterus*, *lugubris*, *gregarius*, *cinereus*, *resplendens*, *duvaucelii*, *macropterus*, and *crassirostris*; all *Haematopus* except *ostralegus*; *Cladorhynchus leucocephalus*; *Recurvirostra americana* and *andina*; and all auks (*Endomychura hypoleuca*, *Uria aalge*, and *Cepphus grylle*). Consequently, all of them were marked as having missing data for characters 24–30 in my revision of Strauch's data matrix.

APPENDIX 2:

REVISED STRAUCH DATA MATRIX

The data matrix employed in the present study is identical to that in Strauch's (1978) table 1, with the following exceptions.

(1) The modifications described in the Revision of Strauch's data matrix were implemented.
(2) Modifications to Strauch's matrix rendered some of his terminal taxa identical. To avoid redundancy, identical terminals were subsumed under single taxon labels. These taxon labels, followed by the species they include, are: Jacanidae A (*Actophilornis africana*, *Irediparra gallinacea*); *Gallinago* A (*G. megala*, *G. nigripennis*); *Gallinago* B (*G. macrodactyla*, *G. media*); *Numenius* A (*N. tahitiensis*, *N. madagascariensis*); *Limosa* A (*L. limosa*, *L. haemastica*, *L. lapponica*); *Phalaropus* A (*P. lob-*

atus, P. fulicarius); *Actitis* (*A. macularia, A. hypoleucos*); *Calidris* A (*C. melanotos, C. acuminata*); *Calidris* B (*C. pusilla, C. minuta*); Charadriidae A (*Charadrius mongolus, C. bicinctus, C. asiaticus, Pluvialis dominica*); Charadriidae B (*Charadrius collaris, C. venustus, C. ruficapillus, C. alticola, C. veredus, Thinornis novaeseelandiae*); *Charadrius* A (*C. marginatus, C. alexandrinus dealbatus*); *Haematopus* A (*H. finschi, H. moquini, H. frazari, H. bachmani, H. ater*); *Recurvirostra* A (*R. americana,*

R. andina); *Cursorius* A (*C. coromandelicus, C. temminckii*); Stercorariinae A (*Catharacta skua, Stercorarius longicaudus*); Sterninae A (*Sterna hirundo, Anous minutus*); Sterninae B (*Chlidonias niger, Phaetusa simplex, Hydroprogne caspia, Sterna trudeaui*); Larinae A (*Larus scoresbii, Pagophila eburnea, Larus philadelphia, L. minutus, Rhodostethia rosea, Rissa tridactyla*); and Larinae B (*Larus heermanni, L. delawarensis, L. argentatus, L. serranus, L. novaehollandiae, Creagrus furcatus*).